SYSTEMATIC REVISION OF SOUTHERN AFRICAN SPECIES IN THE GENERA *Eptesicus, Neoromicia, Hypsugo and Pipistrellus* (CHIROPTERA: VESPERTILIONIDAE)

By

Teresa Catherine Kearney

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Dedicated to my parents, Rae and Brian,
and my husband, Ernest.

ABSTRACT

Patterns of variation in GTG-banded chromosomes, bacula morphology and cranio-dental characters among ten vespertilionid species from southern Africa were studied to clarify generic and specific relationships among the taxa previously assigned to the genera *Eptesicus* and *Pipistrellus*.

GTG-banded chromosomes provided characters to support the elevation of *Neoromicia* to generic rank. Hence, *Eptesicus hottentotus* is the only true *Eptesicus* of the six southern African species (*capensis*, cf. *melckorum*, *rendalli*, *somalicus* and *zuluensis*) formerly classified as *Eptesicus*. GTG-banded chromosomes also provided characters to support the transfer of *P. (Hypsugo) africanus* to the genus *Neoromicia*.

Bacula morphology, although useful for specific identification of males and the distinction of the genus *Eptesicus* (which has a small, triangular bacula), was less suitable for phylogeny estimation in genera with a medium to large and elongated bacula (*Hypsugo, Neoromicia, Pipistrellus*).

Geometric and traditional morphometric techniques identified slightly different intra-specific patterns of cranio-dental sexual dimorphism and tooth wear class variation. The single geometric morphometric intra-population test of *N. capensis* found no significant sexual dimorphism and tooth wear class variation. Traditional morphometric analyses, however, identified significant sexual dimorphism in a single population of six populations of *N. capensis* tested, and significant tooth wear class variation in one of two populations of *E. hottentotus* tested to merit separate treatments in subsequent intra and inter-specific analysis.

Geometric morphometric analysis identified clinal centroid size variation negatively and significantly correlated with latitude and longitude in three of six species tested: *E. hottentotus*, *N. capensis*, and *P. hesperidus*. Only *N. capensis* showed a highly significant correlation between skull centroid size and different biomes and ecoregions. *Neoromicia capensis* was also the only species tested to show a significant clinal variation in skull shape; dorsal skull shape was negatively correlated with longitude and different biomes and ecoregions, while ventral skull shape was negatively correlated with longitude, latitude and different biomes and ecoregions. Traditional morphometric methods, however, identified the following patterns of significant intra-specific clinal variation: in *N. capensis* negatively correlated with latitude and longitude; in *N. zuluensis* positively correlated with longitude and negatively correlated with latitude; in *H. anchietae*, *P. hesperidus* and *P. rusticus* negatively correlated with latitude.

Both geometric and traditional morphometric techniques used to assess cranio-dental variation indicated inter-specific variation was dominated by overall size, which was allometrically constrained and hence there was considerable inter-specific homology. The measurements used in traditional morphometric analysis, however, allowed better separation between the species than the landmarks captured in the geometric morphometric analysis.

PREFACE

The initial research work described in this dissertation was carried out in the School of Life and Environmental Sciences, University of Natal, Durban, from 1995. Since January 2002 to March 2005 I have completed the analyses and writing whilst being employed as a Collection Manager in the Vertebrate Department at the Transvaal Museum in Pretoria.

The work presented here was supervised jointly by Dr. Giancarlo Contrafatto and Dr. Peter J. Taylor. This work has not been submitted in any form to another University. Where use was made of the work of others, this has been duly acknowledged in the text.

Kearney
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T.C. Kearney

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CHAPTER 1

INTRODUCTION

1.1 INTRODUCTION

Vespertilionid bats of the genera *Pipistrellus* and *Eptesicus* s.l. have posed a taxonomic problem for some time (Meester *et al.*, 1986) and a clearer understanding of their generic and specific relationships will have definite benefits for their future conservation (Friedmann and Daly, 2004). The task of conserving biodiversity and ensuring that development is sustainable is a daunting one faced with rising pressures around the globe of growing human populations and loss and degradation of habitats. Since biodiversity conservation is usually based on the unit of the species, conservation efforts will always be hampered unnecessarily if we do not attempt to clarify the units that form the foundation for conservation efforts. Furthermore an understanding of species within the context of their relationship to other species and some idea of their biogeography and evolutionary history will only serve to strengthen conservation assessments and efforts. Against this background, contributions that demonstrate phylogenies are not just tools for classification but also provide critical frameworks for other fields of study including conservation biology (Simmons and Hand, 1998).

1.2 BACKGROUND TO *EPTESICUS, HYPSUGO, NEOROMICIA* AND *PIPISTRELLUS*

Vespertilionidae, the family to which *Eptesicus*, *Hypsugo*, *Neoromicia* and *Pipistrellus* belong is the largest, most speciose family of small, primarily insectivorous microchiropteran bats with 31 genera and 301 species (Koopman, 1993) occurring through most of the world (with the exception of areas unable to sustain their nutritional requirements i.e. alpine and polar regions, and very remote islands) (Rosevear, 1965). Vespertilionidae is also a morphologically diverse group with no unique characteristics that are not found in any other microchiropteran taxon (Simmons 1998). These insectivorous bats have a plain face unadorned by noseleaves or slits, and their long tails are fully enclosed in the tail membrane (Taylor, 2000).

The 10 species of *Eptesicus*, *Hypsugo*, *Neoromicia* and *Pipistrellus* occurring in southern Africa (Table 1.1) show some differences in external morphology, ranging in size from the largest *Eptesicus hottentotus* (average forearm length of larger females 49.5 mm) to the smallest *Neoromicia africanus* (average forearm length of larger males 31.0 mm). There is also variation in colour with *N. rendalli* having pale coloured wing and tail membranes whereas the other species have dark brown membranes, and *N. rueppellii* having contrasting greyish-brown dorsal and white ventral colour pelage. However, the majority of the species vary little in size and shades of brown dorsal pelage, which makes field identification of the species relatively difficult.

The different species have different distributions in southern Africa, which appear in part to be related to roost site and habitat to which they are adapted (Taylor, 2000). *Eptesicus hottentotus* has a patchy distribution over a wide part of southern Africa with new distribution localities still being recorded (Taylor, 2000). Their distribution appears to be related to craggy cliffs, which probably provide roosting sites (Kearney and Seamark, 2004). *Neoromicia capensis* has the most widespread distribution of the species in southern Africa, possibly as a result of their use of man-made structures as roost sites (Taylor, 2000). *Neoromicia africanus* has a broad distribution across the most northern parts of the southern African subregion, which is then limited to the east coast of South Africa, being recorded as far south as Bedford in the Eastern Cape Province (Taylor, 2000). They are associated with *Strelitzia* or banana plants since they roost in the unfurled leaves, but they have also been recorded from thatched and other roofs (Taylor, 2000).

Neoromicia rendalli and *N. rueppellii* are the most poorly represented and poorly known of the species in southern Africa. *Neoromicia rendalli* is known from few well-watered localities, in the northern parts of the region from the Okavango Delta in Botswana and Mana Pools on the Zambezi River in Zimbabwe, with a southerly locality on the northern KwaZulu-Natal Province coast (Taylor, 2000). *Neoromicia rueppellii* is known from a few riverine localities in the north-eastern part of southern Africa, with a single, most westerly record from Augrabies on the Orange River in the Northern Cape Province (Taylor, 2000). The distribution of *N. zuluensis* is sparsely scattered in savanna woodland areas along the northern, north-western and north-eastern parts of the subregion (Taylor, 2000). Their distribution relative to that of *N. somalicus*, from which they were distinguished on chromosome diploid number (Rautenbach *et al.*, 1993), has, however, never been clearly identified, other than what one can gather from the subspecies distributions.

Another poorly known species within the subregion, *Hypsugo anchietae*, has a scattered distribution on the eastern side of southern Africa (Taylor, 2000). Southward extensions to the

Table 1.1 Taxa central to the analysis of this study within the family Vespertilionidae and the subfamily Vespertilioninae. [See text in taxonomy section for justification of taxonomy reflected here. Subspecies listings are for southern Africa only and follow Meester *et al.* (1986) and Koopman (1994)]

Genus	Species	Subspecies
Eptesicus Rafinesque, 1820	*hottentotus* (A. Smith, 1833)	*E. h. hottentotus* *E. h. pallidior* Shortridge, 1942 *E. h. bensoni* Roberts, 1946.
Hypsugo Kolenati, 1856	*anchietae* (Seabra, 1900)	monotypic
Neoromicia Roberts, 1926	*capensis* (A. Smith, 1829)	monotypic
	cf. *melckorum*	?
	africanus (Rüppell, 1842)	*N. a. africanus* *N. a. fouriei* (Thomas, 1926)
	rendalli (Thomas, 1889)	monotypic
	rueppellii (Fischer, 1829)	*N. r. rueppellii* *N. r. vernayi* (Roberts, 1932).
	zuluensis (Roberts, 1924)	monotypic
Pipistrellus Kaup, 1829	*hesperidus* (Temminck, 1840)	*P. h. hesperidus* *P. h. subtilis* (Sundevall, 1846) *P. h. broomi* (Roberts, 1948)
	rusticus (Tomes, 1861)	monotypic

distributional range of *H. anchietae* with identifications based on bacula and chromosome diploid number, indicated that the current identification key (Meester *et al.*, 1986) is inadequate for the identification of this species (Kearney and Taylor, 1997). *Pipistrellus hesperidus* also has an easterly distribution in southern Africa associated with coastal and Afromontane forests (Taylor, 2000), while *P. rusticus* is distributed in savanna woodland in the northern and north-eastern parts of the subregion (Taylor, 2000). The distribution of *Pipistrellus hesperidus,* extending westwards across the Limpopo Province in South Africa as described initially by Rautenbach (1982) and subsequently followed by Smithers (1983), Skinner and Smithers (1990), Taylor (2000) and Friedmann and Daly (2004) is incorrect given the re-identification of most of the specimens indicated by Rautenbach (1982) as *P. hesperidus* to *P. rusticus* by K. Koopman (in January 1988, see Transvaal Museum specimen records).

For many of these species diet, reproduction, habitat, habits and roosts are poorly known (Taylor, 2000).

1.3 TAXONOMY

A recent molecular analysis of the Vespertilionidae (Hoofer and Van Den Bussche 2003) provided results for studies of higher-level relationships (Simmons 1998), since it recognised more than one family within Vespertilionidae and elevated the subfamily Miniopterinae to its own family Miniopteridae. It also provided evidence that the subfamily Vespertilioninae is not monophyletic, due to the position of *Myotis*, and that the subfamily Nyctophilinae is not valid. The molecular results of Hoofer and Van Den Bussche (2003) also suggested relationships corresponding closely with the arrangement suggested by Volleth and Heller (1994) based on karyotypic revisions of Pipistrellus-like genera and tribes, including the monophyly of the Vespertilioninae in which the Pipistrellus-like bats are divided into three tribes, Nycticeiini (rather than Eptesicini, sensu Volleth and Heller, 1994), Pipistrellini and Vespertilionini. Hoofer and Van Den Bussche (2003) also found deep branching patterns within Vespertilioninae, characterised by short inter-nodal distances suggesting contemporaneous diversification for many (if not all) primary lineages within the subfamily.

At a lower level of relationship within Vespertilionidae, bats of the genera *Eptesicus* and *Pipistrellus* have been difficult to classify due to similar morphological characteristics (Volleth *et al.* 2001). The presence or absence of the second upper premolar was traditionally used to distinguish between *Eptesicus* and *Pipistrellus* and the classification followed by Meester *et al.* (1986) reflecting this feature, identified five species occurring in southern Africa in the genus *Eptesicus* (*rendalli, hottentotus, melckorum, somalicus*, and *capensis*), and five in the genus *Pipistrellus* (*rueppellii, nanus, rusticus, kuhlii*, and *anchietai*). *Pipistrellus rueppellii* was classified in the separate subgenus *Vansonia* Roberts, 1946, whereas the other *Pipistrellus* species were in the subgenus *Pipistrellus* Kaup, 1829.

There have also been several changes at the species level. Both Meester *et al.* (1986) and Koopman (1993) recognised that *E. melckorum* had not been clearly distinguished from *E. capensis*. Rautenbach *et al.* (1993) questioned the taxonomic validity of *E. melckorum* and suggested it should be recognised as a synonym of *E. capensis*, on the basis of unpublished morphometric data which showed clinal variation within *E. capensis*. Rautenbach *et al.* (1993), however, also found specimens from the "interior of South Africa" being intermediate in size between *N. capensis* and *E. hottentotus,* which matched the description of *E. melckorum*. These specimens have a different chromosome number (i.e., $2n = 40$) to *E. capensis* (Rautenbach and Schlitter, 1985), and allozyme results (Morales *et al.*, 1991) have shown them to be biochemically well differentiated, although closely allied to *E. capensis*. Rautenbach *et al.* (1993) suggested these specimens found in northern South Africa and Zimbabwe be called *E.* cf. *melckorum* pending formal description, which is currently being undertaken by Dr Duane Schlitter (pers. comm.).

Thorn (1988) recognised four distinct subspecies of *N. capensis* (on the basis of colour and size), most of which were previously incorporated in classifications of Roberts (1951) and Ellerman *et al.* (1953). Koopman (1994) also recognised four subspecies, however one of these, *notius*, was different to those recognised by Thorn (1988). This inclusion of *notius* was surprising given Koopman (1975) had earlier suggested *E. notius* be synonymised with *E. capensis* given the characteristic warts found in *notius* were probably the result of nematode infection. Given variability in colour and size across their range (Rosevear, 1962), it has long been recognised that *N. capensis* might be a complex of species widely spread over the African continent. Rautenbach and Schlitter (1985) indicated that they had found as yet undocumented clinal variation in size across the distribution of *N. capensis* in South Africa. But, whether this variation in colour and size is indicative of different species, races, or is ecologically induced has been cause for confusion (Rosevear, 1962), and still remains to be answered. However, until a complete analysis of the species across their entire distribution is undertaken there has been some reluctance to make any subdivisions and hence Meester *et al.* (1986) recognised no subspecies in *N. capensis*.

Although the specific name *P. nanus* has been used more frequently in publications, which is the basis of the application by Happold (2003) to the International Commission on Zoological Nomenclature to have the name conserved, the species does have a senior name, *africanus*. Two bat specimens collected from Shoa Province in Ethiopia were given the same catalogue number and identified as *Vespertilio pipistrellus* varietas *africanus* by Ruppell (1842). Koopman (1975) and Kock (2001a) identified that one of these specimens represented a specimen of *Pipistrellus nanus* (Peters, 1852), and hence that the name *P. africanus* was a senior synonym of *P. nanus*. The other specimen was identified by Kock (2001a) as *P. hesperidus*. Although the senior name *africanus* appears not to have gained use in publications given the confusion over its existence, two responses to the recommendation by Happold (2003) to conserve the more widely used name have pointed out that to suppress the name *africanus* would be premature as the taxon as currently understood is apparently not monotypic and the names are thus likely not to be synonyms (Van Cakenberghe, 2003; Kock, 2004). Van Cakenberghe (2003) pointed out that while similar in size of some measurements, the lectotype of *P. africanus* was marginally larger than specimens of *P. nanus* from north-eastern Africa in length of the maxillary tooth row, width across the upper molars and length of the mandibula and tibia. Until a comprehensive revision of the complex has been achieved it would be unwise to suppress a potentially valid name.

The presence or absence of the second upper premolar, however, is not a useful character for separation of the genera *Pipistrellus* and *Eptesicus* as tooth reduction has taken place independently in several lineages of the family Vespertilionidae (Volleth *et al.*, 2001). Using variations in tooth morphology and cusp patterns, Menu (1985) classified vespertilionid species into different groups. Hill and Harrison (1987) used baculum shape to re-assign all of the southern African species classified as *Eptesicus* in Meester *et al.* (1986), to the subgenus *Neoromicia* in the genus *Pipistrellus* with the exception of *E. hottentotus*. Hill and Harrison (1987) also re-assigned two species classified as *Pipistrellus* (*Pipistrellus*) in Meester *et al.* (1986), *P. nanus* and *P. anchietae*, to the subgenus *Hypsugo* within *Pipistrellus*. The generic changes suggested by Hill and Harrison (1987) were followed by Koopman (1994).

A difference in chromosome diploid number (Rautenbach *et al.*, 1993) was used to support the elevation to species level of specimens previously assigned in Meester *et al.* (1986) to the subspecies *E. somalicus zuluensis*. A reduced chromosome diploid number was also used to support re-assigning specimens from southern Africa and Madagascar assigned in Meester *et al.* (1986) to *Pipistrellus kuhlii*, to distinguish them from specimens in North Africa and Europe which have a different diploid chromosome number (Volleth *et al.*, 2001; Kearney *et al.*, 2002). This same distinction, albeit identified on the basis of different parasites and cranial morphology, had been noticed by Kock (2001a) who provided the name *P. hesperidus* for the Afrotropical specimens south of the Sahara. Kock (2001b) also justified the emendation to the spelling of *N. anchietae*. Meester *et al.* (1986) recognised two subspecies of *P. hesperidus* in southern Africa, *P. h. subtilis* and *P. h. broomi*; of these, Koopman (1994) only recognised *P. h. subtilis*.

Chromosomal characteristics (Volleth *et al.*, 2001; Kearney *et al.*, 2002) have also been useful at the generic level to distinguish between *Eptesicus* and *Pipistrellus*, and to provide support for the elevation of various subgenera from within *Eptesicus* and *Pipistrellus* to generic level, including *Neoromicia* and *Hypsugo*. The elevation of *Hypsugo* to generic level was also supported by detailed morphological (Horáček and Hanák, 1986) and biochemical (Ruedi and Arlettaz, 1991) analyses. The characteristics of *Neoromicia* (defined by the presence of three Robertsonian fusion chromosomes: 7/11, 8/9, 10/12) also supported the re-assignment of *Hypsugo africanus* to the genus *Neoromicia* (Kearney *et al.*, 2002).

Although the molecular results of Hoofer and Van Den Bussche (2003) corroborated reclassification of species from *Eptesicus* (Hill and Harrison, 1987, Volleth *et al.*, 2001; Kearney *et al.*, 2002), the molecular results contradicted the monophyly of *Neoromicia* and *Hypsugo* (in which they included *H. nanus* sensu Hill and Harrison, 1987). However, had Hoofer and Van Den Bussche (2003) considered *H. nanus* as *N. nanus*, as suggested by GTG-banded chromosome characters (Kearney *et al.*, 2002), the polyphyly in *Hypsugo* might not have occurred and the degree of polyphyly seen in *Neoromicia* may have been smaller. Regarding the problem of the polyphyly in *Hypsugo*, Hoofer and Van Den Bussche (2003) suggested that, pending further study, their results supported the restriction of the genus *Hypsugo* to the type species *H. savii* and transferred the species (*H.*) *eisentrauti* to *Nycticeinops*. The polyphyly in *Neoromicia*, with *N. somalicus* being a sister taxon to *Laephotis*, led Hoofer and Van Den Bussche (2003:32) to suggest retaining *Neoromicia* for "the type species of *Neoromicia*, *N. somalicus* (= *Eptesicus zuluensis*; Roberts 1926)", and allocating (*Hypsugo*) *nanus* and (*Neoromicia*) *brunneus* and *rendalli* to a separate as yet unnamed genus. However, since Rautenbach *et al.* (1993) proposed the elevation to species of *N. zuluensis* , and given the proximity of the locality (Kenya: Coastal Province) of the specimen used in the study by Hoofer and Van Den Bussche (2003) to the type locality of *N. somalicus* (Hargeisa: Somalia), rather than the type locality of *N. zuluensis* (South Africa: White Umfolosi Game Reserve), it is possible that Hoofer and Van Den Bussche (2003) did not include the type species of *Neoromicia* in their study.

The taxonomy used in this study generally follows Meester *et al.* (1986), but with the following exceptions: Volleth *et al.* (2001) for *Hypsugo*, Volleth *et al.* (2001) and Kearney *et al.* (2002; see Appendix I) for *Neoromicia*, Koopman (1975 and 1993) for *N. africanus*, Rautenbach *et al.* (1993) for *N.* cf. *melckorum*, Kock (2001a) for *P. hesperidus*, Kock (2001c) for *N. a. meesteri*, and Kearney and Seamark (2005; see Appendix I) for *Laephotis*. The spelling of *N. anchietae* follows the emendation justified by Kock (2001b).

1.4 PROJECT AIM AND SCOPE

This study attempted to clarify the generic and species relationships among 10 southern African taxa of the bat genera *Eptesicus*, *Neoromicia*, *Hypsugo* and *Pipistrellus* (Table 1.1), using a multifaceted assessment of variation in baculum morphology, GTG-banded chromosomes (Chapter 2) and skull and mandible shape and size using geometric (Chapter 3) and traditional morphometric techniques (Chapters 4 to 7). Additional species from other genera within the family Vespertilionidae and subfamily Vespertilioninae were also included in some of the analyses to provide a broader familial and sub-familial context for the taxa under review. As detailed later in this introduction, Meester *et al.* (1986) recognised the problems at both the genus and species levels within the complex subfamily Vespertilioninae and identified that *Pipistrellus* and *Eptesicus* required revision.

The above methods of analysis were chosen for this study because only limited karyotypical investigations had been carried out on southern African species of *Eptesicus, Neoromicia, Hypsugo* and *Pipistrellus* (Peterson and Nagorsen, 1975; McBee *et al*., 1987; Rautenbach *et al*., 1993). Aside from the morphometric analysis of *E. hottentotus* by Schlitter and Aggundey (1986), no other morphometric work had been published on southern African *Neoromicia, Hypsugo* and *Pipistrellus*. The relatively new technique of geometric analysis was undertaken to complement the traditional method of morphometric analysis. Baculum morphology, although having limited application to male specimens only, had been used for species identification and assessing generic relationships within Vespertilioninae in the study by Hill and Harrison (1987), and while their analysis included all the species of *Eptesicus, Neoromicia, Hypsugo* and *Pipistrellus* occurring in the southern African sub-region, few of the specimens studied were from southern Africa.

Species concepts abound and are still much debated (Guy *et al*., 2003) and it has been indicated that the choice of a particular concept is often determined by the aspect or process in nature that forms the focus of the study (Miller III, 2001). This study was made within the framework of the evolutionary species concept. Simpson's (1961, p.153) description says, "An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies". This lineage species concept although not operational, offers a view of species as historical entities, whose attributes and patterns can be correctly interpreted with respect to their unique descent (Claridge *et al*., 1997; Miller III, 2001). Hence, in clarifying the relationships between the vespertilionid species in this analysis, the aim was to present relationships between species that reflect true phylogeny, free from homoplasies. The evolutionary species concept does not prescribe operational procedures for species delimitation since it allows a number of different approaches, applicable in different circumstances to different requirements, attempting to serve as a primary concept that encompasses all evolutionary outcomes in all kinds of cellular life (Miller III, 2001).

The secondary approach used in this study for practical species delimitation included the use of bacula and karyotype information as absolute species markers against which shape and morphometric characters were tested. Both the bacula and karyotype information were used as indicators of the species "evolving separately from others and with its own unitary evolutionary role and tendencies" (Simpson, 1961, p.153). Such an approach may be seen as pluralist in that the use of chromosomal characters emphasises reproductive isolation suggesting the use of the biological species concept ["A species is a group of interbreeding natural populations that is reproductively isolated from other such groups" (Mayr and Ashlock, 1991)] as a secondary concept, whereas, the use of bacula morphology, which may be important for mate coupling, suggests the use of the recognition species concept ["A species is that most inclusive population of individual, bi-parental organisms which share a common fertilisation system" (Paterson, 1993 p.105)] as a secondary concept.

Disagreements over different results from genetic and morphological data have led some authors to reconsider the reliability of craniodental characters to assess species diversity or to support phylogenetic hypotheses (Guy *et al*., 2003). It has also been suggested that the ultimate test of validity of a morphological analysis is congruence with multiply supported, robust, gene-based trees (Pilbeam, 2000). Others, however, have taken to combining several types of data to improve resolution and stability of resulting phylogenetic hypotheses (see contributions in Part One: Phylogeny and Evolution in Kunz and Racey, 1998). Such studies based on maximising information suggest there is no single "best" data set for answering phylogenetic questions, and point out that molecular data, although highly informative, are subject to most of the same problems that complicate interpretations of morphological data i.e., homoplasy (Simmons and Hand, 1998).

Recent molecular analyses of species in the genus *Myotis* (from the same family, Vespertilionidae, as the taxa central to this analysis) (Ruedi and Mayer, 2001), and on the family Vespertilionidae as a whole (Hoofer and Van Den Bussche, 2003) have indicated that morphological characters traditionally used in vespertilionid systematics have little phyletic information. Instead, Ruedi and Mayer (2001) found morphological similarities that had been used in classification represented independent convergent adaptive radiations of similar ecomorphs, rather than reflecting phylogenetic relationships. Hoofer and Van Den Bussche (2003) suggested the zoogeographic history of the vespertilionid bats may have been far less complex than traditionally thought, especially regarding New World / Old World dispersal events, and that much of the morphological and ecological similarity has resulted from repeated episodes of convergent evolution. The mitochondrial DNA analysis of Hoofer and Van Den Bussche (2003) also supported the karyotypic data of Volleth and Tidemann (1991) and Volleth and Heller, (1994) which indicated a shared common ancestry for the majority of Australian vespertilionids, the range of observed phenotypes having resulted from radiation into a wide range of niches. Although many of the phenotypes resemble vespertilionids from other continents, Australian vesper bats traditionally regarded as belonging to *Pipistrellus* or *Eptesicus* are not closely related to members of either genus (Hoofer and Van Den Bussche, 2003). The mitochondrial DNA results of Hoofer and Van Den Bussche (2003) also suggested similar changes for other traditional morphological groups such as *Eptesicus* and New World '*Pipistrellus*'.

Clearly, the taxonomic validity of morphological variation and interpretations of morphological variation relevant to an appropriate taxonomic level (i.e. determining the threshold of morphological difference between subspecies, species and genera) require thorough testing (Guy *et al.*, 2003). In the context of these recent suggestions, the use of morphological data in this effort to resolve generic and specific relationships was approached with some caution and relationships were examined for phyletic signal and congruence with the phylogenetic relationships suggested by the analysis of GTG-banded chromosomes (this study) and mitochondrial DNA (Hoofer and Van Den Bussche, 2003). The assessment of morphological characters was also pursued recognizing that, although they may not contain much phyletic signal themselves, they could provide characters with which to interpret morphological evolution and convergence once a robust phylogeny has been achieved using other techniques. Morphological evolution (e.g. convergence versus divergence) is an important topic in its own right, and morphological characters superimposed onto existing phylogenies can give important insights into the evolution of morphological and behavioural innovations i.e. foraging strategies and dietary specialisations (Van Cakenberghe *et al.*, 2002).

This work was, for the most part, limited to the distribution of the species within the southern Africa region, defined as south of the Cunene and Zambezi Rivers, including Namibia, Botswana, Zimbabwe, part of Mozambique, South Africa, Lesotho and Swaziland. Systematic analyses based on limited geographic regions within a species distribution have been criticised for potentially misconstruing results, for being biased to a restricted sample and not being sufficiently useful because of the limited application of the results (Adams *et al.,* 1982). However, while many of the species in the taxa in question in this study have extensive distribution ranges, it was deemed more practical to delimit the study region and make a start revising the relationships within a more manageable grouping of southern African species. The southern African species are broadly representative of the group as a whole and, therefore, provide a good test of generic relationships. Another practical issue, which benefited from the delimitation of the study region, was access to museum collections which in South Africa largely represent southern African species.

Field work at localities from Zimbabwe, the Western Cape and north-eastern KwaZulu-Natal in South Africa was undertaken to collect material for the chromosome study (Chapter 2). These specimens were also used in the other assessments made, and for the traditional morphometric investigations provided specimens of known identity (Chapters 4 to 7). For the geometric morphometric assessment (Chapter 3), 708 specimens from eight collections were digitised. Measurements were also made from 1064 specimens from eight different museum collections for the traditional morphometric investigations (Chapters 4 to 7).

CHAPTER 2

SYSTEMATIC IMPLICATIONS OF CHROMOSOME GTG-BAND AND BACULA MORPHOLOGY

2.1 INTRODUCTION

Differences between *Eptesicus* Rafinesque, 1820 and *Pipistrellus* Kaup, 1829, two genera of insectivorous bats of the family Vespertilionidae have long been problematic (Koopman, 1975; Horáček and Hanák, 1986. Heller and Volleth (1984) proposed that *Eptesicus* is chromosomally conservative, all species having a diploid number of 50, while *Pipistrellus* is chromosomally variable, having diploid numbers of 44 or less. At the time of Heller's and Volleth's work (1984), the only species occurring in southern Africa that had been karyotyped were *E. hottentotus* (A. Smith, 1833) and *E. capensis* (A. Smith, 1829) (Peterson and Nagorsen, 1975). *Eptesicus capensis* with a diploid number of 32 was placed in the genus *Pipistrellus*.

On the basis of bacular morphology, Heller and Volleth (1984) and Hill and Harrison (1987) suggested the *Eptesicus* and *Pipistrellus* could be distinguished from each other by *Eptesicus* having a small, triangular baculum, and *Pipistrellus* having a medium to large, "stick-like", elongated baculum. Applying these characters, Hill and Harrison (1987) transferred all, but one southern African species of *Eptesicus* [*capensis, melckorum* Roberts, 1919, *somalicus* (Thomas, 1901), *zuluensis* Roberts, 1924 and *rendalli* (Thomas, 1889)], with the exception of *E. hottentotus*, to the subgenus, *Neoromicia*, in the genus *Pipistrellus*. A subsequent allozyme analysis by Morales *et al.* (1991), which included several southern African species of *Eptesicus* (*hottentotus, capensis, zuluensis*, cf. *melckorum*) and *Pipistrellus* (*africanus*), showed biochemical relationships between the taxa to be consistent with the suggestions of Heller and Volleth (1984) and Hill and Harrison (1987).

Several authors (Ansell and Dowsett, 1988; Cotterill, 1996; Fenton and Rautenbach, 1998; Taylor, 2000) and at least one museum (Natural History Museum of Zimbabwe, Bulawayo) have followed the suggestions of Heller and Volleth (1984) and Hill and Harrison (1987). But for the most part, the caution by Meester *et al.* (1986: 56) appears to have been followed, that until all southern African species of *Eptesicus* and *Pipistrellus* have been tested against the bacula and chromosome criteria "it would be premature to depart from established generic synonymy".

Various studies have subsequently confirmed on the basis of diploid number (from non-differential staining), that *E. rendalli, E. somalicus* (McBee *et al.*, 1987; Rautenbach and Fenton, 1992), *E.* cf. *melckorum* (*sensu* Rautenbach *et al.*, 1993), and *E. zuluensis* (Rautenbach *et al.*, 1993) all have diploid numbers less than 50.

Chromosome banding has also proved a useful source of characters, enabling Volleth and Heller (1994) to infer phylogenetic relationships for the Vespertilionidae. Two chromosomal characters, i.e. the banding pattern of chromosomes 11 and 23, were found to separate the tribes Vespertilionini and Pipistrellini. According to those characters, *Pipistrellus* (*Neoromicia*) *capensis* is a member of the tribe Vespertilionini, and not Pipistrellini. In order to prevent a polyphyletic classification for the genus *Pipistrellus*, Volleth *et al.* (2001) suggested the subgenus *Neoromicia* be elevated to generic rank, as had been done before for all other *Pipistrellus* subgenera *sensu* Hill and Harrison (1987) (*Hypsugo*: Horáček and Hanák, 1986; *Perimyotis*: Menu, 1984; *Vespadelus*: Volleth and Tidemann, 1991; *Falsistrellus*: Kitchener *et al.*, 1986; *Arielulus*: Csorba and Lee, 1999). This study follows the above-mentioned authors and treats all subgenera of *Pipistrellus* (sensu Hill and Harrison, 1987) as separate genera.

In this study, the first GTG-banded karyotypes of five southern African *Pipistrellus*-like species, and the outgroup *Myotis tricolor* (Temminck, 1832) are presented. Bacular morphology is revisited to confirm the usefulness of this structure for identifying relationships. GTG-banded chromosomes and bacular morphology provided characters for cladistic analyses to assess inter- and intra-generic relationships among southern African *Pipistrellus*-like species.

2.2 Materials and Methods

2.2.1 Chromosomes

GTG-banded (Seabright, 1971) karyotypes were constructed from bone-marrow metaphase spreads (for method see Green *et al.*, 1980) of *E. hottentotus, N. capensis, N. rendalli, N. zuluensis, N. africanus, P. hesperidus, P. rusticus* (Tomes, 1861), and *M. tricolor*, from specimens captured at various localities in South Africa (Appendix I). Chromosomes were arranged following a standardised numbering system introduced by Bickham (1979*a*) for *Myotis*, where chromosome arms instead of chromosomes are numbered. This numbering system has been used subsequently in analyses of European and Asian Vespertilionidae, including *Eptesicus* and *Pipistrellus* species, by Zima (1982), Volleth (1987), Volleth and Heller (1994), and Volleth *et al.* (2001). Since complete chromosomal arms are conserved extensively in the family, it should be possible to trace the changes that have given rise to different diploid numbers, and thus infer phylogenetic relationships. Most often the chromosome changes are due to Robertsonian rearrangements, but occasionally due to inversions and tandem fusions (Baker *et al.*, 1982; Zima, 1982; Volleth and Heller, 1994).

Seven chromosome rearrangements (see Appendix 2.3), i.e., the presence or absence of five synapomorphic Robertsonian fusion products, the state of chromosome 11 due to a small paracentric inversion (Volleth and Tidemann, 1989; Volleth and Heller, 1994; Volleth *et al.*, 2001), and the state of the X chromosome, were used to construct a data matrix (Appendix 2.3). Following Ando *et al.* (1977), Bickham (1979*b*), Zima (1982), Baker *et al.* (1985), and Volleth and Heller (1994) who all considered the *Myotis* karyotype, $2n = 44$, FN = 52, as closest to the hypothetical ancestral karyotype of Vespertilionidae, the present study used *M. tricolor* ($2n = 44$, FN = 52) as the outgroup.

Robertsonian fusion chromosomes are denoted as the fusion chromosome numbers linked by a forward slash. Tandem fusions are denoted as the fusion chromosome numbers linked by a hyphen.

2.2.2 Bacula

Bacula were dissected, stained (Hill and Harrison 1987), cleared in glycerin (Lidicker 1968), and drawn (Fig. 2.1) for *E. hottentotus, N. capensis, N. rendalli, N. zuluensis, N.* cf. *melckorum, N. africanus, P. rusticus, P. hesperidus, P. rueppellii,* and *Hypsugo anchietae* (Seabra, 1900). There were also included bacula from *M. tricolor, Laephotis* cf. *wintoni* (*sensu* Kearney and Taylor, 1997), *L. namibensis* Setzer, 1971, *L. botswanae* Setzer, 1971, *Nycticeinops schlieffenii* (Peters, 1859) and *Scotophilus dinganii* (A. Smith, 1833), which are all genera within the same subfamily Vespertilioninae, as *Pipistrellus* and *Eptesicus*. Specimen details are given in Appendix 2.2. Since bacula of different *Laephotis* species are almost identical, their results were combined as *Laephotis* spp.

For each baculum, seven qualitative characters were scored, two of which were multistate and a matrix of bacula characters was created (see Appendix 2.4). As described for the chromosome analysis above, *Myotis tricolor* was used as the outgroup.

2.2.3 Analyses

Data matrices of phylogenetically informative bacula and chromosome characters, and a matrix combining bacula and chromosome characters were analysed with Hennig86 (version 1.5; Farris, 1988). Character polarity was determined by the outgroup. Multistate characters were run as nonadditive. Characters were not weighted. The shortest possible trees were found using implicit enumeration (the `ie*' command in Hennig86). Hennig86 (version 1.5; Farris, 1988) also provided information about how many characters showed convergences and parallelisms (i.e. homoplasy) in the construction of trees with the calculation of tree length, or number of steps (S), the consistency index (CI), and the retention index (RI). The number of steps (S) is the total number of character state changes necessary to support the relationship of taxa in a tree (Camin and Sokal, 1965). The consistency index (CI) is calculated as the number of steps expected given the number of character states in the data, divided by the actual number of steps multiplied by 100 (Kluge and Farris, 1969). The retention index (RI) is a measure of the synapomorphy expected from a data set that is retained as synapomorphy on a cladogram, and is calculated by the maximum number of steps on a tree minus the number of state changes on the tree, divided by the maximum number of steps on a tree minus the number of state changes in the data, multiplied by 100 (Farris, 1991).

In order to assess whether there was a lack of congruence between the bacula and chromosome data sets, two measures of incongruence were used, the Mickevich-Farris incongruence metric (i_{MF}) (Kluge, 1989), and the incongruence length difference (D_{xy}) (Mickevich and Farris, 1981). The robustness of the resulting trees was assessed using the '\\x;' command in Dos-equis mode of Hennig86. This identifies the additional length gained when branches are lost, by successively collapsing nodes leading to at least two taxa in the tree. This is analogous to Bremer's branch support (Bremer, 1994), which although not useful for comparison between analyses, because it is positively correlated with the number of characters in a particular analysis,

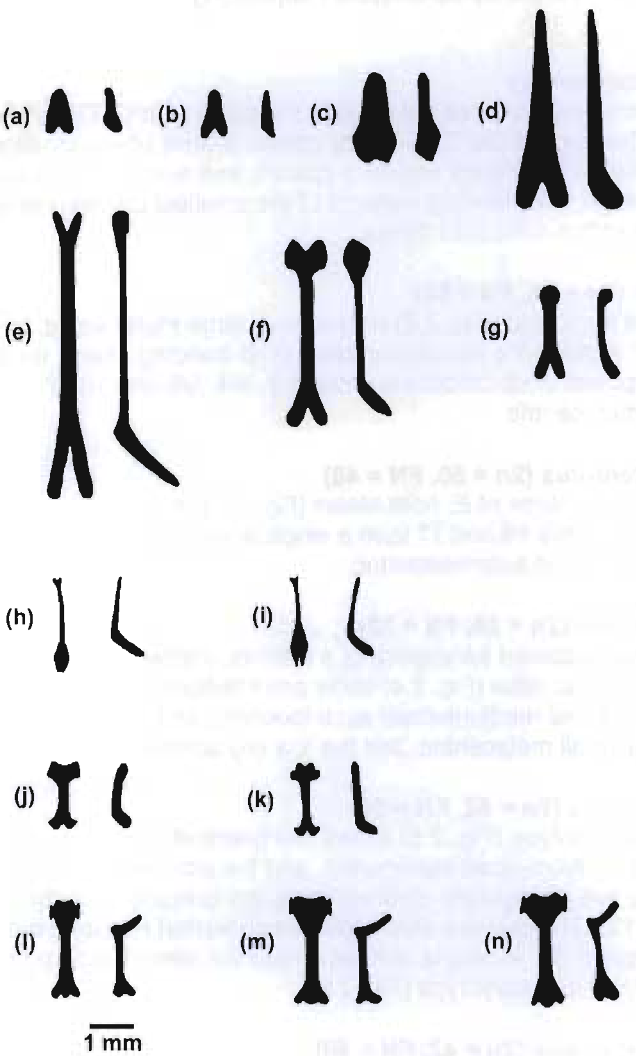


Figure 2.1 Dorsal (left) and lateral (right) views of bacula from: (a) *Myotis tricolor*, (b) *Eptesicus hottentotus*, (c) *Scotophilus dinganii*, (d) *Nycticeinops schlieffenii*, (e) *Pipistrellus rueppellii*, (f) *Neoromicia rendalli*, (g) *Neoromicia africanus*, (h) *Pipistrellus rusticus*, (i) *Pipistrellus hesperidus*, (j) *Hypsugo anchietae*, (k) *Neoromicia zuluensis*, (l) *Neoromicia capensis*, (m) *Neoromicia* cf. *melckorum*, (n) *Laephotis* cf. *wintoni* from southern Africa.

it is informative within an analysis (Bremer, 1996). As a further measure of topology support, the number of unique and unreversed synapomophies supporting each node were counted.

2.3 RESULTS

2.3.1 Chromosome morphology

Unfortunately, bone marrow does not provide the same high GTG-band resolution that cell-cultured spreads do. Thus, not all the GTG-bands obtained were of a resolution to allow detection and confirmation of possible inversions and intra-specific variations, other than a possible polymorphism in *N. rendalli*. The banding patterns of the smallest chromosomes (including the Y chromosome) were also often difficult to detect.

2.3.1.1 *Myotis tricolor* (2*n* = 44, FN = 52)

The GTG-banded karyotype (Fig. 2.2) shows three large metacentric, one small submetacentric, and 17 acrocentric autosomal pairs. GTG-banding shows the four biarmed chromosomes are composed of chromosome arms: 1/2, 3/4, 5/6 and 16/17. The X chromosome is a medium-sized submetacentric.

2.3.1.2 *Eptesicus hottentotus* (2*n* = 50, FN = 48)

The GTG-banded karyotype of *E. hottentotus* (Fig. 2.3) shows all 24 pairs of autosomes are acrocentric. Chromosome arms 16 and 17 form a single acrocentric chromosome. The X chromosome is a medium-sized submetacentric.

2.3.1.3 *Hypsugo anchietae* (2*n* = 26, FN = 32)

The non-differentially stained karyogram of a male *H. anchietae* (Fig. 2.4) and GTG-banded karyogram of a female *H. anchietae* (Fig. 2.4) show one medium-sized submetacentric, one small metacentric, two large and one medium-sized subtelocentric, and seven acrocentric autosomes. The X chromosome is a small metacentric, and the Y a tiny acrocentric.

2.3.1.4 *Pipistrellus rusticus* (2*n* = 42, FN = 50)

The GTG-banded karyotype (Fig. 2.5) shows five biarmed, and 15 acrocentric autosomes. The X chromosome is a medium-sized metacentric, and the acrocentric Y is the same size as the smallest autosome. The five metacentric chromosomes are composed of chromosome arms: 1/2, 3/4, 5/6, 16/17, and 11/12. GTG-banded chromosomes show that *P. rusticus* and *P. hesperidus*, which have the same diploid chromosome number, share the same fusion pairs, including 11/12, which is not present in the basic karyotype (Fig. 2.6).

2.3.1.5 *Pipistrellus hesperidus* (2*n* = 42, FN = 50)

The GTG-banded karyotype (Fig. 2.7) shows five biarmed, and 15 acrocentric autosomes. The X chromosome is a medium-sized metacentric. The biarmed chromosomes are composed of arms 1/2, 3/4, 5/6, 16/17, and 11/12. The Robertsonian fusion chromosome 11/12 is the same as in *P. rusticus* (Fig. 2.6).

2.3.1.6 *Neoromicia africanus* (2*n* = 36, FN = 50)

The GTG-banded karyotype (Fig. 2.8) shows eight biarmed, and nine acrocentric autosomes. The X chromosome is a medium-sized metacentric, and the acrocentric Y chromosome is smaller than the smallest autosome. GTG-banding shows, besides the metacentric chromosomes 1/2, 3/4, 5/6 and 16/17, four chromosomes which are the result of Robertsonian fusions between chromosome arms 7/11, 8/9, 10/12, and 13/14. *Neoromicia africanus* shares fusion of pairs 7/11, 8/9, and 10/12 with *N. zuluensis*, *N. rendalli*, and *N. capensis* (Fig. 2.6), and it is, therefore, suggested transferring it to the genus *Neoromicia*.

2.3.1.7 *Neoromicia zuluensis* (2*n* = 28, FN = 48)

This GTG-banded karyotype (Fig. 2.9) shows 12 biarmed, and one acrocentric autosomes. The X chromosome is a medium-sized subtelocentric. GTG-bands show the reduced chromosome number in *N. zuluensis* is due to Robertsonian fusion pairs between chromosome arms 7/11, 8/9, 10/12, 13/18, 14/21, 15/19, 20/22, and 23/24. *Neoromicia zuluensis* shares pairs 7/11, 8/9, 10/12 with *N. africanus*, *N. rendalli*, and *N. capensis*, and pair 13/18 with *N. capensis* (Fig. 2.6).

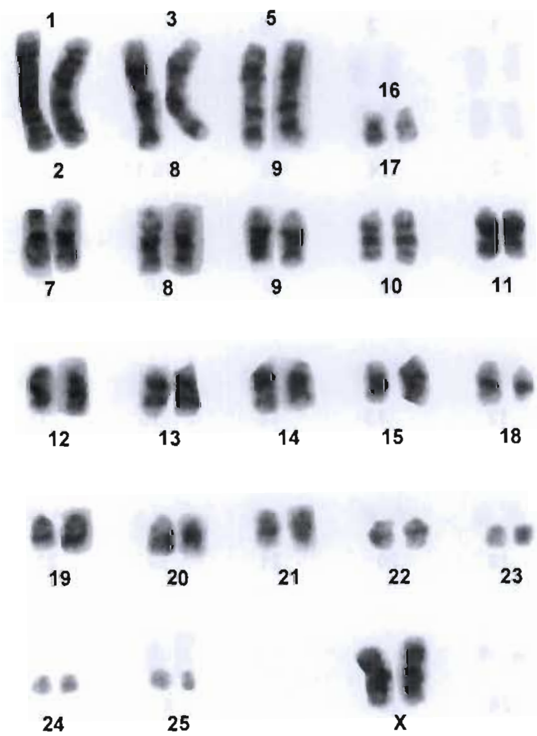


Figure 2.2 GTG-banded karyotype of *Myotis tricolor* from southern Africa.

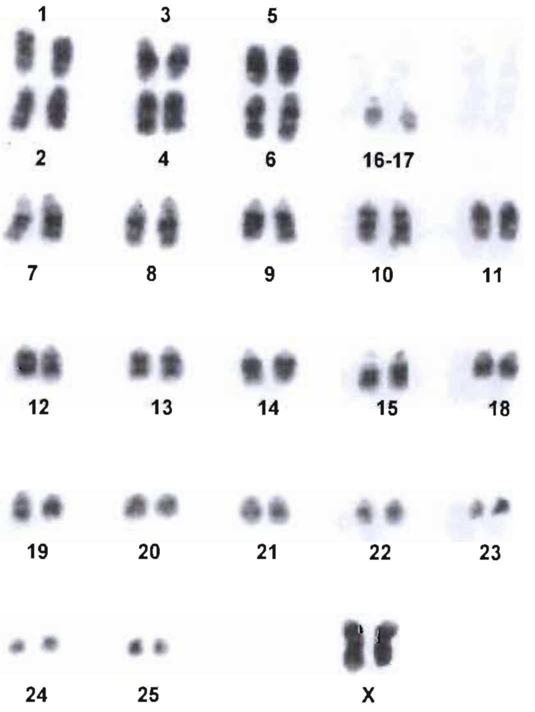


Figure 2.3 GTG-banded karyotype of *Eptesicus hottentotus* from southern Africa.

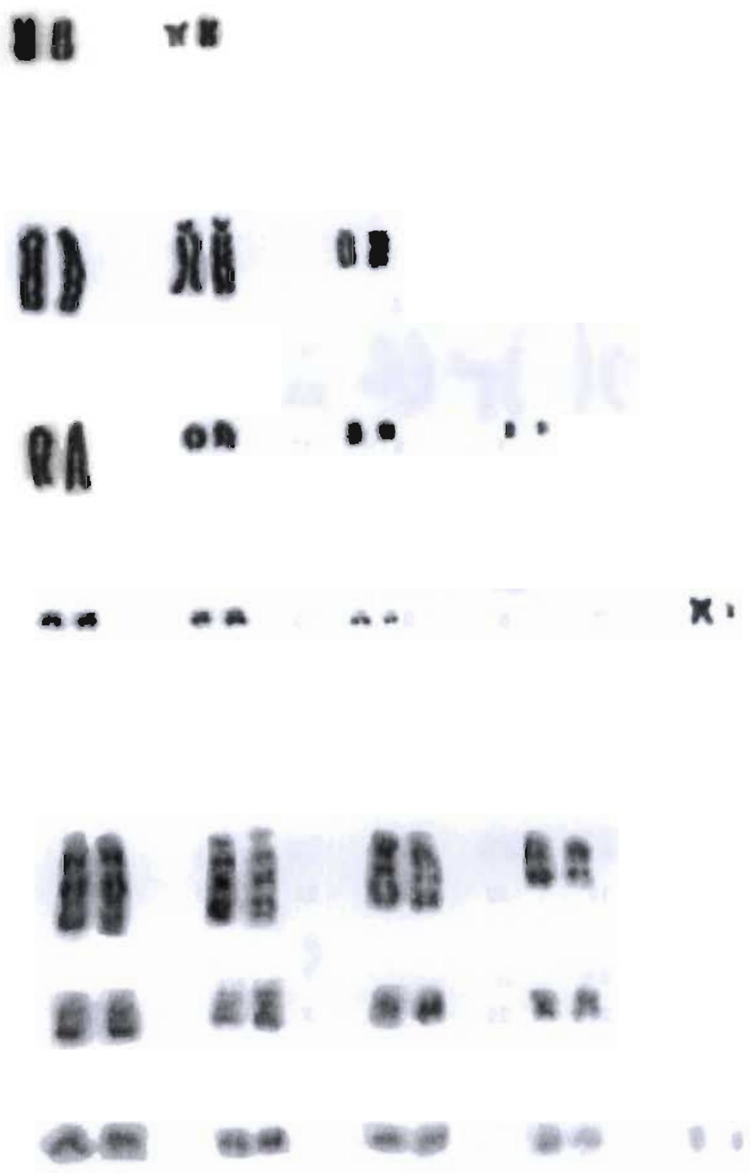


Figure 2.4 Non-differentially stained karyotype of a male (top) and GTG-banded karyotype of a female (below) of *Hypsugo anchietae* from southern Africa

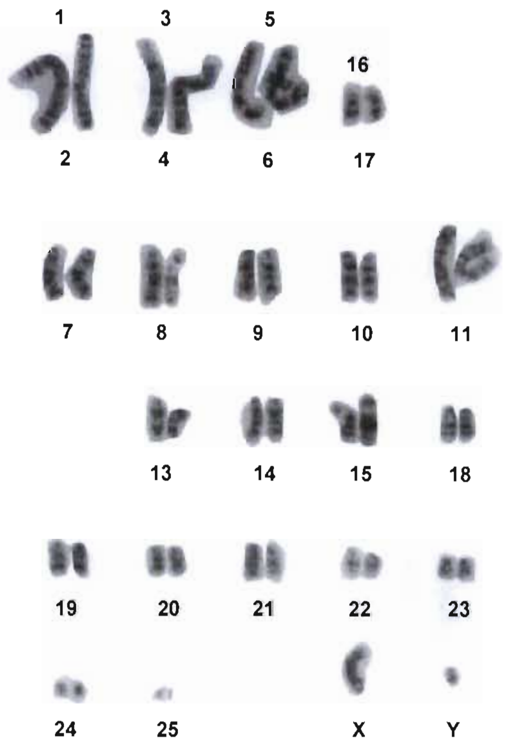


Figure 2.5 GTG-banded karyotype of *Pipistrellus rusticus* from southern Africa.

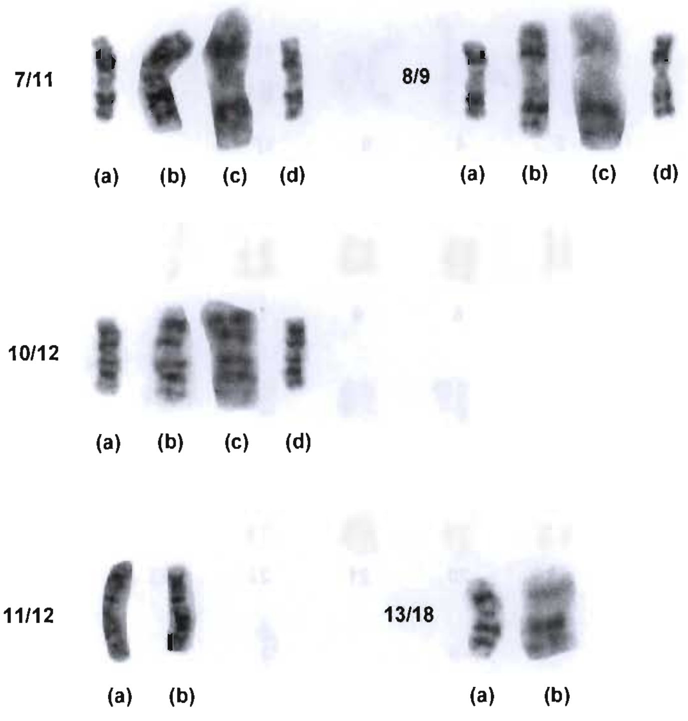


Figure 2.6 Comparison of GTG-banded chromosome pairs between species: 7/11, 8/9, 10/12: (a) *Neoromicia africanus*, (b) *N. zuluensis*, (c) *N. capensis*, (d) *N. rendalli*; 11/12: (a) *Pipistrellus rusticus*, (b) *P. hesperidus*; 13/18: (a) *N. zuluensis*, (b) *N. capensis* from southern Africa.

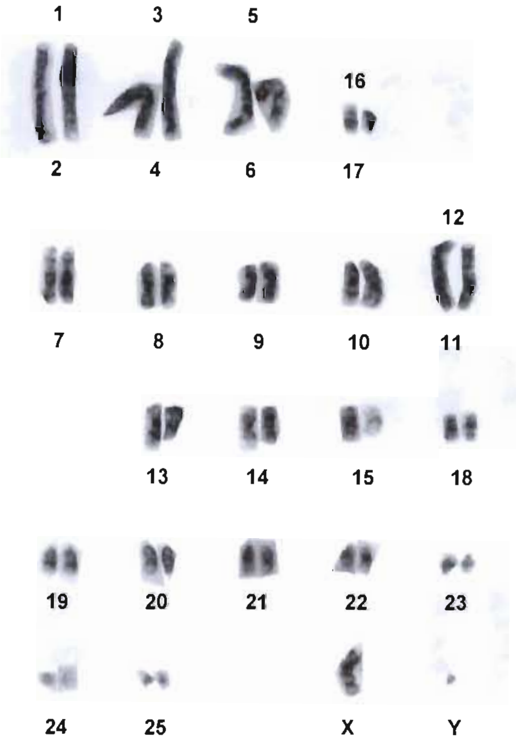


Figure 2.7 GTG-banded karyotype of *Pipistrellus hesperidus* from southern Africa.

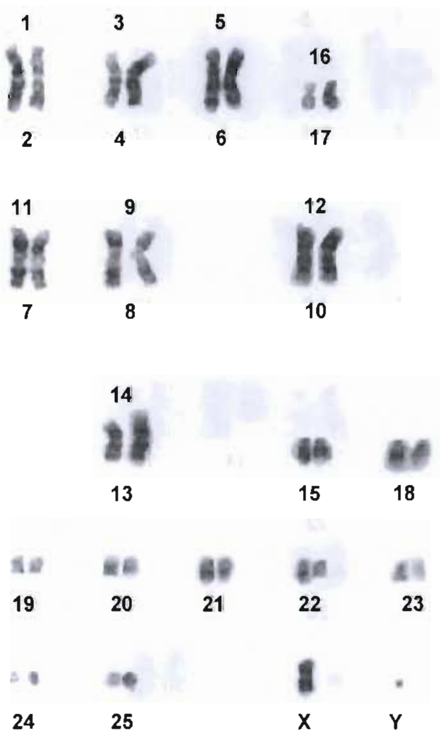


Figure 2.8 GTG-banded karyotype of *Neoromicia africanus* from southern Africa.

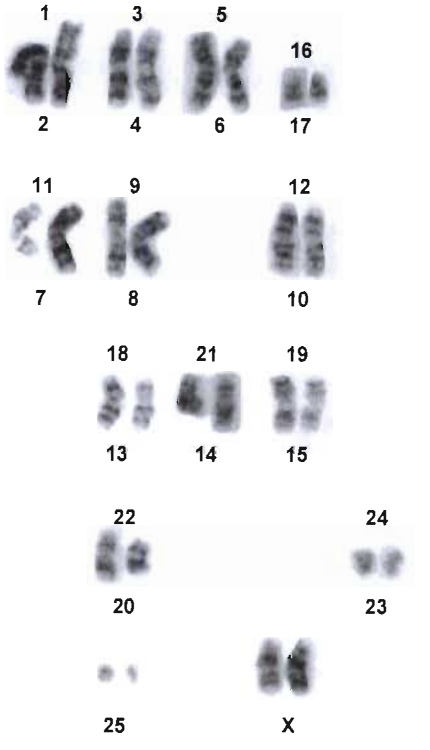


Figure 2.9 GTG-banded karyotype of *Neoromicia zuluensis* from southern Africa.

2.3.1.8 *Neoromicia capensis* (2*n* = 32, FN = 50)

The GTG-banded karyotype (Fig. 2.10) shows 10 biarmed and 5 acrocentric autosomes. The X chromosome is a medium-sized metacentric. Robertsonian fusion pairs are between chromosome arms: 1/2, 3/4, 5/6, 16/17, 7/11, 8/9, 10/12, and 13/18. *Neoromicia capensis* shares pairs 7/11, 8/9, 10/12 with *N. africanus*, *N. rendalli*, and *N. zuluensis*, and pair 13/18 with *N. zuluensis* (Fig. 2.6).

2.3.1.9 *Neoromicia rendalli* (2*n* = 38, FN = 50)

The GTG-banded karyotype (Fig. 2.11) shows seven biarmed, and 11 acrocentric autosomes. The X chromosome is a medium-sized metacentric, and the acrocentric Y is as small as the smallest autosomes. GTG-bands show the seven biarmed chromosomes are composed of 1/2, 3/4, 5/6, 16/17, 7/11, 8/9, 10/12. All pairs are shared with *N. africanus*, *N. zuluensis* and *N. capensis* (Fig. 2.6).

2.3.2 Cladistic Analysis of Chromosomes

Analysis of the chromosome data (Appendix 2.3) resulted in one most parsimonious tree (length (S) = 8; consistency index (CI) = 100; retention index (RI) = 100) (Fig. 2.12). The tree is not fully resolved. A trichotomy at the base is made up of the outgroup *Myotis tricolor*, forming one of the branches, *E. hottentotus* forms the second branch, while the rest of the species form the third branch.

The third branch of the trichotomy forms two clades. *Pipistrellus rusticus* and *P. hesperidus* form one clade supported by a single synapomorphy (fusion of chromosomes 11 and 12), while *N. africanus*, *N. rendalli*, *N. zuluensis* and *N. capensis* form the other clade, as a result of four synapomorphies (fusions of chromosome 7 and 11, 8 and 4, 10 and 12, and state II of chromosome 11). The relationship between these species is not fully resolved as they form a trichotomy. However, *N. zuluensis* and *N. capensis* form the terminal clade separated from *N. africanus* and *N. rendalli* due to the fusion of chromosomes 13 and 18.

As reflected by CI and RI values of 100, the steps at each node are unique and unreversed synapomorphies, and there is no homoplasy. Branch support is highest (four) for the branch linking the trichotomy, while all the other branches have the same, lower support (one).

2.3.3 Bacular Morphology

Although differences in bacular morphology are slight between certain species, there is considerable variation in the bacular morphology of all the species represented (Fig. 2.1). These variations in bacular morphology provided characters (see Appendix 2.4) for cladistic analysis.

2.3.3.1 Cladistic Analysis of Bacula

Analysis of bacular characters (Appendix 2.4) produced one most parsimonious tree (S = 14; CI = 85; RI = 94) (Fig. 2.13), in contrast to the result which appeared in error in the published paper (Appendix I). The root is an unresolved polychotomy. The outgroup, *M. tricolor* forms one branch, *E. hottentotus* another branch, *S. dinganii* yet another branch, while the rest of the species united by a single synapomorphy, bacula shape being medium to large, elongated and 'stick-like' (BS/1), form the fourth branch.

A single synapomorphy, the tip not being distinct from the rest of the bacula (TD/1), separates *N. schlieffenii* from the next unresolved trichotomy. In the trichotomy, *Pipistrellus rueppellii* (Fischer, 1829) forms one branch. *Pipistrellus hesperidus* and *P. rusticus* as sister taxa separated by two synapomorphies, unique basal lobe shape (BL/4), and more than 50% of the bacula being deflected (PBD/1) form the second branch. The rest of the taxa (*N. africanus, H. anchietae*, *N. zuluensis*, *N. rendalli*, *N. capensis*, *N.* cf. *melckorum*, and *Laephotis* spp.) form the third branch, united by the tip shape being either flat and broad (TS/2) or triangular (TS/3), with the triangular shape (TS/3) then evolving from the flat broad shape (TS/2). A synapomorphy, the bacula base being narrower than the tip (TB/1), then separates *N. africanus* from the rest of the taxa (*H. anchietae*, *N. zuluensis*, *N. rendalli*, *N. capensis*, *N.* cf. *melckorum*, and *Laephotis* spp.). *Neoromicia rendalli* is separated from *Hypsugo anchietae*, *N. zuluensis*, *N. capensis*, *N.* cf. *melckorum*, and *Laephotis* spp. by the basal lobe shape being either 'V' shaped, short, broad, with wide edges (BL/1) or semi-circular, skirt-like (BL/2), with the semi-circular, skirt-like (BL/2) shape then evolving from the 'V' shaped, short, broad, with wide edges (BL/1). *Neoromicia capensis*, *N.* cf. *melckorum*, and *Laephotis* spp. form a trichotomy resolved from *Hypsugo anchietae*, *N. zuluensis* by three synapomorphies, a unique tip and basal shape (TS/3 and BL/2),

Figure 2.10 GTG-banded karyotype of *Neoromicia capensis* from southern Africa.

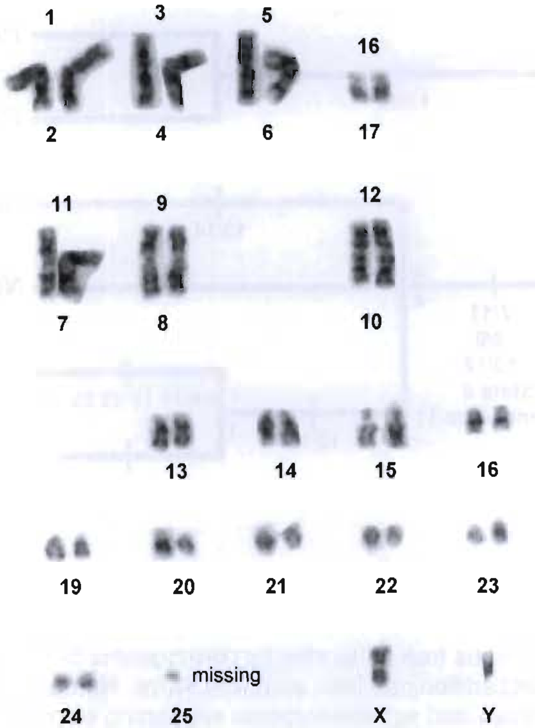


Figure 2.11 GTG-banded karyotype of *Neoromicia rendalli* from southern Africa.

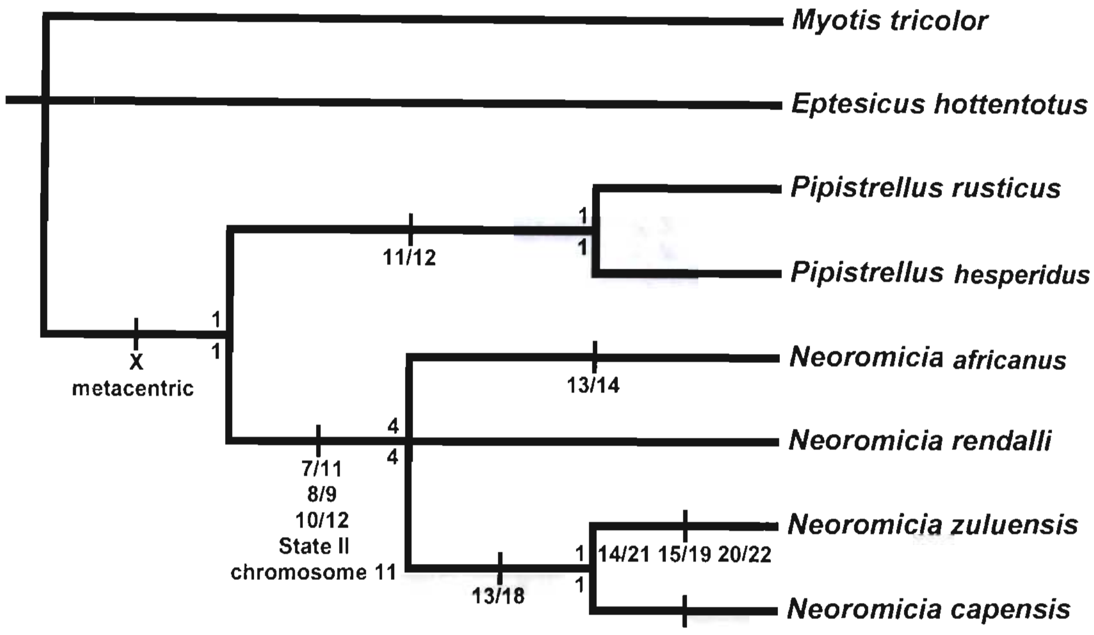


Figure 2.12 Most parsimonious tree generated by chromosome GTG-band characters, for seven taxa, of four genera of Vespertilioninae from southern Africa. Numbers above clade nodes are the number of unique and unreversed synapomorphies supporting each clade. Numbers below the clade nodes are branch support values (which is the number of extra steps required to collapse the particular node). Synapomorphic characters are shown below branches (abbreviations are explained in Appendices 2.3 and 2.4).

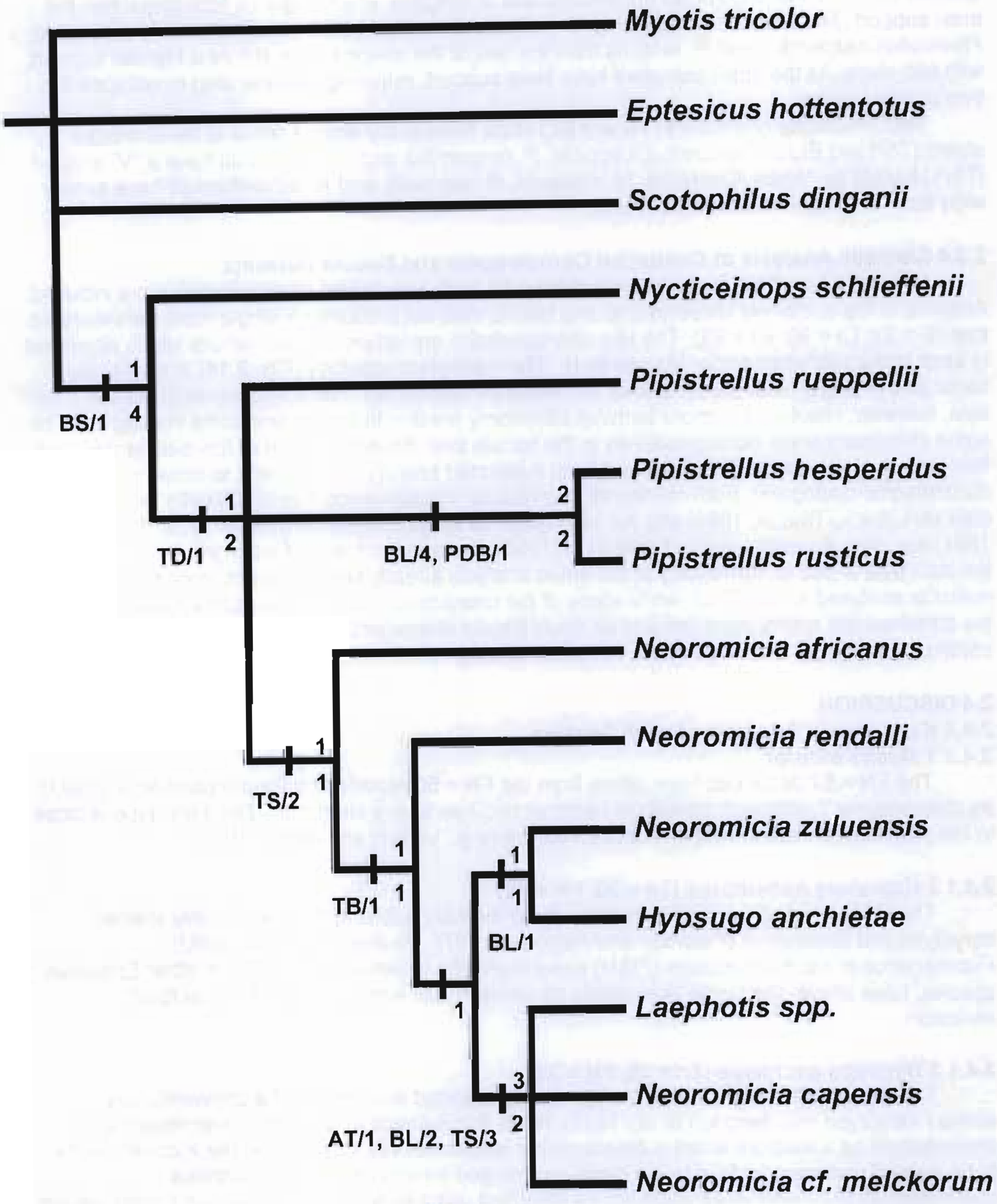


Figure 2.13 Most parsimonious tree generated by bacula characters for fourteen taxa, of eight genera of Vespertilioninae from southern Africa. Numbers above clade nodes are the number of unique and unreversed synapomorphies supporting each clade. Numbers below the clade nodes are branch support values (which is the number of extra steps required to collapse the particular node). Synapomorphic characters are shown below branches (abbreviations are explained in Appendices 2.3 and 2.4).

and a ventrally deflected tip (AT).

Branch support of different nodes varies from one to four steps. The branch uniting all species other than *M. tricolor*, *E. hottentotus* and *S. dinganii* which requires four steps, has the most support. The branches separating *N. schlieffenii* for the rest of the species, and separating *Pipistrellus hesperidus* and *P. rusticus* from the rest of the species have the next highest support, with two steps. All the other branches have least support, requiring just one step to collapse the tree at those points.

Both multistate characters (TS and BL) show homoplasy among some of the character states (TS/1and BL/3). *Pipistrellus rueppellii, P. hesperidus* and *P. rusticus* all have a "V" shaped (TS/1) bacula tip. While *N. rendalli*, *N. africanus*, *P. rueppellii*, and *N. schlieffenii* all have evenly wide and "V" shaped basal lobes (BL/3).

2.3.4 Cladistic Analysis of Combined Chromosome and Bacula Datasets

Only taxa for which there was information for both bacula and chromosomes were included. Analysis of the combined chromosome and bacula data set produced a single most parsimonious tree (S = 22; CI = 90; RI = 93). The tree characteristics are different to the results which appeared in error in the published paper (Appendix I). The cladogram topology (Fig. 2.14) is almost the same as the single most parsimonious chromosome cladogram. The combination of the two data sets, however, resolves the more terminal trichotomy present in the chromosome cladogram. The same characters show homoplasies as in the bacula tree. Branch support of the cladogram varies from one to seven steps. The most and least supported branches are similar to those in the chromosome cladogram. Both measures of character incongruence due to disparity between the data sets, the i_{MF} (Kluge, 1989) and the incongruence length difference (Mickevich and Farris, 1981) are zero. As explained by Farris *et al.*(1995), the apparent lack of incongruence between the data sets is due to homoplasy of the entire analysis already being present when the bacula matrix is analysed alone. Thus, while some of the characters in the bacula matrix dispute those in the chromosome matrix there are just as many bacula characters that agree with the chromosome matrix, which gives the net effect of zero.

2.4 DISCUSSION

2.4.1 Karyological Analysis of each Species

2.4.1.1 *Myotis tricolor*

The FN = 52 described here differs from the FN = 50 reported by Rautenbach *et al.* (1993), as chromosome 7, although considered acrocentric, has a very short arm. This karyotype is close to the proposed ancestral vespertilionid karyotype (e.g., Volleth and Heller, 1994).

2.4.1.2 *Eptesicus hottentotus* (2*n* = 50, FN = 48)

The GTG-banded karyotype confirms the previously published conventionally stained karyotype and description (Peterson and Nagorsen, 1975; Rautenbach *et al.*, 1993). Fluorescence *in situ* hybridization (FISH) experiments by Volleth *et al.* (2001) on other *Eptesicus* species, have shown the single acrocentric chromosome of arms 16 and 17 is due to an inversion.

2.4.1.3 *Hypsugo anchietae* (2*n* = 26, FN = 32)

The results differ slightly from the previously reported description of a conventionally stained karyotype (Rautenbach *et al.*, 1993). While Rautenbach *et al.* (1993) described the X-chromosome as a medium-sized submetacentric autosome, this study found the X chromosome to be a small metacentric. Due to the highly rearranged karyotype, the GTG-banded chromosomes of *H. anchietae* could not be identified using Bickham's (1979a) numbering system. For karyological reasons, a classification of *anchietae* is impossible.

2.4.1.4 *Pipistrellus rusticus* (2*n* = 42, FN = 50)

The results identified a different X chromosome to that described by Rautenbach *et al.* (1993). We found the X chromosome to be a medium-sized metacentric, while Rautenbach *et al.* (1993) described the X chromosome as a medium-sized submetacentric.

2.4.1.5 *Pipistrellus hesperidus* (2*n* = 42, FN = 50)

The GTG-banded karyotype is identical to the GTG-banded karyogram published by Volleth *et al.* (2001) for a specimen from Madagascar. The results are in agreement with the previously

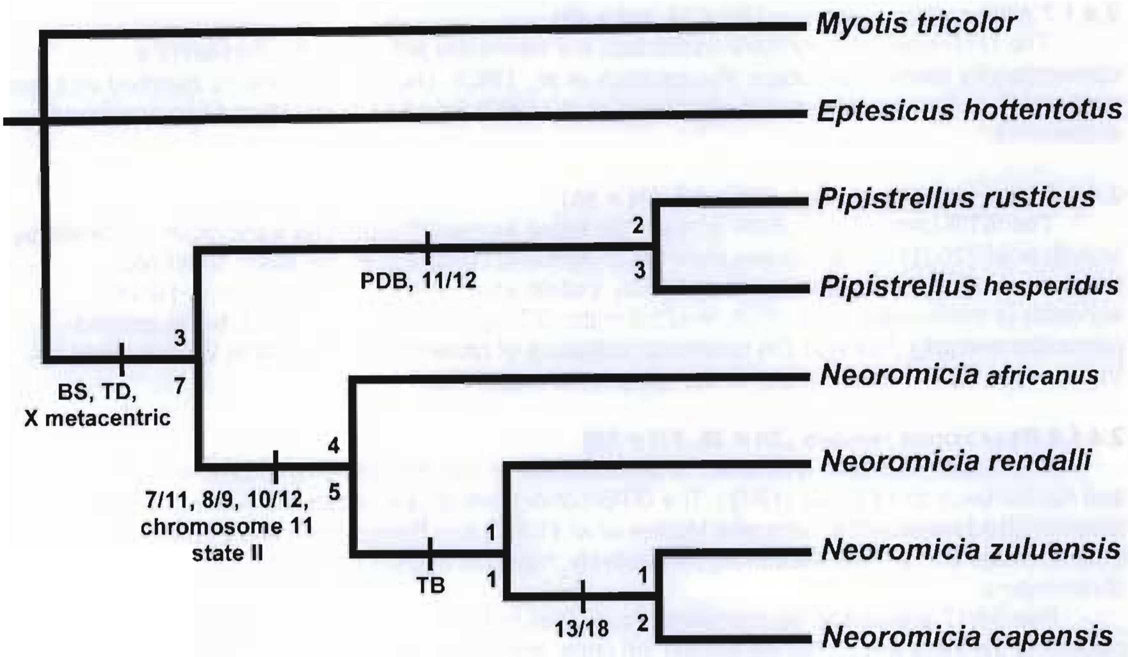


Figure 2.14 Most parsimonious tree generated by bacula and chromosome GTG-band characters for eight taxa, of four genera of Vespertilioninae from southern Africa. Numbers above clade nodes are the number of unique and unreversed synapomorphies supporting each clade. Numbers below the clade nodes are branch support values (which is the number of extra steps required to collapse the particular node). Synapomorphic characters are shown below branches (abbreviations are explained in Appendices 2.3 and 2.4

described conventionally stained karyotype (Rautenbach *et al.*, 1993).

2.4.1.6 *Neoromicia africanus* (2*n*=36, FN=50)

The GTG-banded karyotype confirms the previously published conventionally stained karyotype and description (Peterson and Nagorsen, 1975; Rautenbach *et al.*, 1993).

2.4.1.7 *Neoromicia zuluensis* (2*n* = 28, FN = 48)

The GTG-banded karyotype contradicts the previously published description of a conventionally stained karyotype (Rautenbach *et al.*, 1993). The results show 12 biarmed and one acrocentric autosome, whereas Rautenbach *et al.* (1993) found 11 biarmed and two acrocentric autosomes.

2.4.1.8 *Neoromicia capensis* (2*n* = 32, FN = 50)

The GTG-banded karyotype is much the same as the GTG-banded karyogram published by Volleth *et al.* (2001) for specimens from South Africa. GTG-bands in this study could not, however, verify a rearrangement identified by Volleth *et al.* (2001) on chromosome 1/2 in *N. capensis* (a centromere shift which resulted in the GTG-positive band of arm 2 being located pericentromerically. Nor was the polymorphic feature of chromosome pair 24 or 25 described by Volleth *et al.* (2001) found in any of the specimens examined.

2.4.1.9 *Neoromicia rendalli* (2*n* = 38, FN = 50)

The results identified a different X chromosome to that described by McBee *et al.* (1987) and Rautenbach and Fenton (1992). The GTG-banded karyotype shows the X chromosome is a medium-sized metacentric, whereas McBee *et al.* (1987) and Rautenbach and Fenton (1992), from a female and a male specimen, respectively, reported a large submetacentric as the X chromosome.

Pair 16/17 appears to be rearranged as it does not entirely match the ancestral banding pattern, since there are no bands around the centromere. Surprisingly, the short arms are consistently faintly stained, compared to the other darker stained chromosomal arms. Pale short arms can also be seen in the equivalent chromosomes in the conventionally stained karyotype by McBee *et al.* (1987). It also appears as if the short arm of the 16/17 pair in *N. rendalli* could be polymorphic. Of the male and female studied, the short arms in the male are two sizes, whereas both arms in the female are the same size. Besides the possibility that this indicates a polymorphism in the population concerning the size of the short arm, it could also indicate that chromosome pair 16/17 is forming a 'new' chromosome via pericentric inversion. In which case, the male might have both the 'old' and the 'new' version of the chromosome. However, in the absence of better metaphase GTG-band spreads and CBG-bands, this study can provide no definitive solution to this variation.

2.4.2 Karyological Analysis of all Species

Bickham (1979*b*) and Baker and Bickham (1980) described three types of vespertilionid chromosomal evolution, all three of which are represented by the species examined in this study. *Myotis tricolor* and *E. hottentotus* represent conservative taxa. *Myotis tricolor* like the rest of the *Myotis*-group has a karyotypically primitive karyotype, characterised by a high diploid number and many acrocentric chromosomes. *Eptesicus hottentotus* as a member of the *Eptesicus*-group has also retained a primitive karyotype which is thought to have evolved from the *Myotis*-like karyotype by centric fissions and a pericentric inversion, resulting in a karyotype with acrocentric autosomes only.

Pipistrellus rusticus, *P. hesperidus*, *N. africanus*, *N. zuluensis*, *N. rendalli* and *N. capensis* have all undergone karyotypic specialisation, or orthoselection, due to centric fusions, which have produced karyotypes with reduced diploid numbers. *Hypsugo anchietae* has undergone a radical reorganisation of the genome, called 'karyotypic megaevolution' by Baker and Bickham (1980), whereby the diploid chromosome number has been greatly reduced and the GTG-banding pattern totally altered.

Volleth and Heller (1994) found several chromosome fusion products have evolved more than once (in more than one genus or species). The 13/18 chromosome pair found in *N. zuluensis* has also been found in two unrelated lineages, in the Plecotini (*Barbastella*, *Plecotus)* and in *Rhogeesa alleni* (Volleth and Heller, 1994). The 10/12 chromosome fusion pair shared by *N. capensis, N. zuluensis, N. rendalli* and *N. africanus* has also been found in three Asian

Pipistrellus species (Volleth and Heller, 1994).

On the basis of chromosome GTG-bands, *P. hesperidus* and *P. rusticus* are identical. Their bacula are also very similar, to the extent that they cannot always be accurately assigned to either species. However, they are recognised as separate species on the basis of fur length, palatal area, skull length and forehead shape (Meester *et al.*, 1986).

These results support the suggestion by Volleth *et al.* (2001) to recognise specimens of *P. hesperidus* (identified then as *P. cf. kuhlii*) with a reduced chromosome diploid number ($2n = 42$), due to a fusion of chromosome 11 and 12, as a separate species from *P. kuhlii* ($2n = 44$) which occurs in North Africa and Europe.

GTG-banded chromosomes confirm that *N. capensis*, *N. rendalli* and *N. zuluensis* share very little with *E. hottentotus*, all have biarmed chromosome pairs 1/2, 3/4, 5/6 and 16/17, unlike *E. hottentotus. Neoromicia capensis*, *N. rendalli* and *N. zuluensis* have three Robertsonian fusions in common with *N. africanus* (7/11, 8/9, 10/12), and all show state II of chromosome 11. The latter feature makes them members of the tribe Vespertilionini rather than Pipistrellini (Volleth and Heller, 1994). Unfortunately, without R-banding results this study could not assess the state of chromosome 23, which is the other character used for identifying members of the tribes Vespertilionini and Pipistrellini. On bacular morphology, Hill and Harrison (1987) identified the subgenus *P.* (*Neoromicia)* was closely related to *P.* (*Hypsugo*), the subgenus in which they included *N. africanus*. GTG-banded chromosomes now indicate an even closer relationship of *africanus* to *Neoromicia* than Hill and Harrison (1987) suggested, since this study proposes to transfer *africanus* to the genus *Neoromicia.* On karyological reasons, the following species now are members of the genus *Neoromicia*: *N. africanus, N. capensis*, *N. rendalli* and *N. zuluensis*.

Based on bacular morphology and diploid chromosome number *N. somalicus* and *N.* cf. *melckorum* do not belong to the genus *Eptesicus* (Hill and Harrison, 1987; McBee *et al.*, 1987). Allozyme analysis (Morales *et al.*, 1991) has also shown that *N.* cf. *melckorum* is closely allied with *N. capensis* and does not form part of the *E. hottentotus* group. Unfortunately, not having GTG-banded karyograms for these species, it is not known whether they share the same Robertsonian fusion products as *N. capensis*, *N. zuluensis*, *N. rendalli* and *N. africanus*.

2.4.3 Bacular Analysis

As suggested by GTG-banded chromosomes, the bacular cladogram (Fig. 2.13) also indicates the separation of *E. hottentotus* from the *Neoromicia* species. Heller and Volleth (1984) and Hill and Harrison's (1987) suggestion that *E. hottentotus* is the only true *Eptesicus* of the southern African species assigned to the genus *Eptesicus*, has been validated by GTG-band chromosomes and cladistic analyses of chromosome and bacular characters.

Inclusion of several species in the bacular analysis that did not have GTG-banded karyotypes introduced some differences to the relationships suggested by GTG-band chromosome characters. In the bacular cladogram, *N. africanus* is not in the same group as the other species sharing three common Robertsonian fusion chromosomes, while *H. anchietae* and *Laephotis* spp. cluster with the other *Neoromicia* species, which includes *N.* cf. *melckorum* for which there are no GTG-banded karyotypes.

It is not surprising that bacular morphology does not support the genus *Neoromicia*, as identified by three common Robertsonian fusion chromosomes, since each of the four species (*N. africanus, N. rendalli, N. zuluensis* and *N. capensis*) have a different bacular morphology (Fig. 2.1). While all are elongated and stick-like, they have different bacular tip shapes, cover three different basal lobe morphologies, and both tip relative to the base categories (Appendix 2.4). Volleth and Heller (1994) found several instances when mapping overall bacular shape and size onto a chromosome cladogram of Vespertilionidae, where they had to assume independent reductions.

Bacular morphology indicates it is not just the generic relationship between *Eptesicus* and *Pipistrellus* species that requires revision, but also the generic boundary of *Laephotis*. Further analyses using alternative characters would be required to confirm this suggestion. However, *Laephotis* has previously been distinguished as a distinct genus on the basis of morphological characters (Meester *et al.*, 1986).

Many advocate the combination of all data in a single analysis, believing that all data potentially contributes to a phylogenetic analysis, and that a species phylogeny makes less sense considering data sets separately, even if one data set swamps another (Doyle, 1992; Honeycutt and Adkins, 1993; Shaffer, Clark and Kraus, 1997). However, there are instances when incongruence between data sets indicates different rates or modes of evolution, or even different underlying phylogenetic histories, and these would be important arguments against combining data sets (Graham *et al.*, 1998; Normark and Lanteri, 1998; Wiens, 1998). Incongruence can also result from sampling error, especially with small numbers of characters (Cannatella *et al.*, 1998; Graham *et al.*, 1998), characters not being independent of one another (Doyle, 1992), errors in polarity assessment (Baker *et al.*, 1989; Patterson, Williams and Humphries, 1993), and/or homoplasy (Baker *et al*, 1989; Shaffer *et al.*, 1991).

It is possible that several homoplasies have occurred in the evolution of certain bacula shapes and sizes in Vespertilioninae, as sexual selection might directly be acting on these features (Eberhard, 1996). If so, bacula characters used in an analysis without additional characters that accurately reflect phylogenetic history, would cause convergent taxa to cluster together. Possibly when combined with a larger data set from different sources, bacula morphology will provide useful characters.

The possibility also exists that bacula should be represented by just a single character, as the numerous characters derived in this study might not be independent (Doyle, 1992). Hill and Harrison's (1987) bacular arrangements have been criticised for the lack of discussion of character transformational polarity (Frost and Timm, 1992; Bogdanowicz *et al.*, 1998). In this study, besides using the outgroup to indicate polarity, for characters which have multiple states there is little basis on which to suggest a pattern of transformation, without becoming trapped in circular reasoning. The lack of understanding of bacular morphology transformation might mean this study used plesiomorphic characters, which have constrained the phylogenetic relationships. However, it appears bacular morphology is not entirely useful for resolving relationships between taxa at the generic level. Certainly, bacular morphology is useful for identifying species.

Interestingly, Frost and Timm (1992), in trying to recover the phylogenetic history of plecotine vespertilionid bats, also found disagreement between bacula morphology and other lines of evidence including karyology, osteology and dental evidence. They suggested certain bacula shapes could be plesiomorphic within vespertilionids, in which case, similarities would be phylogenetically uninformative. As a result, they dismissed bacula as a morphological system whose application seemed to be at a considerably lower level than the generic, subgeneric and group level at which Hill and Harrison (1987) applied it. These findings also support Frost's and Timm's (1992) criticism of Hill's and Harrison's (1987) analysis for being subjective, as bacula which appear from their illustrations to be similar are not always found in the same taxonomic groups. Clearly, a wider revision of the family Vespertilionidae incorporating more taxa, GTG-banded karyotypes and other techniques and characters will be required to test the relationships suggested above.

GTG-banded chromosomes support the close relationship of *N. rendalli*, *N. capensis* and *N. zuluensis*. Banding data further suggest transferring *africanus* to the genus *Neoromicia*. This study supports the generic rank of *Neoromicia* as defined by three Robertsonian fusion products (7/11, 8/9, 10/12). It still remains to be shown whether *Neoromicia* can be defined by additional characters. Possibly, on-going analyses of skull morphology by traditional and geometric morphometrics, might provide additional characters for the genus *Neoromicia*.

While gross bacular morphological differences (small, triangular or medium to large, and elongated) support the separation of *N. rendalli*, *N. capensis*, *N. zuluensis* and *N.* cf. *melckorum* from *Eptesicus*, the generic relationships of taxa with medium to large, elongated bacula are poorly resolved by bacular characters. Bacular morphological characters are useful for species identification, but appear less suitable for phylogeny estimation in the above genera.

APPENDIX 2.1

Specimens examined for chromosome analyses

Acronyms: DM – Durban Natural Science Museum, Durban; MM – McGregor Museum, Kimberley; TM – Transvaal Museum, Pretoria; ZM – South African Museum, Cape Town.

Eptesicus hottentotus: **SOUTH AFRICA**: WESTERN CAPE PROVINCE: Cederberg, Algeria (32° 22'S, 19°03'E): ZM41419, female. Cederberg, Kliphuis (32°08'S, 19°00'E): ZM41416, female, (Fig. 2.3).

Neoromicia capensis: **SOUTH AFRICA**: LIMPOPO PROVINCE: Messina (22°23'S, 30°02'E): DM5398, female. KWAZULU NATAL: Ithala Game Reserve (27°30'S, 31°12'E): DM5903, male, (Fig. 2.11). WESTERN CAPE PROVINCE: Vrolijkheid (33°54'S, 19°53'E): DM7194, male. Kersefontein (32°54'S, 18°20'E): DM7193, female.

Neoromicia rendalli: **SOUTH AFRICA**: KWAZULU-NATAL: Bonamanzi Game Reserve (28°06'S, 32°18'E): DM5877, male, (Fig. 2.12); DM5878, female.

Neoromicia zuluensis: **SOUTH AFRICA**: LIMPOPO PROVINCE: Messina (22°23'S, 30°02'E): DM5375, female, (Fig. 2.10).

Neoromicia africanus: **SOUTH AFRICA**: KWAZULU-NATAL: Ithala Game Reserve (27°32'S, 31° 22'E): DM5901, male. Durban, Yellowwood Park, Stainbank (29°54'S, 30°56'E): DM5870, male, (Fig. 2.9); DM5871, male.

Pipistrellus hesperidus: **SOUTH AFRICA**: KWAZULU-NATAL: Harold Johnson Nature Reserve (29°07'S, 31°15'E): DM5369, male. Eshowe, Dlinza Forest (28°54'S, 31°27'E): DM5406, female. Durban, Cowies Hill, (29°50'S, 30°53'E): DM7201, male. Durban, Yellowwood Park, Stainbank, (29°54'S, 30°56'E): DM5868, male, (Fig. 2.8).

Pipistrellus rusticus: **SOUTH AFRICA**: LIMPOPO PROVINCE: Messina, Messina Nature Reserve (22°23'S, 30°02'E): DM5379, male, (Fig. 2.6); DM5389, male; DM5391, male; DM5867, female.

Hypsugo anchietae: **SOUTH AFRICA**: KWAZULU-NATAL: 17.5 km SWW of Richmond, Hella-Hella, Game Valley Estate (29°54'S, 30°05'E): DM5362, female, (Fig. 2.5). 1.5 km NWW of Umkomaas, Empisini Nature Reserve (30°12'S, 30°48'E): DM5377, female.

Myotis tricolor: **SOUTH AFRICA**: KWAZULU-NATAL: Ithala Game Reserve (27°30'S, 31°12'E): DM5897, female, (Fig. 2.2).

APPENDIX 2.2

Specimens examined for bacula analyses

Acronyms: DM – Durban Natural Science Museum, Durban; MM – McGregor Museum, Kimberley; TM – Transvaal Museum, Pretoria; ZM – South African Museum, Cape Town.

Eptesicus hottentotus: **SOUTH AFRICA:** KWAZULU-NATAL: 10 km NW Louwsburg, Itala Game Reserve, Doornkraal Farm (27°31'S, 31°12'E): TM31756. WESTERN CAPE PROVINCE: Clanwilliam, Algeria Forest Station (32°22'S, 19°15'E): TM38412, ZM41418.

Neoromicia zuluensis: **SOUTH AFRICA:** MPUMALANGA: Kruger National Park (KNP), 1.5 km NW of Skukuza, dense woodland of western reservoir (24°59'S, 31°35'E): TM39761. KNP, 2 km E confluence Letaba and Olifants Rivers (23°59'S, 31°50'E): TM39697.

Neoromicia capensis: **SOUTH AFRICA:** KWAZULU-NATAL: 10 km NW Louwsburg, Ithala Game Reserve (27°30'S, 31°12'E): DM5894, DM5899, DM5902. 15 km E of Mkuze village, Mkuzi Game Reserve. (27°38'S, 32°16'E): DM5380, DM5400. Drakensberg, Loteni Nature Reserve (29°27'S, 29°32'E): DM1912, DM1947. Drakensberg, Royal Natal National Park (28°41'S, 28°56'E): DM2389. Natal Midlands, Nottingham Road, Clifton School (29°21'S, 30°00'E): DM5873. Natal Midlands, Merrivale (29°30'S, 30°15'E): DM5387. Durban, Forest hills, Epping Crescent (29°45'S, 30°49'E): DM7017. Durban, Westriding, 22 Ashley Road (29°47'S, 30°46'E): DM7018. Durban, Westriding, 14 Marion Rd (29°47'S, 30°46'E): DM5881. 17.5 km SWW of Richmond, Hella-Hella, Game Valley Estate (29°54'S, 30°05'E): DM6894. NORTH WEST PROVINCE: Ganyesa (26° 32'S, 24°07'E): MM7061. NORTHERN CAPE: 58 km S of Kuruman, Wonderwerk Cave (27°49'S, 23°35'E): MM7064, MM7066, MM7067. WESTERN CAPE: 16 km N of Hopefield, Kersefontein Farm (32°54'S, 18°20'E): DM7196. Cederberg, Algeria (32°22'S, 19°03'E): ZM41452. Cederberg, Kliphuis (32°08'S, 19°00'E): ZM41457. 15 km SW Robertson, Vrolijkheid Nature Reserve (33° 54'S, 19°53'E): DM7194, DM7197.

Neoromicia rendalli: **SOUTH AFRICA**: KWAZULU-NATAL: 5 km S of Hluhluwe Village, Bonamanzi Game Reserve (28°06'S, 32°18'E): DM5370, DM5361, DM5877.

Neoromicia africanus: **ZIMBABWE**: Eastern Highlands, 15 km SE Juliesdale, Chingamwe Estates (18°27'S, 32°45'E): DM 5366. Rusito Forest, along Rusito River (20°02'S, 32°59'E): TM34782. **SWAZILAND**: 10 km N Simunye (26°07'S, 31°57'E): DM5879, DM5880. **SOUTH AFRICA**: KWAZULU-NATAL: Itala Game Reserve (27°32'S, 31°22'E): DM5900, DM5901. Jozini Dam Wall, (27°25'S, 32°04'E): DM5367. Durban, Yellowwood Park, Stainbank (29°54'S, 30°56'E): DM5869, DM5870, DM5871. Renishaw, Old Community Health Hall (30°17'S, 30°44'E): DM5365, DM5402, DM5404.

Neoromicia cf. *melckorum:* **SOUTH AFRICA**: LIMPOPO PROVINCE: KNP, Pafuri, Old picnic site (22°25'S, 31°18'E): TM39506.

Hypsugo anchietae: **SOUTH AFRICA**: KWAZULU-NATAL: St. Lucia, Sobhengu Lodge (27°59'S, 32°24'E): DM6885. St. Lucia, False Bay Park (27°48'S, 32°23'E): DM2269. 8.5 km S of Mandini, Harold Johnson Nature Reserve (29°07'S, 31°15'E): DM5353. 1.5 km NWW Umkomaas, Empisini Nature Reserve (30°12'S, 30°48'E): DM5358.

Pipistrellus hesperidus: **ZIMBABWE**: Eastern Highlands, 15 km SE Juliesdale, Chingamwe Estates (18°27'S, 32°45'E): DM4692. Rhodes Inyanga National Park (18°17'S, 32°46'E): TM34757. **SOUTH AFRICA**: KWAZULU-NATAL: 8.5 km S of Mandini, Harold Johnson Nature Reserve (29°07'S, 31°15'E): DM 5369. Eshowe, servitude into Dlinza Forest (28°54'S, 31°27'E): DM 5360, 5374, 5397, 5356. Mtunzini, Twin Streams Farm (28°57'S, 31°30'E): DM5872. Mount Edgecombe, Sugar Research Association Estate (29°42'S, 31°04'E): DM7143. Kloof, Kranskloof Nature Reserve, Kloof Falls Road/ Bridle Road picnic site (29°46'S, 30°49'E): DM5876, DM6219. Hillcrest, 26 Hathaway (29°47'S, 30°46'E): DM7016. Pinetown, Cowies Hill (29°50'S, 30°53'E): DM7201. Durban, Hillary School (29°53'S, 30°56'E): DM6150. Durban, Rossburgh, 183 Sarnia Road (29°54'S, 30°58'E): DM5378. Durban, Yellowwood Park (29°54'S, 30°56'E): DM5868. Durban, North Park Nature Reserve (29°52'S, 30°52'E): DM5403. Durban, Pigeon Valley Park

APPENDIX 2.2 continued

(29°52'S, 30°59'E): DM5384, DM5385.

Pipistrellus rusticus: **SOUTH AFRICA**: LIMPOPO PROVINCE: 30 km NE of Vaalwater, Farm Klipfontein (24°08'S, 28°18'E): TM39887, TM39885. Messina, Messina Nature Reserve (22°23'S, 30°02'E): DM5379, DM5318, DM5390, DM5389, DM5391.

Pipistrellus rueppellii: **SOUTH AFRICA**: LIMPOPO PROVINCE: KNP, Pafuri, Anthrax Camp (22° 25'S, 31°15'E): TM36609, TM37908.

Myotis tricolor: **SOUTH AFRICA**: GAUTENG: Krugersdorp District, Farm Uitkomst, American Cave(25°55'S, 27°45'E): TM19210. Krugersdorp, Uitkyk (26°05'S, 27°46'E): TM9058.

Laephotis botswanae: **SOUTH AFRICA**: KWAZULU-NATAL: 17.5 km SWW of Richmond, Hella-Hella, Game Valley Estate (29°54'S, 30°05'E): DM5351, DM6899. WESTERN CAPE: Cederberg, Algeria (32°22'S, 19°03'E): ZM41415, ZM41417. LIMPOPO PROVINCE: KNP, Punda Maria, Mahogany Drive, Manditobe Dam (22°41'S, 31°02'E): TM38123, TM38155. 30 km NE Vaalwater, Farm Klipfontein (24°08'S, 28°18'E): TM39946.

Laephotis namibensis: **NAMIBIA**: 3 km W Aus, Klein Aus 8 (26°39'S, 16°13'E): TM37547.

Nycticeinops schlieffenii: **SOUTH AFRICA**: KWAZULU-NATAL: 15 km E of Mkuze Village, Mkuzi Game Reserve (27°38'S, 32°16'E): DM5401.

Scotophilus dinganii: **SOUTH AFRICA**: KWAZULU-NATAL: Kloof, Kranskloof Nature Reserve, Kloof Falls Road/ Bridle Road picnic site (29°46'S, 30°49'E): DM5874, DM5875.

APPENDIX 2.3

Chromosome characters

1) **Chromosome fusion 7/11** - absent (0), present (1).
2) **Chromosome fusion 8/9** - absent (0), present (1).
3) **Chromosome fusion 10/12** - absent (0), present (1).
4) **Chromosome fusion 11/12** - absent (0), present (1).
5) **Chromosome fusion 13/18** - absent (0), present (1).
6) **State of chromosome 11**: (0) GTG- negative band close to the centromere (state I), (1) or found more terminally (state II)
7) **State of X chromosome**: (0) submetacentric, (1) metacentric, (2) subtelocentric.

Matrix of chromosome characters used for Vespertilioninae species from southern Africa. MTR. *Myotis tricolor*, EHO. *Eptesicus hottentotus*, NCA. *Neoromicia capensis*, NZU. *Neoromicia zuluensis*, NRE. *Neoromicia rendalli*, NAF. *Neoromicia africanus*, PRU. *Pipistrellus rusticus*, PHE. *Pipistrellus hesperidus*.

Character	MTR	EHO	NCA	NZU	NRE	NAF	PRU	PHE
7/11	0	0	1	1	1	1	0	0
8/9	0	0	1	1	1	1	0	0
10/12	0	0	1	1	1	1	0	0
11/12	0	0	0	0	0	0	1	1
13/18	0	0	1	1	0	0	0	0
State 11	0	0	1	1	1	1	0	0
State X	0	0	1	2	1	1	1	1

APPENDIX 2.4

Bacula characters

1) **Bacula shape (BS)**: (0) small, triangular, (1) medium to large, elongate, "stick-like".
2) **Tip not distinct from shaft (TD)**: (0) yes, (1) no.
3) **Tip shape (TS)**: (0) rounded, (1) "V" shaped, (2) flat and broad, (3) triangular.
4) **Tip relative to the base (TB)**: (0) tip narrower, (1) base narrower.
5) **Percent of bacula length deflected (PBD)**: (0) 35% and less, (1) more than 50%.
6) **Angle of tip relative to shaft (AT)**: (0) same plane, (1) ventrally deflected.
7) **Basal lobe shape (BL)**: (0) "V" shaped, small and rounded, (1) "V" shaped, short, broad, with wider ends, (2) semi-circular, skirt-like, with a "W" shaped edge, (3) "V" shaped, longer, evenly wide, (4) triangular.

Matrix of bacular characters used for Vespertilioninae species from southern Africa. MTR. *Myotis tricolor*, EHO. *Eptesicus hottentotus*, NCA. *Neoromicia capensis*, NZU. *Neoromicia zuluensis*, NRE. *Neoromicia rendalli*, NAF. *Neoromicia africanus*, NcM. *Neoromicia* cf. *melckorum*, PRU. *Pipistrellus rusticus*, PHE. *Pipistrellus hesperidus*, PRP. *Pipistrellus rueppellii*, HAN. *Hypsugo anchietae*, NYS. *Nycticeinops schlieffenii*, LAE. *Laephotis wintoni*, SDI. *Scotophilus dinganii.*

Charac	MTR	EHO	NCA	NZU	NRE	NAF	NcM	PRU	PHE	PRP	HAN	NYS	LAE	SDI
BS	0	0	1	1	1	1	1	1	1	1	1	1	1	0
TD	0	0	1	1	1	1	1	1	1	1	1	0	1	0
TS	0	0	3	2	2	2	3	1	1	1	2	0	3	0
TB	0	0	1	1	1	0	1	0	0	0	1	0	1	0
PDB	0	0	0	0	0	0	0	1	1	0	0	0	0	0
AT	0	0	1	0	0	0	1	0	0	0	0	0	1	0
BL	0	0	2	1	3	3	2	4	4	3	1	3	2	0

CHAPTER 3

GEOMETRIC MORPHOMETRIC ANALYSIS OF CRANIAL SIZE AND SHAPE VARIATION

3.1 INTRODUCTION

Additional characters and techniques are required to test the relationships suggested by GTG-banded chromosomes (Volleth *et al.*, 2001; Kearney *et al.*, 2002 - see Appendix I), and mtDNA (Hoofer and Van Den Bussche, 2003). Since current taxon identification keys utilise many cranial characters (Meester *et al.*, 1986; Taylor, 2000), a study of dorsal and ventral cranial shape was undertaken applying the technique of geometric morphometrics. Geometric morphometrics methods are more effective at taking into account spatial relationships obtained from the relative positions of landmarks (i.e. the geometry of an object is retained) than traditional morphometric methods, and thin plate splines provide useful graphical representations of shape change (Dryden and Mardia, 1998). Although geometric morphometric analyses are based on Kendall shape space which has a non-Euclidian geometry, spaces tangent to Kendall shape space can be treated with Euclidian geometry (standard multivariate methods), and thus provide a useful tool for the analysis of shape and centroid size (Rohlf, 1999).

The aim of this part of the study was thus to try and capture and describe any variation in dorsal and ventral skull shape and size occurring within species between different sexes, tooth wear classes and OTUs and between 16 species of vespertilionid bats occurring in southern Africa. A further aim was to identify whether any morphological relationships suggested by skull shape and size contain phylogenetic signal and are congruent with the generic relationships suggested by GTG-chromosome banding characters (Volleth *et al.*, 2001; Kearney *et al.*, 2002), or the molecular phylogenetic study of Vespertilionidae (Hoofer and Van Den Bussche, 2003). In addition, since a particular morphology embodies not only an organism's developmental and evolutionary history but also the requirements of present life (Swartz *et al.*, 2003), this study alternatively questions whether skull shape and size represent convergent ecological adaptations. As was suggested by a molecular analysis of thirty-three taxa of *Myotis* Kaup, 1829 by Ruedi and Mayer (2001) which showed that morphological characters (including cranial characters), that had been used in the classification of species, did not correspond to true phylogenetic groupings and instead represented independent convergent adaptive radiations to similar ecomorphs.

Various other authors have suggested that cranial morphology in bats shows little phyletic signal, but rather reflects interrelated associations of diet, echolocation, and habitat (Jacobs, 1996; Freeman 1998; Pedersen 1998; Sanchez-Villagra and Williams, 1998; Stadelmann *et al.*, 2004). Hence skull shape was also assessed using a basic and widely applied approach in ecomorphological analyses, correlating form with ecological attributes and seeking to describe patterns of interrelationship between them (Swartz *et al.*, 2003). In this study, skull shape was correlated with ecogeographical and bioclimatic factors of latitude, longitude, ecoregion and biome information (Olson *et al.*, 2001), as well as information about dominant frequency of the echolocation call (Taylor, 2000). Such analyses seek to understand the interconnections between morphological design and function that are central to biology. Yet, the results should be viewed with caution as the causative or adaptive advantages of patterns of morphological variation are challenging and often difficult to appraise (Kennedy *et al.*, 2002; Swartz *et al.*, 2003), since the relationship between an animals structure and its interactions with it environment are often complicated and multifactorial (Swartz *et al.*, 2003). In addition the results of this analysis could be used as a hypothesis for further experimental testing.

The biome and ecoregion information of Olsen *et al.* (2001) and Olsen and Dinerstein (2002), available in a useful electronic format at the website http://www.worldwildlife.org/wildlife, was used. The terrestrial ecoregions of the world map devised by Olson *et al.* (2001) primarily as a tool for conservation action, provides information at both the biome and ecoregion scales, and is built on existing biogeographical knowledge (for the African region, they cite White, 1983) and hence is very similar to the more commonly used information for the southern African subregion (Cowling, Richardson and Pierce, 1997; Low and Rebelo, 1996; Rutherford and Westerfall, 1994). Olsen *et al.* (2001) define ecoregions as separate biota nested within biomes that contain a distinct assemblage of natural communities and species and hence reflect the distribution of a broad range of flora and fauna, whereas biomes are generally recognised as a broad ecological unit representing a major life zone extending over a large natural area (Olsen *et al.*, 2001; Rutherford and Westfall, 1994). The biome and ecoregion information of Olsen *et al.* (2001) and

Olsen and Dinerstein (2002) extends into the rest of Africa, which the other studies with the exception of White (1983) do not, and hence was useful for specimens incorporated into the study from beyond the southern African region. The current information about the diet and feeding strategies of the species in question is poorly known, although what information does exist for nine of the sixteen species in question suggests considerable similarity in their diet and feeding behaviour (Taylor, 2000).

The focal interest of this study was the inter- and intra-generic relationships and identification of ten species of insectivorous bats occurring in southern Africa from the subfamily Vespertilioninae and the genera *Eptesicus* Rafinesque, 1820, *Neoromicia* Roberts, 1926, *Hypsugo* and *Pipistrellus* Kaup, 1829: *Eptesicus hottentotus* (A. Smith, 1833), *Hypsugo anchietae* (Seabra, 1900), *Neoromicia capensis* (A. Smith, 1829), *Neoromicia* cf. *melckorum* (*sensu* Rautenbach *et al.*, 1993), *Neoromicia africanus* (Rüppell, 1842), *Neoromicia rendalli* (Thomas, 1889), *Neoromicia zuluensis* (Roberts, 1924), *Neoromicia rueppellii* (Fischer, 1829), *Pipistrellus hesperidus* (Temminck, 1840) and *Pipistrellus rusticus* (Tomes,1861). However, a few additional specimens from further afield in Africa, as well as from six additional species were also included in the analyses to provide a context for the genera *Eptesicus*, *Neoromicia*, *Hypsugo,* and *Pipistrellus* which represent the tribes Nycticeiini, Vespertilionini, and Pipistrellini as suggested by the molecular analysis of Hoofer and Van Den Bussche (2003). The additional species represent the following recently suggested changes and relationships within the family Vespertilionidae and subfamily Vespertilioninae (Hoofer and Van Den Bussche, 2003): *Miniopterus schreibersii* (Kuhl, 1819) is from the newly recognised family Miniopteridae, *Myotis tricolor* (Temminck, 1832) is from the newly recognised subfamily Myotinae, *Scotophilus dinganii* (A. Smith, 1833) is from the tribe Scotophilini within the subfamily Vespertilioninae, and *Laephotis botswanae* Setzer, 1971, *L. namibensis* Setzer, 1971 and *Nycticeinops schlieffenii* (Peters, 1859) are in the same tribe Vespertilionini as are the species of *Neoromicia*.

3.2 MATERIAL AND METHODS

Appendix 3.1 gives details of the specimens of *E. hottentotus*, *H. anchietae*, *N. capensis*, *N.* cf. *melckorum*, *N. africanus*, *N. rendalli*, *N. zuluensis*, *N. rueppellii*, *P. hesperidus*, *P. rusticus*, *L. botswanae*, *L. namibensis*, *M. tricolor*, *N. schlieffenii*, *S. dinganii*, and *M. schreibersii* analysed in this study. Table 3.1 gives the numbers of specimens analysed, as well as a breakdown in relation to different sexes and tooth wear classes. Specimens were assigned to one of four tooth wear classes following Rautenbach (1986). Images of dorsal and ventral views of the skulls were digitised using a microscope mounted CCV camera, and a frame grabbing Miro Video PCTV card (Pinnacle Systems). Two-dimensional coordinates were collected using TpsDig (Rohlf, 1998) from nine landmarks on the left side of the dorsal surface of the skull and thirteen landmarks on the right side of the ventral surface of the skull (Fig. 3.1) (see Appendix 3.2 for a written description of the landmark positions). Dorsal and ventral coordinates were analysed separately, initially to ascertain size and shape variation within species and thereafter between species.

Centroid size, the square root of the sum of squared distances between each landmark and the centroid (Bookstein, 1991), calculated using GRF-ND (Slice, 1993) or TpsRelw (Rohlf, 2003) was used as a measure of geometric size. One-way analysis of variance (ANOVA) tests (unbalanced design - Type III) (Zar, 1996) were run to identify if dorsal and ventral skull centroid size varied significantly between different sexes, and tooth wear classes within a single locality of *N. capensis* with sufficient specimens (Jagersfontein in the Free State). One-way ANOVA tests (unbalanced design - Type III) were also run to identify if centroid size varied significantly between different localities, sexes, and tooth wear classes within the six species that had sufficient specimens for the test. One-way ANOVA tests were used rather than multi-way ANOVAs as the homogeneity of variances were significant in multi-way ANOVAs (Zar, 1996), i.e. the error variance of the dependant variable was not equal across the groups. Post-hoc Tukey tests (Zar, 1996) were used to identify any significantly different subsets. Correlation tests were run between centroid size and latitude, longitude, biome and ecoregion for species that showed significant variation in centroid size between localities. Dorsal and ventral centroid size variation between species was displayed using box plots.

In order to generate Procrustes tangent coordinates from shape space, TpsRelw (Rohlf, 2003a) was used to compute Procrustes superimposition and partial warp scores (including the uniform component). In TpsRelw, the "reference" configuration was computed using the generalised orthogonal least-squares Procrustes analysis procedures (Rohlf & Slice, 1990). Specimens were aligned to this average shape scaled to unit centroid size and projected onto the

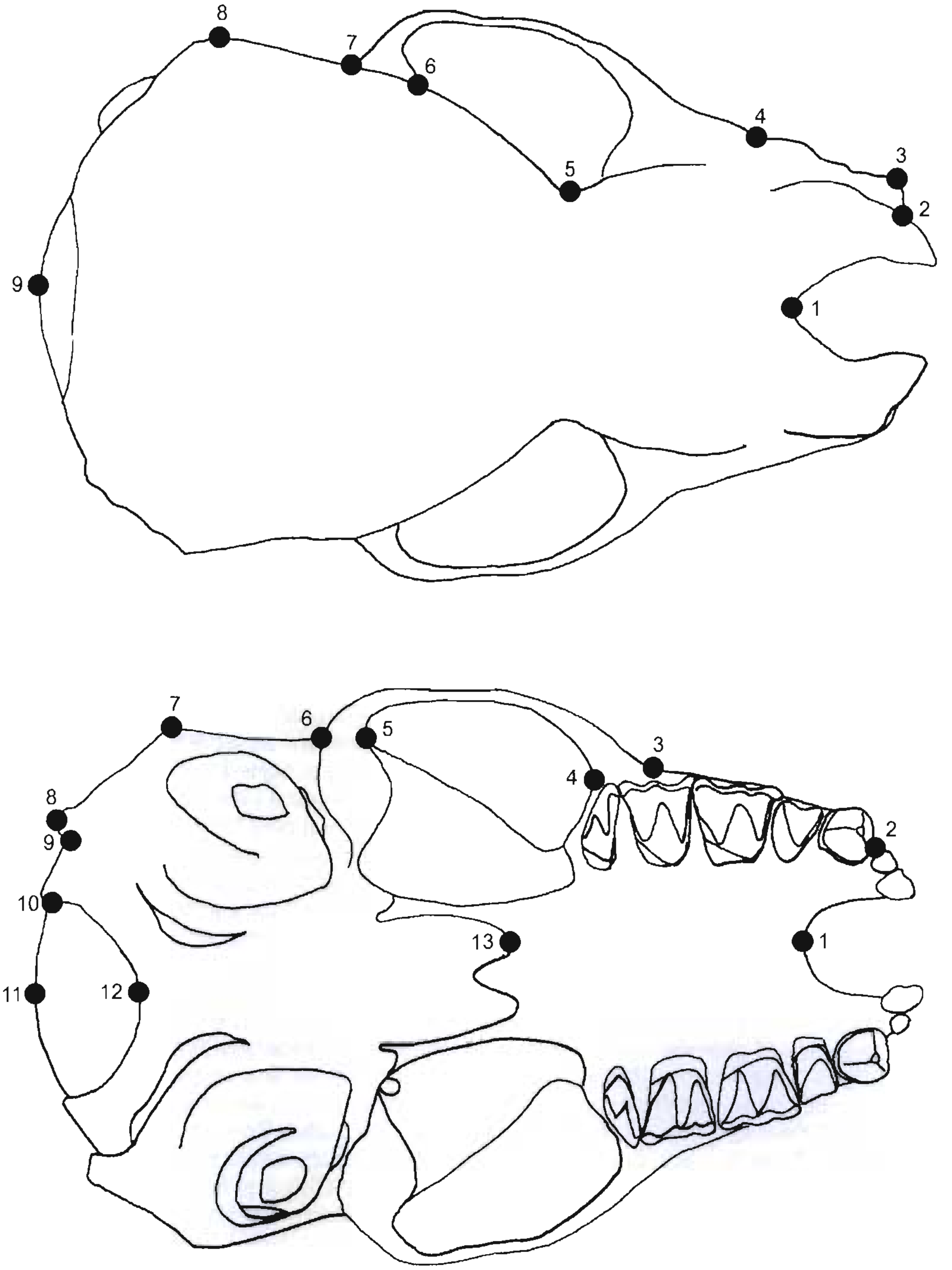


Figure 3.1 Dorsal and ventral views of a vesper skull showing positions of the landmarks (numbered points described in the text).

Table 3.1 The number of specimens of each sex of each Vespertilionid species from southern Africa used in the analyses of dorsal and ventral skull shape. Only the first six species were used for intra-specific analyses.

Species	Dorsal skull			Ventral skull		
	Females	**Males**	**Total**	**Females**	**Males**	**Total**
Eptesicus hottentotus	25	13	38	17	12	29
Neoromicia capensis	102	89	191	90	68	158
Neoromicia nanus	26	26	52	19	20	39
Neoromicia zuluensis	30	10	40	20	8	28
Pipistrellus hesperidus	7	20	27	10	22	32
Pipistrellus rusticus	24	14	38	20	12	32
Neoromicia rendalli	2	4	6	4	1	5
Neoromicia rueppellii	2	3	5	1	2	3
Neoromicia* cf. *melckorum	5	1	6	5	-	5
Hypsugo anchietae	5	4	9	4	1	5
Laephotis botswanae	2	8	10	2	6	8
Laephotis namibensis	-	4	4	-	4	4
Myotis schreibersii	2	1	3	2	1	3
Myotis tricolor	3	1	4	3	-	3
Nycticeinops schlieffenii	-	2	2	-	2	2
Scotophilus dinganii	-	2	2	-	2	2
Total	235	202	437	197	161	358

space orthogonal to the consensus configuration to construct Kendall tangent space coordinates (Rohlf, 1999). Since the geometry of Kendall's shape space is non-linear, specimens were projected from non-linear shape space into a linear tangent space to allow shape variation and co-variation to be studied using linear multivariate statistical techniques (Rohlf, 1996). Partial warps (rotations of Procrustes coordinates) were used as the space tangent to Kendall's shape space, in which the thin plate spline is used to represent shape differences as a smooth deformation of a reference shape into another shape (Rohlf, 1999). The average shape serves as the "reference" configuration in the computation of thin-plate splines (deformation of average shape/ bending energy matrices) (Bookstein, 1989 and 1991). Splines were decomposed into principal warps, and superimposed specimens projected onto these principle warps describe their deviations from the consensus configuration which produces a weight matrix of geometrically orthogonal shape variables called partial warp scores (W) (Rohlf, 1996). Shape variation may be partitioned into a uniform component (infinite scale or uniform stretching or compression of an object in a particular direction; Bookstein, 1996; Rohlf and Bookstein, 2003), and a non-uniform component (localised deformations; Bookstein, 1991). In this study the uniform components (U1 and U2) estimated using the complement approach (Rohlf and Bookstein, 2003) were analysed together with the non-uniform partial warp scores (W) as a W' matrix. Tests of dorsal and ventral inter-specific relative warp analyses without the uniform component showed the distinction between the species was poorer than when the uniform component was included even though the percentage contributions of the first four relative warps were higher. A correlation of 1.0 obtained between Euclidian and Procrustes distances for both dorsal and ventral data, respectively, using TpsSmall (Rohlf, 2003b), indicated tangent space could be used as an approximation of shape space, since the linear tangent space closely approximates shape space.

Relative warp analyses (i.e. principal component analyses of covariance matrices of partial warp scores; Rohlf, 1996) were performed to assess changes in shape within a single locality with sufficient specimens (*N. capensis* from Jagersfontein, Free State), within six species with sufficient specimens, and between the 16 vesper bat species. Analyses were run on individual specimens, as well as the means for each species, and within some species (see Appendix 3.1) the means of different localities or pooled localities (calculated from partial warp scores of the individual specimens). Localities were pooled into Operational Taxonomic Units (OTUs; Sneath and Sokal, 1973) based on closest geographic proximity when they were represented by fewer than three specimens. Minimum-length spanning trees (MST) computed from distance matrices (Sneath and Sokal, 1973) were superimposed on relative warp plots of species means to help clarify nearest-neighbour relationships among species. Thin plate spline deformations calculated in TpsRelw (Rohlf, 2003a) following Rohlf *et al.* (1996) were used to identify shape changes along the important principal component axes. Canonical variate analyses (Rohlf, 1997) were not used to assess variation in skull shape within and between different species, since the critical assumption of multivariate homogeneity of within group covariance matrices, which underlies the construction of canonical axes, was not met in each of six species tested (i.e. those having more specimens than landmark numbers, *E. hottentotus, N. capensis, N. zuluensis, N. africanus, P. hesperidus*, and *P. rusticus*). Cluster analyses (Sneath and Sokal, 1973), using the unweighted pair group method with averages (UPGMA), were computed from distance matrices of partial warp scores. Following Adams and Funk (1997) and Cardini (2003), multivariate multiple regression analyses between shape and centroid size within and between species, as well as tests for common slopes were computed using TpsReg (Rohlf, 2003c). Since other variables of interest were non-normally distributed, non-parametric Spearman rank correlation analyses were used rather than regression analyses. In contrast to analyses that have used TpsPLS (Rohlf, 2002) software to explore possible relationships between shape variation and other variables (Adams and Rohlf, 2000; Fadda and Corti, 1998; Rohlf and Corti, 2000), the method of correlating morphological variation using principal component scores either from traditional morphometric (Kennedy *et al.*, 2002; Smith *et al.*, 2002) or shape variables, i.e. relative warps (O'Higgins and Jones, 1998; Milne & O'Higgens, 2002; Singleton, 2002; Viguier, 2002) with variables of interest was followed. In analyses within species correlation tests were run between principal component scores (PCS) and different OTUs, centroid size (allometric effects), sexes, tooth wear classes, latitude, longitude, biome and ecoregion. In analyses between species correlation tests were run between principal component scores and different species, centroid size (allometric effects), latitude, longitude, biome, ecoregion and dominant frequency of the echolocation call. Scatter plots were produced of significantly correlated PCS and variables, to which were added from TpsRelw the thin plate splines appropriate to the PCS. Regression analyses were used to explore allometric scaling (Huxley, 1932) in significant correlations between skull shape and centroid size.

Of the 16 species, only six species (*E. hottentotus, N. capensis, N. zuluensis, N. africanus, P. hesperidus*, and *P. rusticus*) were represented by a sufficient number of specimens of different sexes, tooth wear classes and from a variety of different geographic localities (mostly in southern Africa) to allow intra-specific analyses. Biome and ecoregion information following Olsen and Dinerstein (2002) was downloaded from the WWF Global 200 Ecoregions website at http://www.worldwildlife.org/wildlife. There are a few differences between the vegetation groupings for South Africa in the data of Olsen and Dinerstein (2002) and that of Low and Rebelo (1996). The results of a test on *P. hesperidus* (the only species with specimens restricted to South Africa) correlating the first four PCs of dorsal and ventral skull shape with the biome data of Olsen and Dinerstein (2002) and that of Low and Rebelo (1996) gave very similar results. Table 3.2 gives a breakdown of the different biomes and the number of different ecoregions represented by the localities of each species included in this study. Information about dominant call frequency was available for 11 of the 16 species (*M. tricolor, M. schreibersii, S. dinganii, L. botswanae, N. schlieffenii, E. hottentotus, N. capensis, N. rueppellii, N. africanus, P. hesperidus, P. rusticus*) in Taylor (2000), but not for *L. namibensis, N.* cf. *melckorum, N. rendalli, N. zuluensis*, and *N. anchietae*.

The TPS suite of statistical programs were available as shareware at the Morphometrics website at http://life.bio.sunysb.edu/morph/.The statistical package SPSS 9.0.1 (SPSS Inc., 1999) was used to test for normality (Kolmogorov-Smirnov; see Zar, 1996), homogeneity of variance (Levene's test; see SPSS 9.0.1, 1999), analysis of variance, correlation and regression, and the computation of box plots, scatter plots and relative warp plots. The statistical package NTSYS-pc, version 2.01h (Rohlf, 1997) was used for the calculation of UPGMA clustering.

3.3 RESULTS

3.3.1 Intra-specific centroid size

Centroid size was normally distributed within the six species with sufficiently large sample sizes (*E. hottentotus, N. capensis, N. zuluensis, N. africanus, P. hesperidus*, and *P. rusticus*), and within *N. capensis* from Jagersfontein in the Free State. However, since latitude, longitude, ecoregion and biome data were not normally distributed, the non-parametric Spearman rank correlation test (Zar, 1996) was used.

One-way ANOVA tests found no significant difference in dorsal or ventral skull centroid size due to sex or tooth wear class within the single locality of *N. capensis* from Jagersfontein (see Tables 3.3 and 3.4 for results), hence these were combined within a species for subsequent analyses. However, one-way ANOVA tests identified the following significant differences in dorsal and ventral skull centroid size within the six different species (see Tables 3.3 and 3.4 for full results): between different OTUs of both the dorsal and ventral skull in *N. capensis* ($P < 0.001$), *E. hottentotus* ($P < 0.001$), and *P. hesperidus* (dorsal $P < 0.05$, ventral $P < 0.01$), between different OTUs of the dorsal skull only in *N. africanus* ($P < 0.05$); between sexes of both dorsal and ventral skull in *N. capensis* ($P < 0.001$) and *P. hesperidus* (dorsal $P < 0.05$, ventral $P < 0.01$), between sexes of the ventral skull only in *N. zuluensis* ($P < 0.05$), between sexes of the dorsal skull only in *N. africanus* ($P < 0.01$); and between different tooth wear classes in both dorsal and ventral skull in *E. hottentotus* (dorsal $P < 0.001$, ventral $P < 0.01$).

In each of the six species tested, with the exception of the dorsal skull of *E. hottentotus*, females were slightly larger than males. Where there was significant sexual dimorphism in centroid size of the skull, females were larger by the following percentages: 4.24% in the dorsal skull and 3.94% in the ventral skull of *N. capensis*; 2.66% in the ventral skull of *N. zuluensis*; 2.27% in the dorsal skull of *N. africanus*; 2.92% in the ventral skull and 2.78% in the dorsal skull of *P. hesperidus*. In those species that did not show significant sexual dimorphism in centroid size of the skull the percent difference between males and females for the ventral skull ranged from 0.40% in *P. rusticus* to 1.27% in *E. hottentotus*, whereas the range for the dorsal skull was from 0.61% in *E. hottentotus* (the only case where females were larger than males) to 1.44% in *N. zuluensis*.

The box plot of centroid size for the ventral skull of *N. capensis* was similar to that of dorsal skull centroid size, even though the data for the dorsal skull included a few more specimens and OTUs; hence only the results of the ventral plot are shown in Figure 3.2. The box plot visually confirms that, with the exception of the specimens from Sengwa in Zimbabwe where the males were larger than a single female, females are larger than males in dorsal skull centroid size. The largest difference in ventral skull centroid size between males and females occurred in specimens

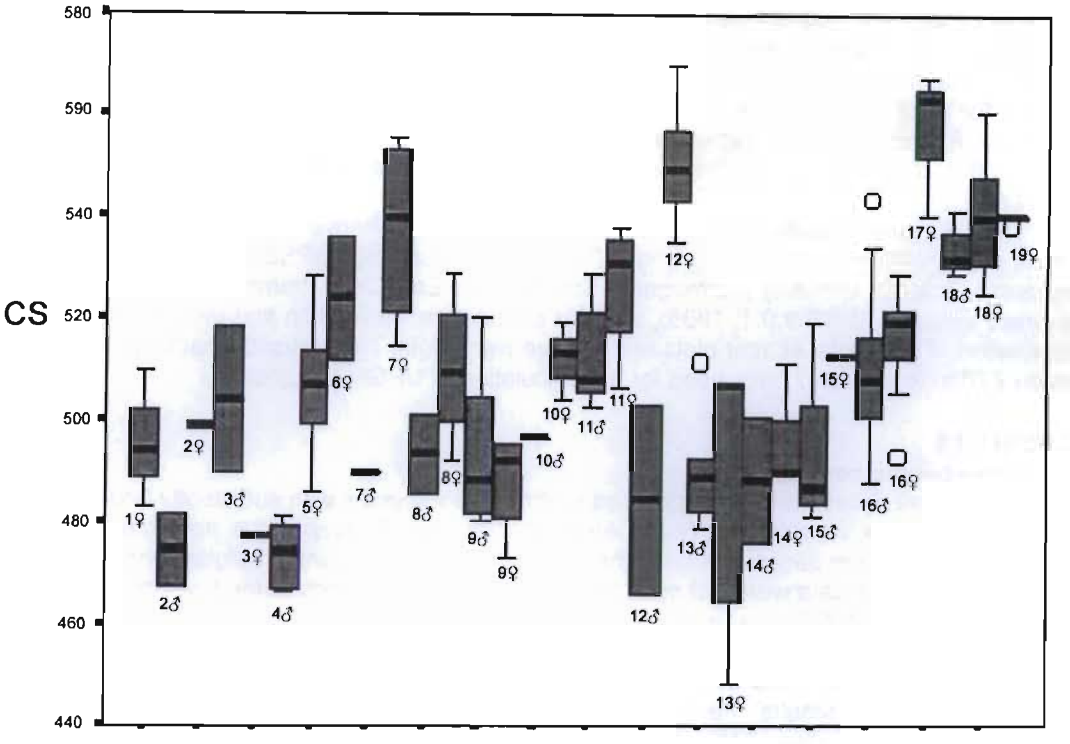


Figure 3.2 Boxplot of centroid size of the ventral skull of *Neoromicia capensis* from southern Africa with different sexes and OTUs separated (codes for the OTUs arranged from north to south and east to west: 1 - Zambia; 2 - Zimbabwe, Harare; 3 - Zimbabwe, Sengwa; 4 - Botswana; 5 - Namibia, Sandfontein; 6 - Namibia, Okaland, Okombake, Liebig's Ranch; 7 - South Africa, Limpopo, Kruger National Park; 8 - South Africa, Limpopo, Farm Ratsegaai; 9 South Africa, Northern Cape, Marie Se Gat; 10 - South Africa, North West, Farm Welgedaan; 11 - South Africa, Free State, Hoopstad; 12 - Namibia, Swartkop; 13 - South Africa, KwaZulu-Natal, Mkuze; 14 - South Africa, KwaZulu-Natal, Royal Natal National Park, Weenan, Himeville; 15 - Lesotho; 16 - South Africa, Free State, Jagersfontein Commonage; 17 - South Africa, Northern Cape, 28 km SSE Narap Farm; 18 - South Africa, Western Cape, Algeria Campsite, Kersefontein Farm; 18 - South Africa, Western Cape, Karoo National Park, Stilbaai). The box represents the inter-quartile range containing 50% (25-75%) of the values; the horizontal line across the box is the median. The whiskers extend to the highest and lowest values from the upper or lower box edge, but exclude outliers (open circles) that are values 1.5 times the box length.

Table 3.2 The number of different ecoregions within each biome represented by specimens of each Vespertilionid species from southern Africa included in this analysis. Biome description abbreviations: forest - tropical and subtropical moist broadleaf forests, savanna - tropical and subtropical grasslands, savannas, and shrublands; grassland - montane grasslands and shrublands; flooded - flooded grasslands and savanna; fynbos - mediterranean forests, woodlands and shrub; xeric - desert and xeric shrublands; and mangrove - mangrove. Species names abbreviations: Eh - *E. hottentotus*, Ncfm - *N.* cf. *melckorum*, Nc - *N. capensis*, Nre - *N. rendalli*, Nru - *N. rueppellii*, Ph - *P. hesperidus*, Ha - *H. anchietae*, Nz - *N. zuluensis*, Pr - *P. rusticus*, Na - *N. africanus*, Sd - *S. dinganii*, Mt - *M. tricolor*, Ln - *L. namibensis*, Ms - *M. schreibersii*, Lb - *L. botswanae*, and Ns - *N. schlieffenii*.

	Eh	Nc	Na	Nz	Nre	Nru	Ncfm	Ha	Ph	Pr	Lb	Ln	Ns	Mt	Ms	Sd
Forest	1	-	1	-	1	-	-	1	2	-	-	-	-	-	-	1
Savanna	1	5	4	4	1	2	1	4	-	3	2	-	1	-	-	-
Grassland	2	4	3	1	-	1	1	1	2	-	1	-	1	1	1	-
Flooded	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-
Fynbos	1	2	-	-	-	-	-	-	-	-	-	1	-	1	1	-
Xeric	3	3	-	1	-	1	-	-	-	-	-	2	-	-	-	-
Mangrove	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-

Tables 3.3 Results of one-way ANOVA tests of dorsal centroid size with different sexes and tooth wear classes (TW) in a single locality of *Neoromicia capensis* from Jagersfontein in the Free State, South Africa, with different sexes, OTUs and tooth wear classes (TW) in *Eptesicus hottentotus*, *Neoromicia capensis*, *Neoromicia africanus*, *Neoromicia zuluensis*, *Pipistrellus hesperidus*, and *Pipistrellus rusticus*, and between different species using all 16 species. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Dorsal	**Type III sum of squares**	**df**	**Mean squares**	**F-value**	**Significance**
Neoromicia capensis	Jagersfontein				
Sex	197.864	1	197.864	1.978	0.167
TW	429.048	3	143.016	1.441	0.246
Eptesicus hottentotus					
OTU	9025.566	7	1289.367	6.440	1.13E-04 ***
Sex	116.409	1	116.409	0.281	0.599
TW	3634.349	2	1817.174	5.580	7.88E-03 **
Neoromicia capensis					
OTU	51933.015	23	2257.957	17.007	0.00E-17 ***
Sex	16607.426	1	16607.426	54.591	4.64E-10 ***
TW	1610.941	3	536.980	1.385	0.249
Neoromicia africanus					
OTU	1370.348	8	171.293	2.297	0.038 *
Sex	845.561	1	845.561	11.329	1.47E-03 **
TW	235.657	3	78.552	0.868	0.464
Neoromicia zuluensis					
OTU	293.809	5	58.762	0.329	0.892
Sex	225.621	1	225.621	1.394	0.245
TW	405.436	3	135.145	0.815	0.494
Pipistrellus hesperidus					
OTU	1.221.268	4	305.317	4.077	0.013 *
Sex	657.774	1	657.774	7.438	0.012 *
TW	4.386	2	2.193	0.018	0.982
Pipistrellus rusticus					
OTU	457.304	4	114.326	0.845	0.507
Sex	123.784	1	123.784	0.929	0.342
TW	562.364	3	187.455	1.462	0.242
All 16 species					
Species	2007039.889	15	133842.660	488.056	0.00E-17 ***

Table 3.4 Results of one-way ANOVA tests of ventral centroid size with different sexes and tooth wear classes (TW) in a single locality of *Neoromicia capensis* from Jagersfontein in the Free State, South Africa, with different sexes, OTUs and tooth wear classes (TW) in *Eptesicus hottentotus*, *Neoromicia capensis*, *Neoromicia africanus*, *Neoromicia zuluensis*, *Pipistrellus hesperidus*, and *Pipistrellus rusticus*, and between different species using all 16 species. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Ventral	Type III sum of squares	df	Mean squares	F-value	Significance
Neoromicia capensis	Jagersfontein				
Sex	260.426	1	260.426	1.563	0.220
TW	418.507	3	139.502	0.810	0.498
Eptesicus hottentotus					
OTU	9368.954	4	2342.239	8.939	1.44E-04 ***
Sex	581.343	1	581.343	1.041	0.317
TW	7161.026	2	3580.513	10.956	3.54E-04 ***
Neoromicia capensis					
OTU	57126.902	18	3173.717	12.824	0.00E-17 ***
Sex	16273.387	1	16273.387	33.734	3.44E-08 ***
TW	1938.130	3	646.043	1.111	0.347
Neoromicia africanus					
OTU	1376.564	8	172.070	2.050	0.074
Sex	184.106	1	184.106	1.836	0.184
TW	340.479	3	113.493	1.118	0.355
Neoromicia zuluensis					
OTU	1311.112	5	262.222	2.501	0.061
Sex	803.241	1	803.241	7.420	0.011 *
TW	301.950	3	100.650	0.728	0.545
Pipistrellus hesperidus					
OTU	1970.018	4	492.504	4.202	0.009 **
Sex	1317.555	1	1317.555	10.355	0.003 **
TW	127.782	2	63.891	0.370	0.694
Pipistrellus rusticus					
OTU	1334.484	4	333.621	2.671	0.054
Sex	20.886	1	20.886	0.134	0.717
TW	13.878	3	4.626	0.028	0.994
All 16 species					
Species	2192468.025	15	146164.535	380.401	0.00E-17 ***

from Swartkop in Namibia, Pafuri in South Africa and Harare and Sengwa in Zimbabwe, which may be an artifact of small sample size since in each of the latter three populations one of the sexes was represented by a single specimen only, or it may indicate misidentified specimens. With regards the significant variation of centroid size between the different OTUs, the box plot visually confirms the ventral skull post-hoc Tukey test which identified eight successively, overlapping subgroups where the first subgroup (the more north-easterly OTUs from Zambia, Zimbabwe and Botswana) and last subgroup (the most south-westerly OTUs from the Cape) did not overlap but were linked by the overlap of the intermediate groups. The post-hoc Tukey test of the dorsal skull centroid size identified a similar pattern of variation between the OTUs although there were 10 overlapping subgroups. The pattern of skull centroid size increasing in OTUs from north to the south and east to west was confirmed by the highly significant correlation of centroid size with both latitude (dorsal skull: r_s = -0.467, P=1.00E-06; ventral skull: r_s = -0.487, P = 2.18E-04) and longitude (dorsal skull: r_s = -0.516, P = 1.00E-06; ventral skull: r_s = -0.493, P = 1.00E-06). Both the box plot and a plot of centroid size against latitude identified females from three different localities (Pafuri, Swartkop and Namaqualand) that are considerably larger than specimens from similar latitudes, as well as specimens from two localities (Mkuze and Swartkop) that are considerably smaller than other specimens from the same latitude. Two females from Pafuri, TM34185 and TM34240, are also larger than other specimens from the same longitude on the plot of centroid size against longitude, and are thus exceptions to the clinal variation of centroid size with latitude and longitude. The larger females from Namaqualand are TM28002 and TM28004, the larger females from Swartkop are TM32657 and TM32683, while the smaller male from Rheinvels is TM32547, and the smaller females from Mkuze are DM5371 and TM35270. Centroid size was also highly significantly correlated with different biomes (dorsal skull: r_s=0.389, P=1.00E-06; ventral skull: r_s=0.290, P=2.18E-04) and ecoregions (dorsal skull: r_s=0.503, P=1.00E-06; ventral skull: r_s=0.400, P=1.00E-06), such that centroid size was larger in *N. capensis* from the westerly OTUs in the Mediterranean forests, woodlands and shrub (fynbos) and deserts and xeric shrubland biomes and smaller in the tropical and subtropical grasslands, savannas and shrubland biome.

Box plots of dorsal and ventral skull centroid size of *E. hottentotus* which separated significantly different OTUs and tooth wear classes were similar even though the dorsal skull plot included a few more specimens and OTUs, hence only the dorsal results are shown in Figure 3.3. In relation to the significantly different tooth wear classes, the box plot visually confirmed the ventral skull post-hoc Tukey test which identified two different subsets. The Tukey test identified one group of tooth wear class B and another of tooth wear classes C and D, while the box plot showed that in five out of six OTUs with all three tooth wear classes tooth wear class B was significantly smaller in centroid size than tooth wear classes C and D, while in the sixth OTU (Aus, Namibia) tooth wear class B was significantly smaller than tooth wear class C but not tooth wear class D. In two of the three OTUs with specimens of both tooth wear classes C and D, tooth wear class C was larger in centroid size than tooth wear class D. In relation to the significantly different OTUs, in which the post-hoc Tukey tests had identified two overlapping subgroups (based on the dorsal skull) and two distinct subgroups (based on the ventral skull), the box plot visually confirmed that specimens from Messina and Pafuri have a smaller skull centroid size than any of the other OTUs of *E. hottentotus*. The pattern of increase in centroid size across the different OTUs correlated significantly with decreasing longitude in the dorsal (dorsal skull: r_s = -0.371, P = 0.022) but not the ventral skull (ventral skull: r_s = -0.131, P = 0.498), and did not correlate significantly with increasing latitude in either the dorsal skull or the ventral skull (dorsal skull: r_s = -0.237, P = 0.152; ventral skull: r_s = -0.269, P = 0.159). Centroid size of the dorsal skull was only slightly significantly correlated with ecoregions (r_s =0.355, P = 0.029), otherwise centroid size was not significantly correlated with either the different biomes (dorsal skull: r_s = 0.299, P = 0.068; ventral skull: r_s = 0.105, P = 0.587) or the ecoregions (ventral skull: r_s = 0.141, P = 0.467).

Boxplots of dorsal and ventral skull centroid size of *P. hesperidus* which separated significantly different OTUs and sexes were similar; hence only the ventral results are shown in Figure 3.4. In two out of three OTUs, females were larger than males of the same OTU, the difference between the sexes being more pronounced in specimens from St Lucia than Eshowe. The boxplot also visually confirms the results of the Post-hoc Tukey tests for both the dorsal and ventral skull which identified two overlapping subgroups of OTUs, in which the most northerly (Ndumu and Kosi Bay) and southerly (greater Durban area) OTUs did not overlap but were connected by the overlap of the intermediate OTUs. The pattern of increase in centroid size across the different OTUs correlated significantly with increasing latitude in both the dorsal and

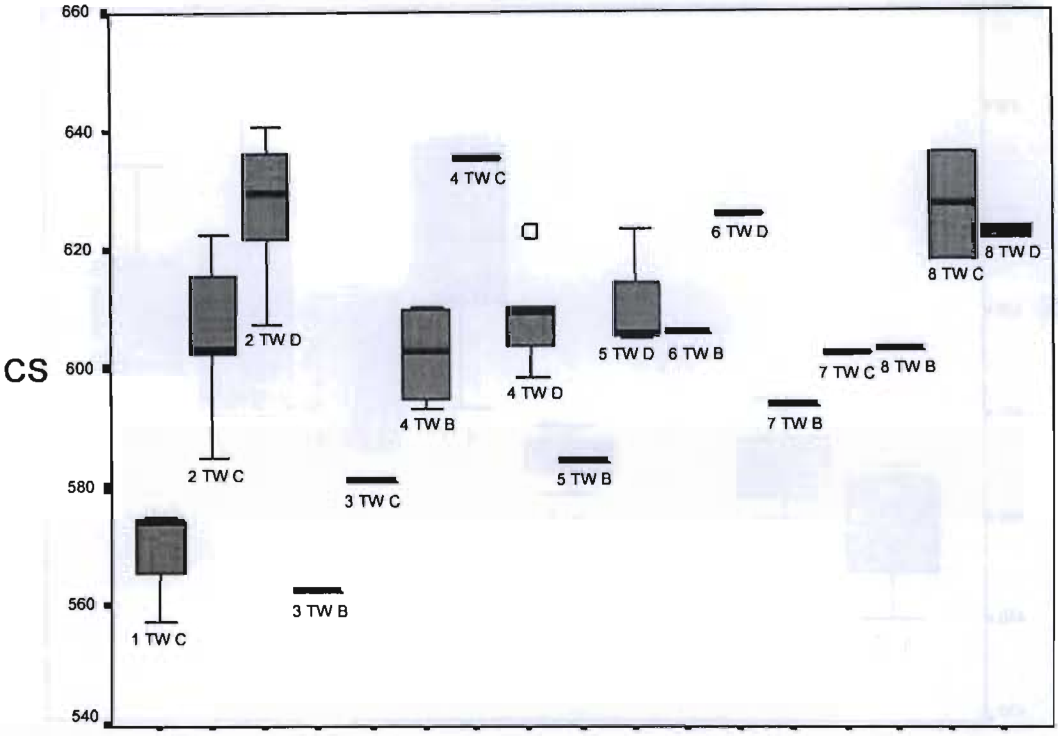


Figure 3.3 Boxplot of centroid size of the dorsal skull of *Eptesicus hottentotus* from southern Africa with different OTUs and tooth wear classes (TW) separated (codes for the OTUs arranged from north to south and east to west: 1 - Zimbabwe; 2 - Namibia, Ombu Eronga Mountains; 3 - South Africa, Limpopo, Greefswald Farm, Pafuri; 4 - Namibia, Klein Aus 8, Zwartmodder 101, Farm Kanaan; 5 - Namibia, Bethanie-Huns 106, Rheinvels Farm; 6 - South Africa, KwaZulu-Natal, Ithala Game Reserve, Kranskloof Nature Reserve; 7 - Lesotho; 8 - South Africa, Western Cape, Algeria and Kliphuis Campsites). The box represents the inter-quartile range containing 50% (25-75%) of the values; the horizontal line across the box is the median. The whiskers extend to the highest and lowest values from the upper or lower box edge, but exclude outliers (open circles) that are values 1.5 times the box length.

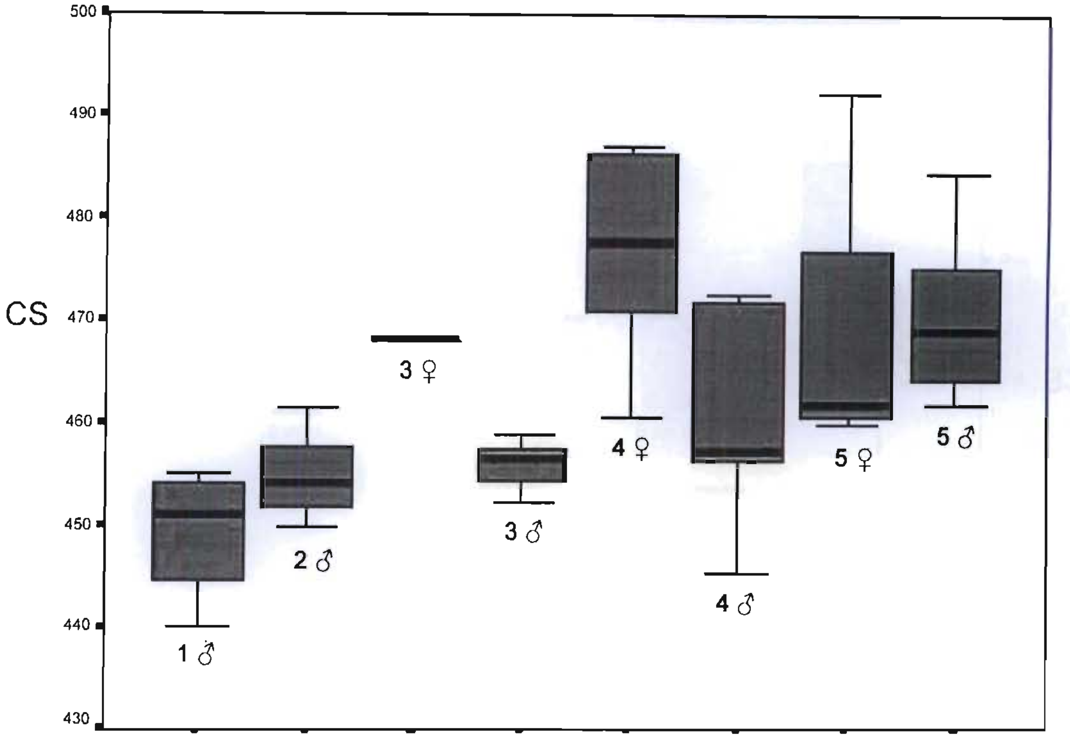


Figure 3.4 Boxplot of centroid size of the ventral skull of *Pipistrellus hesperidus* from southern Africa with different sexes and OTUs separated (codes for the OTUs arranged from north to south:1 = Ndumu Game Reserve, Kosi Lake; 2 = Ngome Forest Reserve, Hluhluwe Game Reserve; 3 = St Lucia, Dukuduku Forest; 4 = Dlinza Forest, Twinstreams Farm; 5 = Greater Durban area. The box represents the inter-quartile range containing 50% (25-75%) of the values; the horizontal line across the box is the median. The whiskers extend to the highest and lowest values from the upper or lower box edge, but exclude outliers (open circles) that are values 1.5 times the box length.

ventral skull (dorsal skull: r_s = -0.485, P = 0.010; ventral skull: r_s = -0.597, P = 3.09E-04), and decreasing longitude in both the dorsal and ventral skull (dorsal skull: r_s = -0.391, P = 0.043; ventral skull: r_s = -0.536, P = 0.002), but was not significantly correlated with either the different biomes (dorsal skull: r_s = 0.150, P = 0.455; ventral skull: r_s = 0.026, P = 0.889) or the different ecoregions (dorsal skull: r_s = 0.131, P = 0.515; ventral skull: r_s = 0.033, P = 0.856).

3.3.2 Inter-specific centroid size

One-way ANOVA tests identified highly significant differences in dorsal ($P < 0.001$) and ventral ($P < 0.001$) skull centroid size between the species of all 16 vespertilionid species (see Tables 3.3 and 3.4 for results). Box plots of dorsal and ventral skull centroid size of all 16 vespertilionid species analysed were similar and hence only the ventral results are shown in Figure 3.5. *Eptesicus hottentotus* was significantly larger in skull centroid size than any of the other species of *Pipistrellus* and *Neoromicia* analysed. Of the other species included from the same subfamily, Vespertilioninae, only *S. dinganii* was similar in skull centroid size to *E. hottentotus*. Of the species of *Pipistrellus* and *Neoromicia* analysed, the smallest to the largest formed an overlapping continuum in skull centroid size. However, if species of intermediate, overlapping skull centroid size (*P. hesperidus*, *H. anchietae*, and *N. zuluensis*) were excluded, *N.* cf. *melckorum*, *N. capensis*, *N. rendalli*, and *N. rueppellii* were significantly larger in skull centroid size than the smallest species, *N. africanus* and *P. rusticus*. Of the other species of Vespertilionidae and Miniopteridae included, *N. schlieffenii*, *L. botswanae* and *M. schreibersii* overlapped in skull centroid size with the various species of *Neoromicia* and *Pipistrellus*, whereas *L. namibensis* and *M. tricolor* although different from each other, were larger than the various species of *Neoromicia* and *Pipistrellus* but smaller than *E. hottentotus* and *S. dinganii*. The box plot visually confirms the post-hoc Tukey tests which identified 16 and 10 different subset for the dorsal and ventral skull centroid size, respectively, of which the subsets of *L. namibensis* and *M. tricolor*, and *S. dinganii* and *E. hottentotus* did not overlap with any other subsets, while the remaining subsets overlapped.

3.3.3 Intra-specific shape

In the analysis of *N. capensis* from Jagersfontein in the Free State, two of the 14 dorsal skull partial warps and two of the 22 ventral skull partial warps were significantly non-normally distributed. In the intra-specific analyses of the six species with sufficiently large sample sizes, all 14 partial warps of dorsal skull shape were normally distributed in *E. hottentotus*, *P. hesperidus*, *P. rusticus*, *N. zuluensis*, and *N. capensis*, while in *N. africanus*, one partial warp was non-normally distributed. In ventral skull shape, all 22 partial warps were normally distributed in *E. hottentotus*, while in *N. capensis*, *P. rusticus*, and *N. africanus* one partial warp, in *P. hesperidus* two partial warps, and in *N. zuluensis* three partial warps were non-normally distributed. Non-parametric Spearman rank correlation tests were also used in correlations with variables of interest that were also significantly non-normally distributed i.e. OTUs, sexes, tooth wear classes, and values of latitude and longitude .

Relative warp analyses of dorsal and ventral skull shape showed no clear patterns of distinction between specimens from a single locality of *N. capensis* from Jagersfontein in the Free State due to different sex or tooth wear classes. However, correlation tests identified the following significant correlations in dorsal and ventral skull shape (see Appendix 3.3 A for the full correlation results): in ventral skull shape between the second principal component scores and centroid size (r = -0.387, P = 0.022), and in dorsal skull shape between the first and second principal component scores and centroid size (r = -0.326, P = 0.035; r = -0.362, P = 0.019), and between the fourth principal component scores and sex (r_s = -0.369, P = 0.016). Although non-parametric rank correlation tests were required, their results were usually no different in significance to parametric Pearson product moment correlation tests (see Appendix 3.3 A). Different tooth wear classes and sexes were combined within species in subsequent analyses of shape, since variation in centroid size was not significantly correlated with either sex or tooth wear class. And, the significant correlation of shape with sex was on the fourth relative warp, which of the four most important relative warps contributed least to the variation in shape, and the level of significance was low.

Thin plate splines (not shown) indicated the following skull shape changes associated with the significant correlations in dorsal and ventral skull shape of *N. capensis* from Jagersfontein in the Free State. In the correlation between the first principal component axis (which described 23.83% of the shape variation) of dorsal skull shape and centroid size, smaller specimens have a

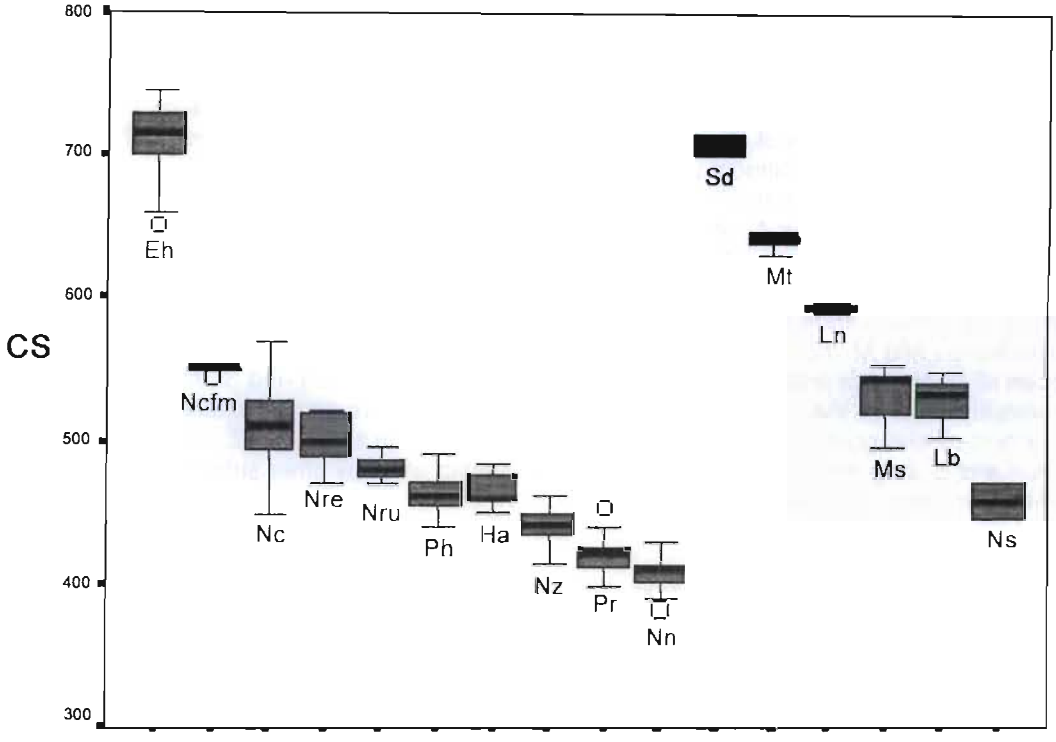


Figure 3.5 Boxplot of centroid size of the ventral skull of all 16 species (Eh = *Eptesicus hottentotus*, Ncfm = *Neoromicia* cf. *melckorum*, Nc = *N. capensis*, Nre = *N. rendalli*, Nru = *N. rueppellii*, Ph = *Pipistrellus hesperidus*, Ha = *H. anchietae*, Nz = *N. zuluensis*, Pr = *P. rusticus*, Nn = *N. africanus*, Sd = *Scotophilus dinganii*, Mt = *Myotis tricolor*, Ln = *Laephotis namibensis*, Ms - *Miniopterus schreibersii*, Lb = *L. botswanae*, Ns = *Nycticeinops schlieffenii*) from southern Africa. The box represents the inter-quartile range containing 50% (25-75%) of the values; the horizontal line across the box is the median. The whiskers extend to the highest and lowest values from the upper or lower box edge, but exclude outliers (open circles) that are values 1.5 times the box length.

broader more laterally displaced muzzle region, and a shorter cranium in the region between posterior insertion of the zygomatic process with the squamosal and the most lateral extension of the mastoid. In the correlation between the second principal component axis of dorsal skull shape (which described 19.68% of the shape variation) and centroid size, specimens with larger centroid sizes have shorter muzzle regions while in the cranium, the most lateral displacement of the mastoid is further back from the posterior insertion of the zygomatic process with the squamosal. In the correlation between the fourth principal component axis (which described 9.90% of the shape variation) of dorsal skull shape and sex, the posterior cranium in females is more laterally displaced than in males, and in females, the distance between the deepest indentation of the premaxilla between the last incisor and canine and the most lateral extension at the canine is shorter than in males. In the correlation between the second principal component axis of ventral skull shape (which described 16.26% of the shape variation) and centroid size, specimens with larger centroid sizes have slightly longer, broader muzzles where the anterior insertion of the zygomatic arch is less laterally displaced. Specimens with larger centroid sizes also have a less rounded cranium due to the most laterally displacement of the mastoid being more posteriorly displaced from the posterior insertion of the zygomatic process with the squamosal.

Relative warp analyses of dorsal and ventral skull shape based on the means of OTUs within each species showed some separation of OTUs into various groups, but no clear distinctions were found between different OTUs in the relative warp analyses of all specimens of each species. The percentage contributions of the first four relative warps to total shape variation were similar between the species, however, the results of the correlation tests between the first four principal component scores of dorsal and ventral skull shape of each specimen and the different OTUs, centroid size, sex, tooth wear class, latitude, longitude, biome and ecoregion were different for each species (see Appendix 3.3 B and C for the full correlation results). There were, however, more significant correlations with ventral than dorsal skull shape, and more significant correlations of skull shape with latitude and fewest significant correlations with tooth wear class. While non-parametric tests were required for most of the correlation tests, their results were very similar to those of parametric Pearson product moment correlation tests (see Appendix 3.3 B and C for the full correlation results).

In *E. hottentotus*, shape variability in the dorsal skull was significantly correlated on the first relative warp with variation between different OTUs (r_s = 0.500, P = 0.001), latitudes (r_s = -0.391, P = 0.015), longitudes (r_s = 0.334, P = 0.040), biomes (r_s = -0.325, P = 0.046) and ecoregion (r_s = -0.414, P = 0.010), and on the second relative warp with sexual dimorphism (r_s = -0.331, P = 0.042). In the ventral skull shape of *E. hottentotus* shape variation was still significantly correlated on the first relative warp with variation between different OTUs (r_s = 0.569, P = 0.001), latitudes (r_s = -0.511, P = 0.005), longitudes (r_s = 0.570, P = 0.001), biome (r_s = -0.385, P = 0.039) and ecoregion (r_s = 0.568, P = 0.001), and on the third relative warp with different OTUs (r_s = 0.498, P = 0.006), longitudes (r_s = 0.468, P = 0.011), ecoregions (r_s = -0.565, P = 0.001) and biomes (r_s = 0.402, P = 0.031), and on the fourth relative warp with different latitudes (r_s = 0.434, P = 0.019).

Skull shape variation in the dorsal skull of *N. capensis* was significantly correlated on the first relative warp with sexual dimorphism (r_s = 0.172, P = 0.018), on the second relative warp with ecoregion (r_s = -0.146, P = 0.044), on the third relative warp with sexual dimorphism (r_s = 0.207, P = 0.004), different centroid sizes (r = -0.355, P = 4.6E-06), latitudes (r_s = -0.166, P = 0.021), longitudes (r_s = -0.320, P = 6.40E-06), biomes (r_s = -0.312, P = 1.10E-05) and ecoregion (r_s = -0.355, P = 1.00E-06), and on the fourth relative warp with different OTUs (r_s = -0.173, P = 0.016) and latitude (r_s = 0.153, P = 0.034). In the ventral skull shape of *N. capensis* skull shape variation was significantly correlated on the first relative warp with different OTUs (r_s = -0.185, P = 0.020), sexual dimorphism (r_s = 0.167, P = 0.036), latitude (r_s = 0.293, P = 1.92E-04), biome (r_s = -0.209, P = 0.008) and ecoregion (r_s = -0.196, P = 0.014), on the second relative warp with centroid size (r = -0.355, P = 4.87E-06), longitude (r_s = 0.317, P = 4.97E-05), biome (r_s = -0.246, P = 0.002) and ecoregion (r_s = -0.278, P = 4.09E-04), and on the fourth relative warp with centroid size (r = -0.161, P = 0.043), sexual dimorphism (r_s = 0.188, P = 0.018), latitude (r_s = 0.191, P = 0.016), biome (r_s = -0.192, P = 0.016) and ecoregion (r_s = -0.272, P = 0.001).

In *N. africanus* shape variability in the dorsal skull was significantly correlated on the first relative warp with variation between tooth wear classes (r_s = 0.361, P = 0.009), and on the second relative warp with different OTUs (r_s = 0.449, P = 0.001), centroid size (r = 0.276, P = 0.048), latitude (r_s = -0.365, P = 0.008) and longitude (r_s = 0.292, P = 0.035). While variation in ventral skull shape in *N. africanus* was significantly correlated on the first relative warp with different OTUs (r_s = -0.394, P = 0.013), centroid size (r = -0.336, P = 0.037), latitude (r_s = 0.345, P = 0.032) and longitude (r_s = -0.417, P = 0.008), and on the fourth relative warp with latitude (r_s = 0.354, P = 0.027). The dorsal skull shape of *N. zuluensis* only showed a significant correlation on the first relative warp with longitude (r_s = 0.359, P = 0.023), while variation in the ventral skull shape showed a significant correlation on the first relative warp with different OTUs (r_s = -0.493, P = 0.008), latitude (r_s = 0.498, P = 0.007) and longitude (r_s = -0.395, P = 0.037), and on the second relative warp with different OTUs (r_s = -0.504, P = 0.006).

The dorsal skull shape variation of *P. hesperidus* was significantly correlated on the second relative warp with centroid size (r = 0.538, P = 0.004) and sexual dimorphism (r_s = 0.629, P = 4.37E-04), while the ventral skull variation was significantly correlated on the first relative warp with sexual dimorphism (r_s = 0.526, P = 0.002), and ecoregion (r_s = 0.358, P = 0.044), and on the second relative warp with different OTUs (r_s = -0.506, P = 0.003), latitude (r_s = 0.466, P = 0.007) and longitude (r_s = 0.435, P = 0.013), on the third relative warp with sexual dimorphism (r_s = 0.372, P = 0.036) and on the fourth relative warp with centroid size (r = -0.421, P = 0.016) and different tooth wear classes (r_s = 0.421, P = 0.017). In *P. rusticus*, dorsal skull shape variation was significantly correlated on the fourth relative warp with different OTUs (r_s = -0.405, P = 0.012), tooth wear classes (r_s = 0.523, P = 0.001), latitude (r_s = 0.439, P = 0.006), and biome (r_s = -0.364, P = 0.025), while variation in the ventral skull shape was significantly correlated on the second relative warp with different tooth wear classes (r_s = 0.574, P = 0.001) and the third relative warp with different OTUs (r_s = -0.415, P = 0.018) and latitude (r_s = 0.429, P = 0.014).

Further investigations were made of the highly significant correlations within species in the analyses of all specimens. A plot of the significantly correlated first principal component scores of the ventral skull of *N. capensis* and latitude of all specimens (Fig. 3.6) identified a general trend for specimens from low latitudes (i.e. further south) to be found on the negative side of the first relative warp, and visa versa. Even so, individuals from a single OTU showed a considerable range in first principal component scores and there were several exceptions to the trend, such as specimen numbers NMZ58818 from Harare in Zimbabwe and KM2222 from Balovale in Zambia, which although from localities of high latitude plotted on the negative side of the first relative warp. The ventral skull shape difference (Fig. 3.6) in *N. capensis* summarised by the first relative warp describes 17.52% of the shape variation. In larger specimens from latitudes further south, the anterior attachment of the zygomatic arch is more laterally displaced with regards the anterior posterior plane of the skull, and they have a shallower angle between the occipital condyle the most lateral angle of the foramen magnum.

A plot of the significantly correlated second principal component scores of the ventral skull and centroid size (Fig. 3.7) showed that specimens of *N. capensis* from Pafuri, Swartkop and Namaqualand-Springbok which had the largest centroid sizes were found at the negative extreme of the second relative warp, while specimens from the Drakensberg, Mkuze, Lesotho, Botswana, Zimbabwe and Ventersdorp which had the smallest centroid sizes were found at the positive extreme of the second relative warp. Two exceptions to this trend were specimen number TM32683 from Swartkop in Namibia which plotted higher along the second relative warp, and specimen number TM32547 from Rheinvels Farm in Namibia which plotted lower along the second relative warp than other specimens of a similar centroid size. Both these specimens were among specimens identified above as having larger and smaller centroid sizes, respectively than other specimens from the same OTU. A plot of second principal component scores of the ventral skull and longitude (Fig. 3.7) identified that although individuals from a single OTU showed a considerable range in second principal component scores, the general trend was for specimens from OTUs of lower longitude (i.e. further west) to be found on the negative side of the second relative warp, and visa versa. The most obvious exception to this trend were specimens from Pafuri (TM37811 and TM34240) which had the lowest second principal component scores although they were from an OTU with one of the highest longitudes. Specimen number TM34240 was one of the specimens identified above as having a larger centroid size than other specimens from Pafuri. A plot of the second principal component scores of the ventral skull and the different ecoregions showed that as with longitude, individuals from a single OTU showed a considerable range in second principal component scores although the general trend was for specimens from OTUs of ecoregions in the mediterranean forests, woodlands and shrub, and deserts and xeric shrublands biomes (i.e. further west) to be found on the negative side of the second relative warp, whereas specimens from OTUs in the montane grassland and shrublands, and tropical and subtropical grasslands, savannas and shrublands biomes were found on the positive side of the second relative warp. As in the plots of skull shape with centroid size and longitude, the exception to the trend with different ecoregions were specimens from Pafuri, which plotted further towards

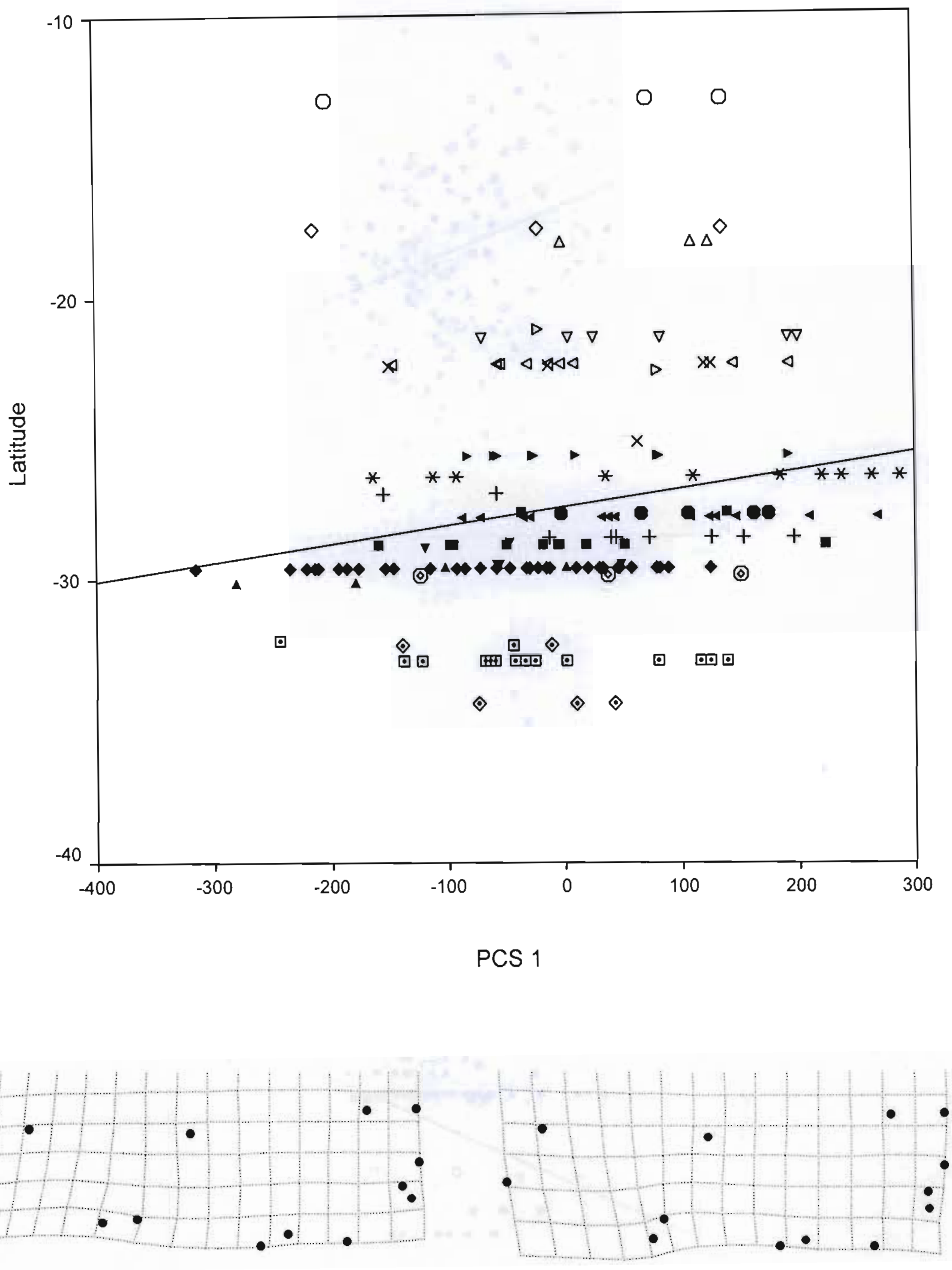


Figure 3.6 Plot of the first principal component scores (PCS1) and latitude with associated thin plate splines of ventral skull of *Neoromicia capensis* from southern Africa. OTU codes used: 1=○, 2=◇, 3=△, 4=▽, 5=◁, 6=▷, 7=+, 8=×, 9=∗, 10=●, 11=■, 12=◆, 13=▲, 14=▼, 15=◀, 16=▶, 17=◎, 18=⊡, 19=◈.

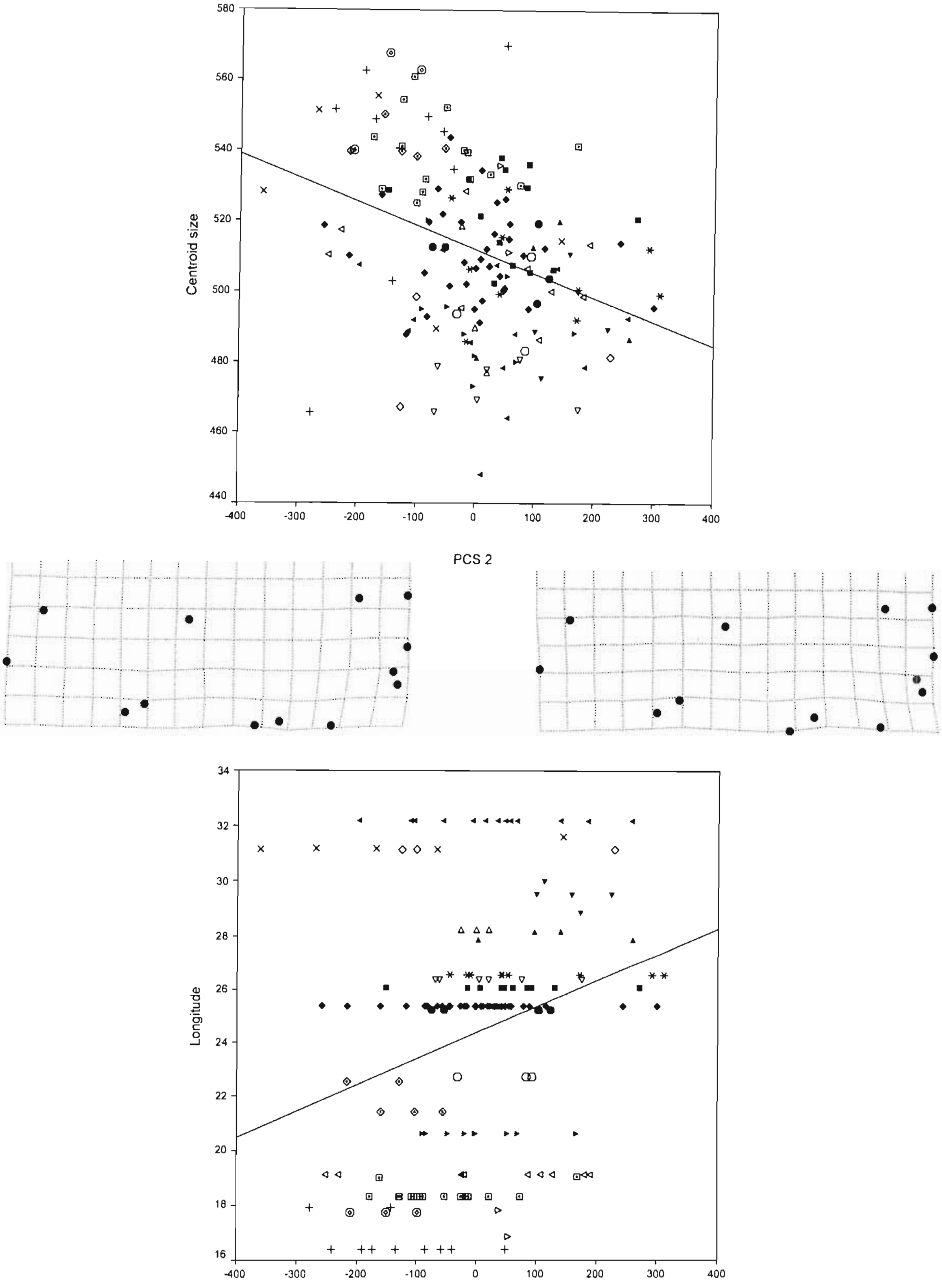


Figure 3.7 Plots of the second principal component scores (PCS2) with centroid size and longitude with associated thin plate splines of ventral skull of *Neoromicia capensis* from southern Africa. OTU codes used: 1=○, 2=◇, 3=△, 4=▽, 5=◁, 6=▷, 7=+, 8=×, 9=✱, 10=●, 11=■, 12=◆, 13=▲, 14=▼, 15=◀, 16=▶, 17=◎, 18=⊡, 19=◈.

the negative side of the second principal component scores compared with other specimens from similar ecoregions. The ventral skull shape difference (Fig. 3.7) in *N. capensis* summarised by the second relative warp described 11.94% of the shape variation. In larger specimens from longitudes further west the anterior attachment of the zygomatic arch is broader, the angle of the posterior attachment of the zygomatic arch relative to the anterior posterior plane of the skull is more laterally displaced, and the distance between the posterior attachment of the zygomatic arch and the most lateral displacement of the mastoid is larger.

Plots between the significantly correlated third principal component scores of dorsal skull shape of *N. capensis* and both centroid size and longitude (Fig. 3.8), indicate that specimens of *N. capensis* from higher longitudes and smaller centroid size were found on the more negative side of the third relative warp and visa versa. The exception to the correlation between dorsal skull shape and longitude was specimen number TM 35583 from Nossob, which although from a locality with a lower longitude, plotted at the most positive side of the third relative warp. This specimen was also an outlier on the plot of centroid size with the third relative warp since it plotted at the most positive extreme of the third relative warp relative to other specimens of the same centroid size, but it was not an outlier on the ventral skull shape. The third principal component scores of dorsal skull shape of *N. capensis* were also highly significantly correlated with different biomes and ecoregions, such that specimens from OTUs of ecoregions in the mediterranean forests, woodlands and shrub, and deserts and xeric shrublands biomes (i.e. further west) were found on the positive side of the third relative warp, whereas specimens from OTUs in the montane grassland and shrublands, and tropical and subtropical grasslands, savannas and shrublands biomes were found on the negative side of the third relative warp. The dorsal skull shape differences summarised by the third relative warp described 14.4% of the shape variation. Specimens with larger centroid size from more westerly longitudes have a shorter nasal in the region between the insertion of the jugal on the maxilla and the point of least inter-orbital width, whereas the frontal and parietal area posterior to the orbit is more elongated. The posterior insertion of the zygomatic arch is narrower, as is the distance from the posterior insertion of the zygomatic arch to the most lateral extension of the mastoid, and the area between the most lateral extension of the mastoid and the middle of the posterior extension of the cranium is greater.

Correlation tests between the first four principal component scores of the means of the different OTUs of *N. capensis* for dorsal and ventral skull shape and centroid size, the different OTUs, latitude, longitude, biomes and ecoregions indicated fewer significant correlations in analyses with individual specimens none of which were highly significant, and the significant correlations were different between the tests with individuals and those with the means of the individuals. In the analysis of mean OTUs of dorsal skull shape of *N. capensis,* the following tests for correlation were significant, between the first principal component scores and centroid size (r = 0.606, P = 0.002), longitude (r_s = -0.517, P = 0.010), biome (r_s = 0.565, P = 0.004) and ecoregion (r_s = -0.626, P = 0.001). While in the analysis of mean OTUs of ventral skull shape of *N. capensis* two of the tests for correlation were significant, between the second principal component scores and latitude (r_s = 0.588, P = 0.008), and between the third principal component scores and the different OTUs (r_s = -0.477, P =0.039) (see Appendix 3.3 D for the full correlation results).

A plot of the first two relative warp scores (Fig. 3.9) identified that the highly significant correlation in the dorsal skull shape of *P. hesperidus* between the second principal component scores and the different sexes was due to females being found only at the positive extreme of the second relative warp, while males occurred across the range of second principal component scores. The subtle dorsal skull shape differences associated with the second relative warp indicate that in female *P. hesperidus* both the distance between the most lateral extension of the canine and the deepest indentation of the premaxilla between the last incisor and the canine, and the attachment of the zygomatic process with the squamosal are narrower than in most males.

Multiple regression analyses of dorsal and ventral skull shape and centroid size in six taxa identified highly significant relationships between dorsal and ventral skull shape and centroid size in *N. capensis* (dorsal skull: Wilks lambda = 0.691, P = 6.165E-09; ventral skull: Wilks lambda = 0.681, P = 9.592E-05) slightly significant relationships between dorsal and ventral skull shape and centroid size in *P. hesperidus* (dorsal skull: Wilks lambda = 0.179, P = 0.012; ventral skull: Wilks lambda = 0.106, P = 0.030), and a significant relationships between dorsal skull shape and centroid size in *E. hottentotus* (dorsal skull: Wilks lambda = 0.327, P = 0.005) (see Appendix 3.5 for full multiple regression results). Thin plate splines indicated all three species (*N. capensis*, *N. zuluensis* and *E. hottentotus*) showed the following similar shape changes associated with

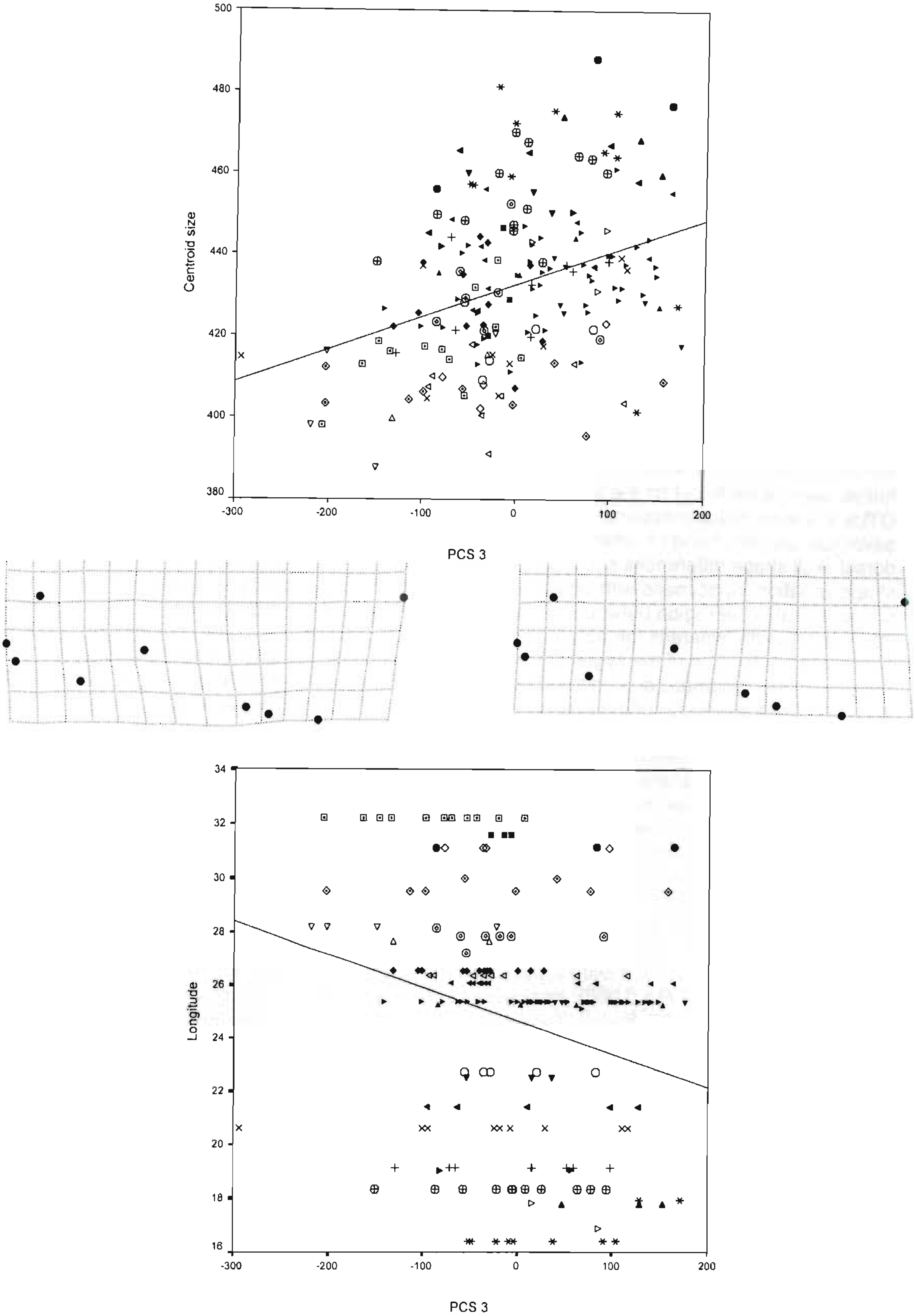


Figure 3.8 Plots of the third principal component score (PCS3) with centroid size and longitude with associated thin plate splines of dorsal skull of *Neoromicia capensis* from southern Africa. OTU codes used: 1=○, 2=◇, 3=△, 4=▽, 5=◁, 6=▷, 7=+, 8=×, 9=✳, 10=●, 11=■, 12=◆, 13=▲, 14=▼, 15=◀, 16=▶, 17=◎, 18=⊡, 19=◈, 20=◬, 21=⊽, 22=⊲, 23=⊳, 24=⊗.

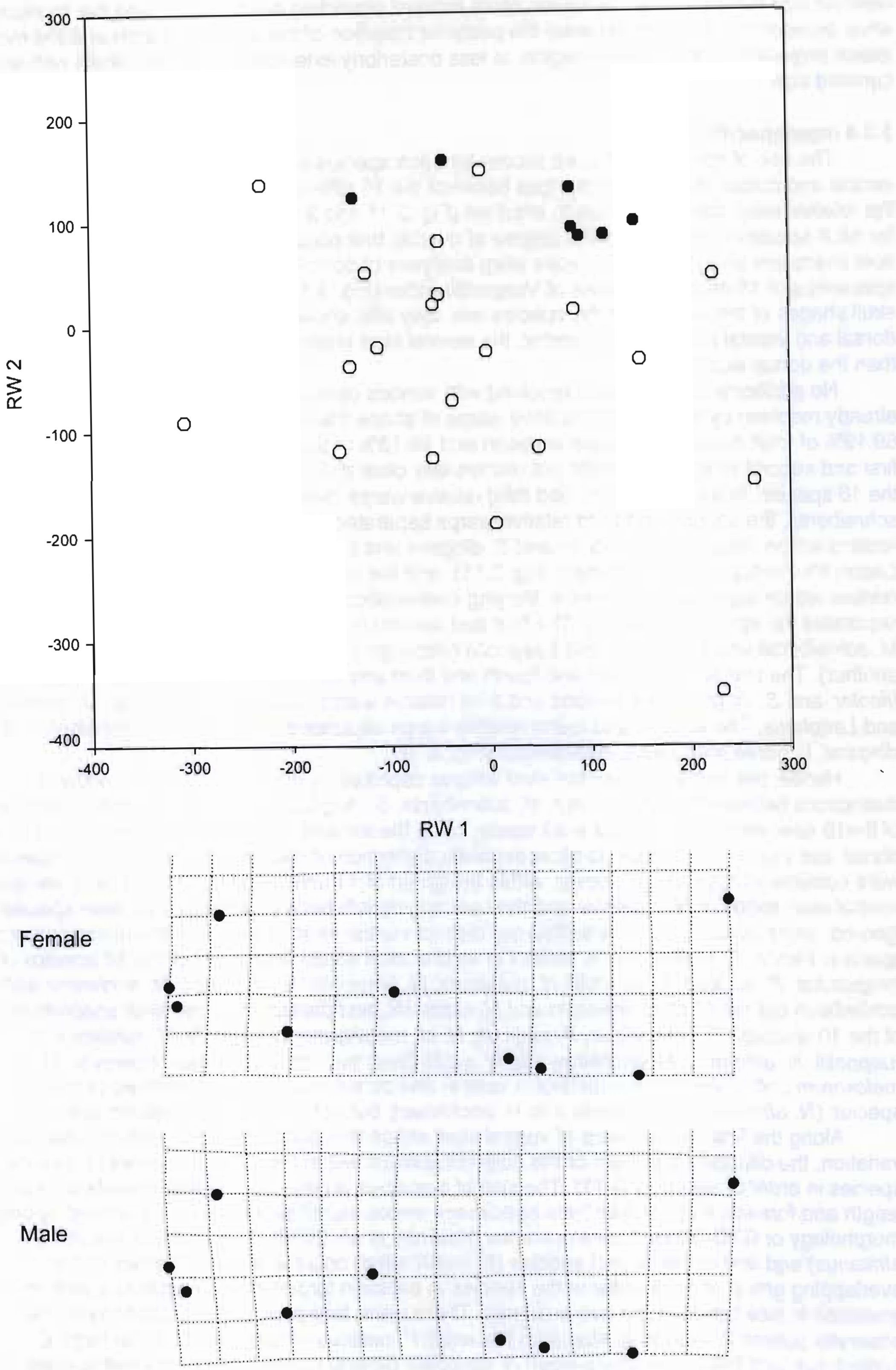


Figure 3.9 Plot of relative warps (RW) 1 and 2 indicating males (○) and females (•), with associated thin plate splines of dorsal skull shape of *Pipistrellus hesperidus* from southern Africa.

centroid size (see Fig. 3.10 for changes in *N. capensis*): dorsal and ventral skulls with larger centroid size have a longer, narrower, more forward projecting nasal region, and the cranium, while broader in the region between the posterior insertion of the zygomatic arch and the most lateral projection of the mastoid region, is less posteriorly extended than in the skulls with smaller centroid size.

3.3.4 Inter-specific shape

The use of mean partial warp scores for each species in the relative warp analyses of ventral and dorsal skull shape changes between the 16 different species of Vespertilionidae made the relative warp analyses easier to interpret (Fig. 3.11 and 3.12), but mean partial warp scores for each species do not reflect the degree of overlap that occurs between species when individual specimens are analysed. The relative warp analyses of dorsal and ventral skull shape of all specimens of 16 different species of Vespertilionidae (Fig. 3.13 and 3.14) show how similar the skull shapes of the majority of the species are, they also show that although the results of the dorsal and ventral analyses are similar, the ventral skull shape resolves species distinctions better than the dorsal skull shape.

No additional species were resolved with various combinations of relative warps than those already resolved by the first four relative warps of shape based on all specimens, which explained 69.19% of total dorsal skull shape variation and 58.13% of total ventral skull shape variation. The first and second relative warps did not resolve any clear distinctions in dorsal skull shape between the 16 species, however, the first and third relative warps clearly separated *M. tricolor* and *M. schreibersii*, the second and third relative warps separated *M. tricolor*, the second and fourth relative warps separated *M. tricolor* and *S. dinganii* and *Laephotis* (although both species of *Laephotis* overlapped one another) (Fig. 3.15), and the first and fourth and third and fourth relative warps separated *S. dinganii*. Varying combinations of relative warps of ventral skull shape separated the species differently. The first and second relative warps clearly separated *M. tricolor*, *M. schreibersii* and *S. dinganii* and *Laephotis* (although both species of *Laephotis* overlapped one another). The first and third, first and fourth and third and fourth relative warps separated *M. tricolor*, and *S. dinganii*. The second and third relative warps separated *M. tricolor*, *M. schreibersii*, and *Laephotis*. The second and fourth relative warps separated *M. tricolor*, *M. schreibersii*, *S. dinganii*, *L. botswanae* and *L. namibensis* (Fig. 3.16).

Hence, the dorsal and ventral skull shapes captured by the landmarks only allowed distinctions between five (*M. tricolor*, *M. schreibersii*, *S. dinganii*, *L. botswanae* and *L. namibensis*) of the16 species on the basis of skull shape, while the remaining 11 species were too similar in dorsal and ventral skull shape to allow separate distinction of each species when all 11 species were considered together. However, within the group of 11 similar species, if the large variation in ventral skull shape in *N. capensis* and the overlapping influence of a number of other species is ignored, some species do have sufficiently distinct ventral skull shapes to allow distinction of the species. Hence, *E. hottentotus* is distinct in ventral skull shape from eight of the 10 species (*P. hesperidus*, *P. rusticus*, *N. rendalli*, *N. zuluensis*, *N. rueppellii*, *N. africanus*, *H. anchietae* and *N. schlieffenii*) but not *N.* cf. *melckorum* and *N. capensis*, and distinct in dorsal skull shape from nine of the 10 species (*P. hesperidus*, *P. rusticus*, *N.* cf. *melckorum*, *N. rendalli*, *N. zuluensis*, *N. rueppellii*, *N. africanus*, *H. anchietae* and *N. schlieffenii*) but not *N. capensis*. However, *N.* cf. *melckorum* and *N. rendalli* are distinct in ventral and dorsal skull shape from three of the 10 species (*N. africanus*, *N. rueppellii* and *H. anchietae*), but not the remaining seven species.

Along the first relative warp of ventral skull shape that accounts for 19.46% of total shape variation, the distribution pattern of the different species within the cluster appears to arrange species in order of size (Fig. 3.13). The size of a species is based on measurements of skull length and forearm length taken from specimens whose identifications were confirmed by bacula morphology or GTG-banded chromosomes (Kearney *et al.*, 2002). The smallest species (*N. africanus*) and one of the largest species (*E. hottentotus*) occur at either extremes of the overlapping group and the order of the species in between largely corresponds to a pattern of gradation in size between the two extremes. There were, however, some exceptions to the observed pattern in relation to size, with the small *P. rusticus* plotting closer to the large *E. hottentotus*, and the intermediate-sized *N. rueppellii* plotting closest to the smallest species, *N. africanus*.

The tests for correlation between dorsal and ventral shape of the skull based on all specimens and five different variables (species, dominant call frequency, longitude, latitude, and centroid size) showed more significant correlations than the tests for correlation between dorsal

A) Dorsal

Larger
CS

Smaller
CS

B) Ventral

Larger
CS

Smaller
CS

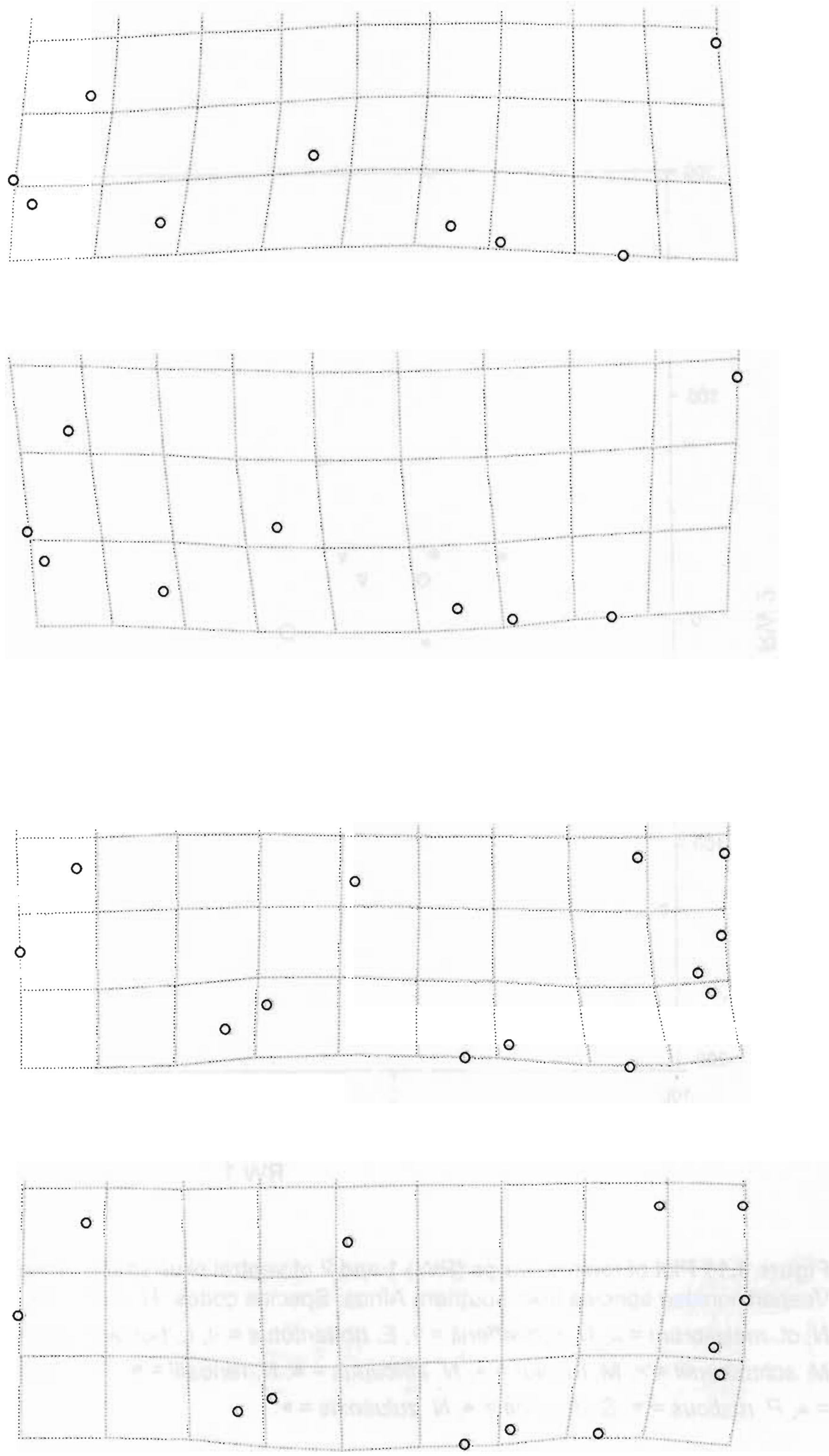


Figure 3.10 Thin plate splines of A) dorsal and B) ventral skull shape of *Neoromicia capensis* from southern Africa correlated with change in centroid size (Larger or Smaller CS).

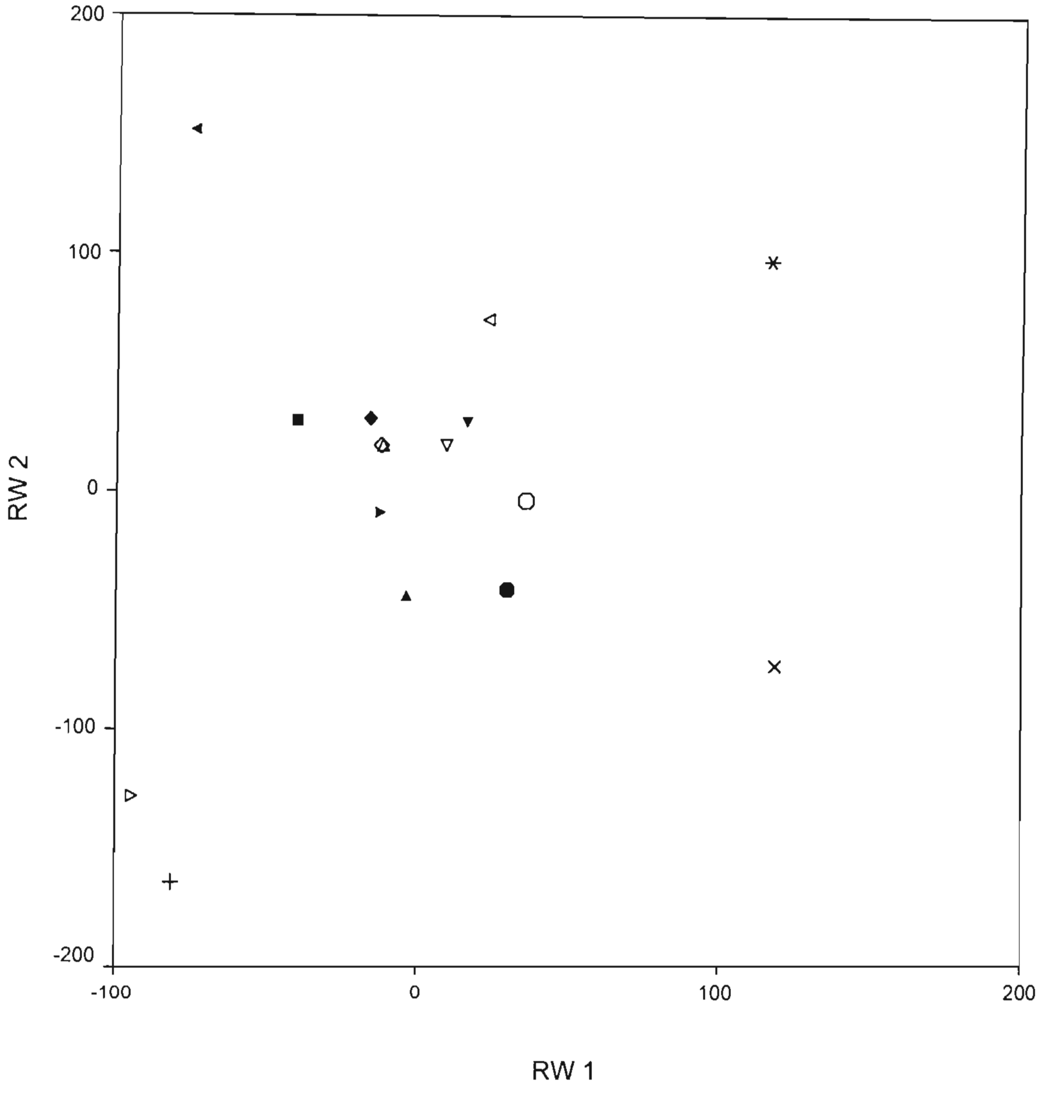


Figure 3.11 Plot of relative warps (RW) 1 and 2 of ventral skull shape of the means of 16 Vespertilionidae species from southern Africa. Species codes: *H. anchietae* = ○, *N. capensis* = ◇, *N.* cf. *melckorum* = △, *N. schlieffenii* = ▽, *E. hottentotus* = ◁, *L. botswanae* = ▷, *L. namibensis* = +, *M. schreibersii* = ×, *M. tricolor* = ∗, *N. africanus* = ●, *N. rendalli* = ■, *P. hesperidus* = ◆, *N. rueppellii* = ▲, *P. rusticus* = ▼, *S. dinganii* = ◀, *N. zuluensis* = ▶.

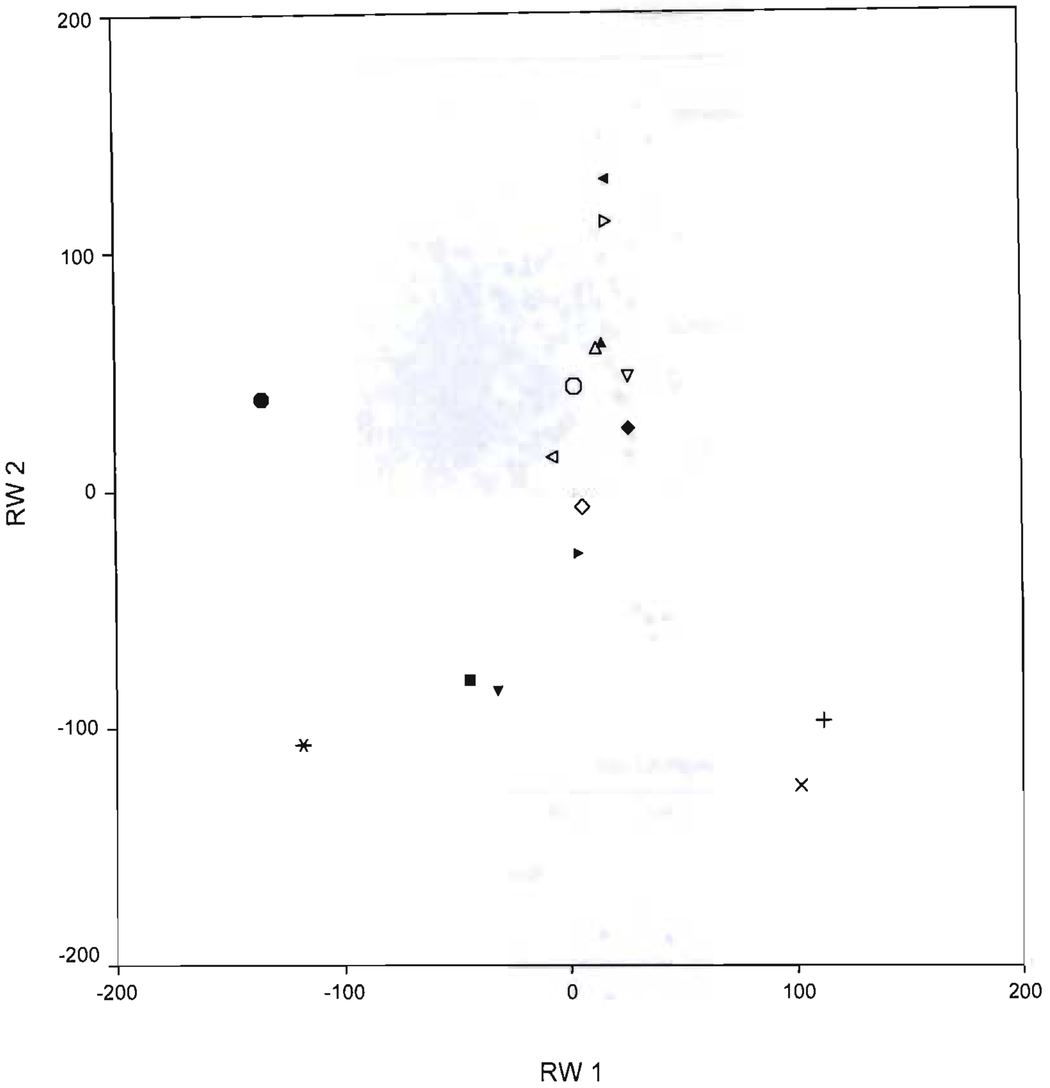


Figure 3.12 Plot of relative warps (RW) 1 and 2 of dorsal skull shape of the means of 16 Vespertilionidae species from southern Africa. Species codes: *E. hottentotus* = ○, *H. anchietae* = ◇, *N. capensis* = △, *N.* cf. *melckorum* = ▽, *P. hesperidus* = ◁, *M. tricolor* = ▷, *L. botswanae* = +, *L. namibensis* = ×, *M. schreibersii* = *, *N. rendalli* = ●, *N. africanus* = ■, *N. schlieffenii* = ◆, *N. zuluensis* = ▲, *N. rueppellii* = ▼, *P. rusticus* = ◀, *S. dinganii* = ▶.

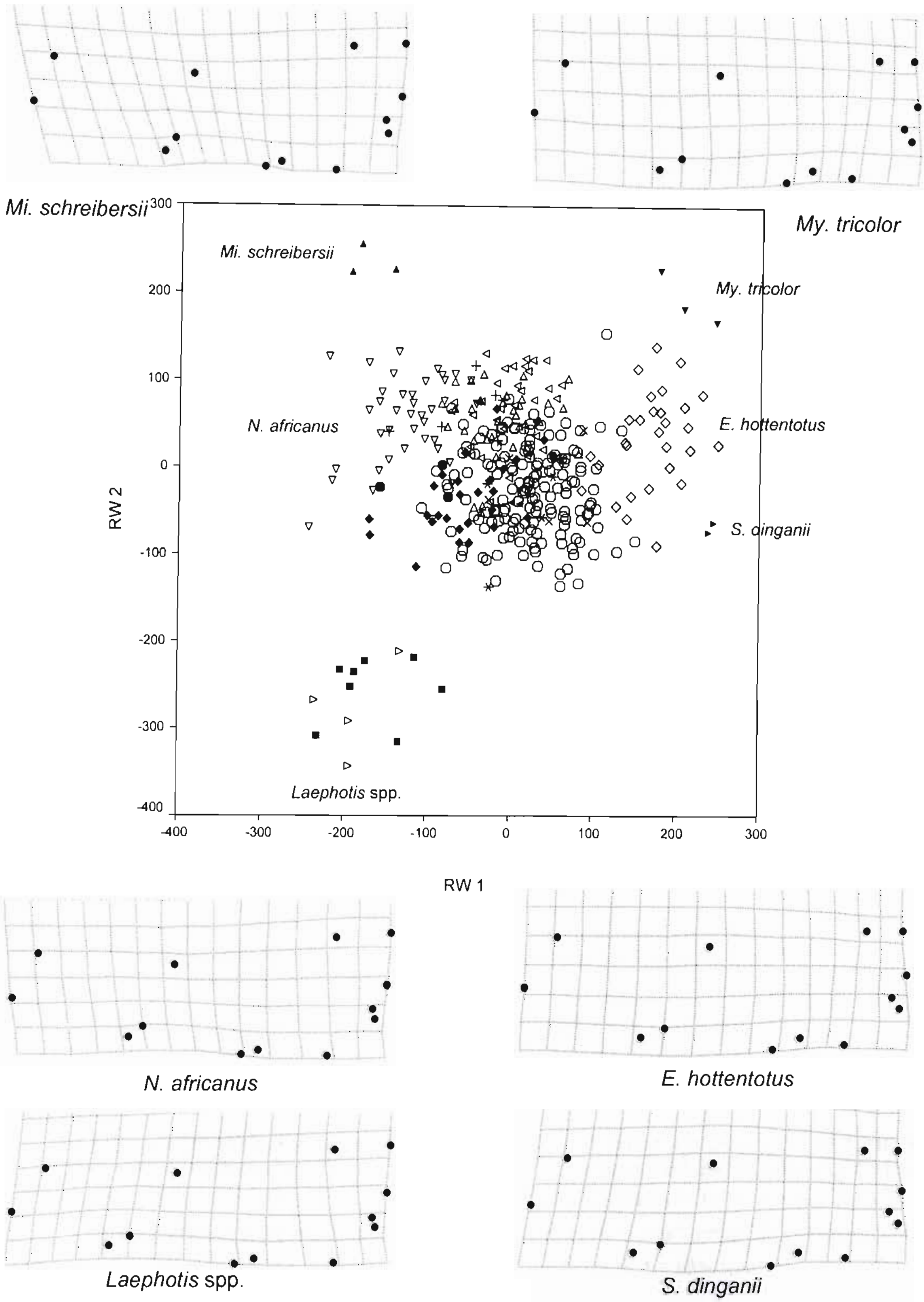


Figure 3.13 Plot of relative warps (RW) 1 and 2 of ventral skull shape of all specimens of 16 Vespertilionidae species from southern Africa, with thin plate splines representing the deformation of dorsal shape implied by variation along the first and second principal component axes. Species codes: *N. capensis* = ○, *E. hottentotus* = ◇, *P. hesperidus* = △, *N. africanus* = ▽, *P. rusticus* = ◁, *N. zuluensis* = ▷, *H. anchietae* = +, *N.* cf. *melckorum* = ×, *N. rendalli* = ∗, *N. rueppellii* = •, *L. botswanae* = ■, *L. namibensis* = ◆, *M. schreibersii* = ▲, *M. tricolor* = ▼, *N. schlieffenii* = ◀, *S. dinganii* = ▶.

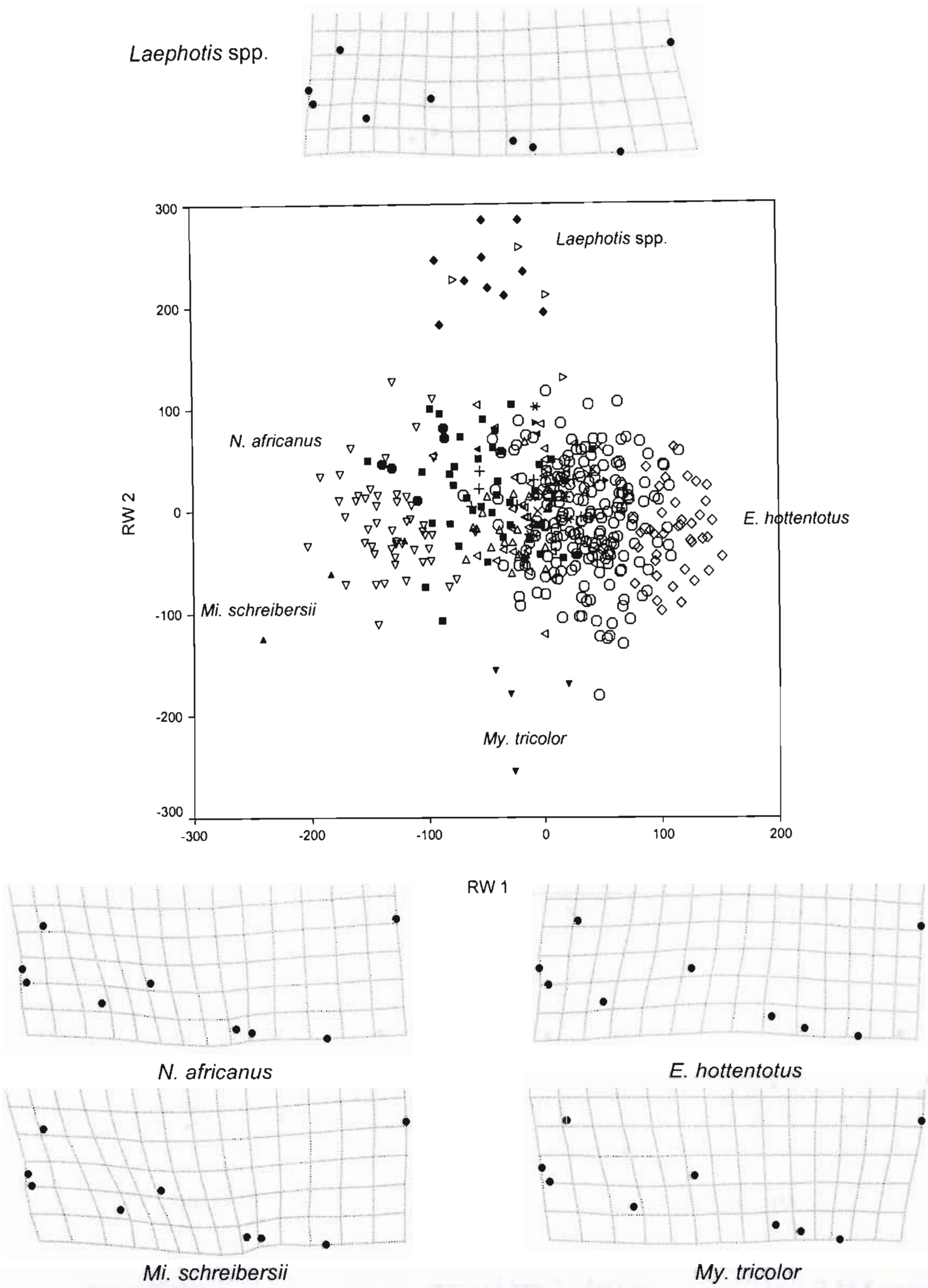


Figure 3.14 Plot of relative warps 1 and 2 (RW) of dorsal skull shape of all specimens of 16 Vespertilionidae species from southern Africa, with thin plate splines representing the deformation of dorsal shape implied by variation along the first and second principal component axes. Species codes: *N. capensis* = ○, *E. hottentotus* = ◇, *P. hesperidus* = △, *N. africanus* = ▽, *P. rusticus* = ◁, *N. zuluensis* = ▷, *H. anchietae* = +, *N.* cf. *melckorum* = ×, *N. rendalli* = ∗, *N. rueppellii* = ●, *L. botswanae* = ■, *L. namibensis* = ◆, *M. schreibersii* = ▲, *M. tricolor* = ▼, *N. schlieffenii* = ◀, *S. dinganii* = ▶.

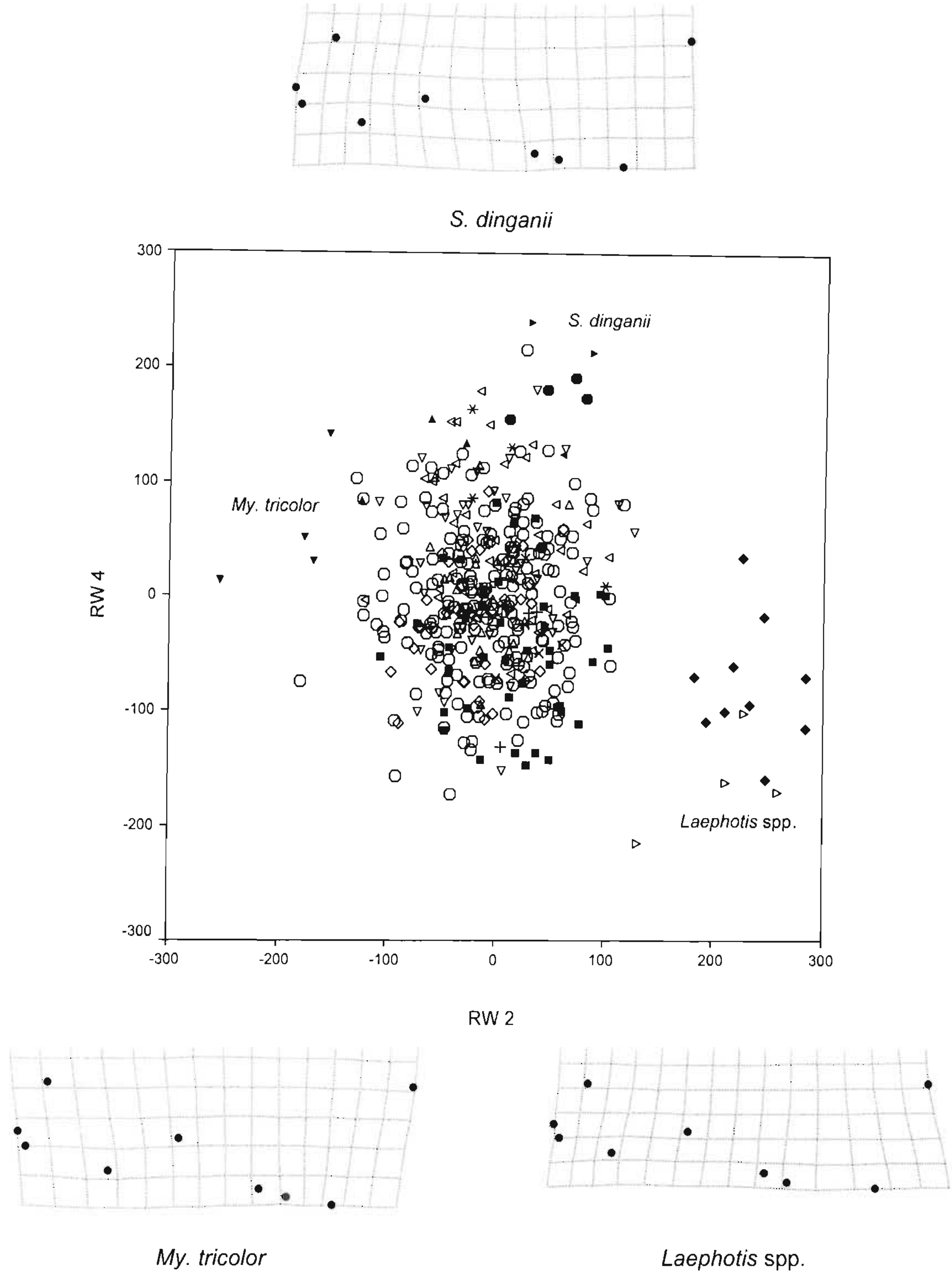


Figure 3.15 Plot of relative warps (RW) 2 and 4 of dorsal skull shape of 16 Vespertilionidae species from southern Africa with associated thin plate splines, showing the separation of *Myotis tricolor*, *Laephotis* and *Scotophilus dinganii*. Species codes: *N. capensis* = ○, *E. hottentotus* = ◇, *P. hesperidus* = △, *N. africanus* = ▽, *P. rusticus* = ◁, *N. zuluensis* = ▷, *H. anchietae* = +, *N.* cf. *melckorum* = ×, *N. rendalli* = *, *N. rueppellii* = ●, *L. botswanae* = ■, *L. namibensis* = ◆, *M. schreibersii* = ▲, *M. tricolor* = ▼, *N. schlieffenii* = ◀, *S. dinganii* = ▶.

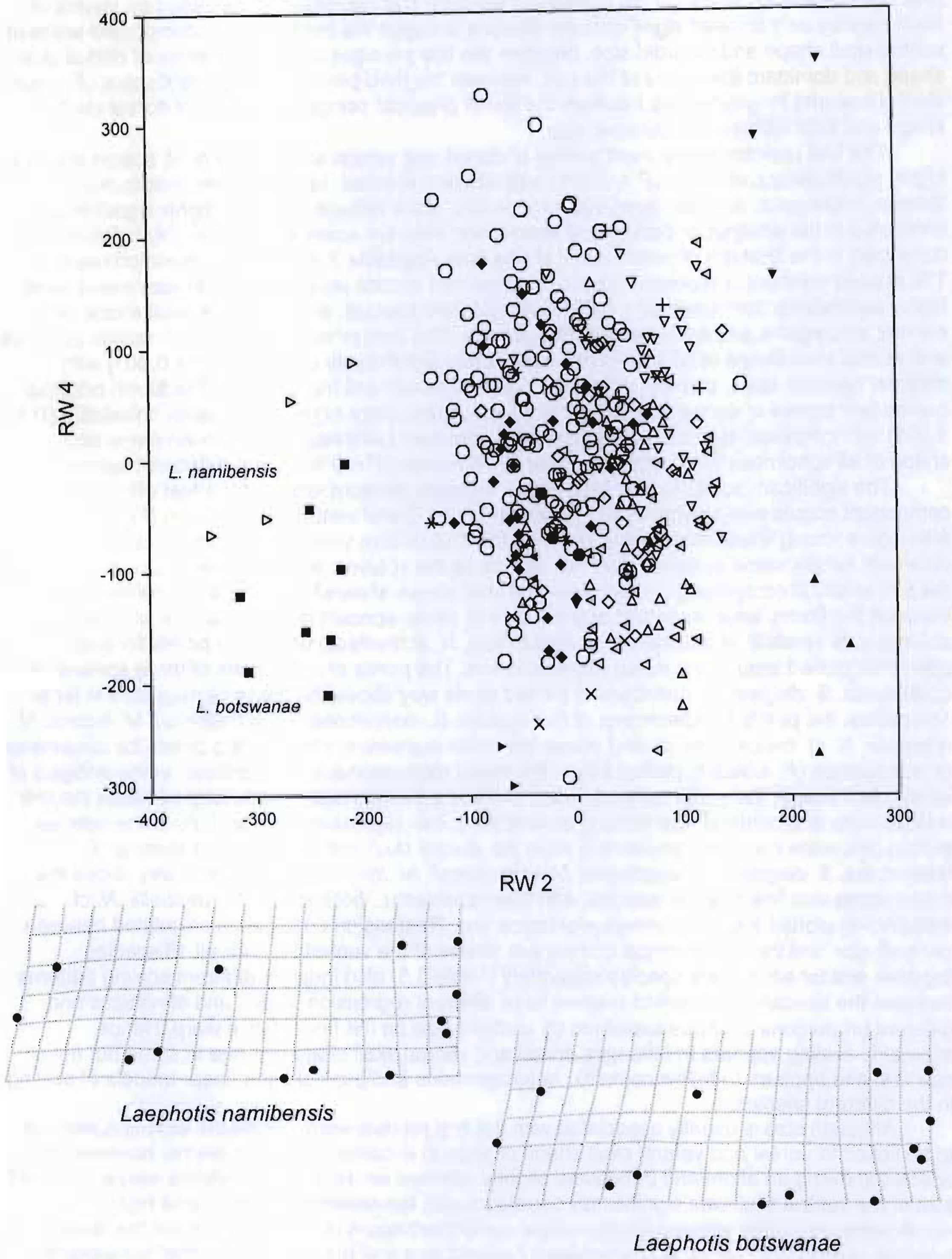


Figure 3.16 Plot of relative warps (RW) 2 and 4 of ventral skull shape of 16 Vespertilionidae species from southern Africa with associated thin plate splines, showing the separation on RW4 between *Laephotis namibensis* and *L. botswanae*. Species codes: *N. capensis* = ○, *E. hottentotus* = ◇, *P. hesperidus* = △, *N. africanus* = ▽, *P. rusticus* = ◁, *N. zuluensis* = ▷, *H. anchietae* = +, *N.* cf. *melckorum* = ×, *N. rendalli* = ∗, *N. rueppellii* = ●, *L. botswanae* = ■, *L. namibensis* = ◆, *M. schreibersii* = ▲, *M. tricolor* = ▼, *N. schlieffenii* = ◀, *S. dinganii* = ▶.

and ventral shape of the skull based on the means of each species and the five different variables (see Appendix 3.3 E and F for full correlation results). The correlation tests based on means of each species only showed significant correlations between the third principal component score of ventral skull shape and centroid size, between the first principal component score of dorsal skull shape and dominant frequency of the call, between the third principal component score of dorsal skull shape and longitude, and between the fourth principal component score of dorsal skull shape and both latitude and centroid size.

The first principal component scores of dorsal and ventral skull shape of all specimens were highly significantly correlated ($P < 0.001$) with different species, centroid sizes, longitudes, biomes, ecoregions, and dominant call frequencies, while latitude was also highly significantly correlated in the analysis of dorsal skull shape, and different sexes was also highly significantly correlated in the analysis of ventral skull shape (see Appendix 3.3 E for full correlation results). The second principal component scores of dorsal and ventral skull shape of all specimens were highly significantly correlated ($P < 0.001$) with different species, and in ventral skull shape only biomes, ecoregions and dominant call frequencies. The third principal component scores of dorsal and ventral skull shape of all specimens were highly significantly correlated ($P < 0.001$) with different centroid sizes, biomes, ecoregions, and dominant call frequencies. The fourth principal component scores of dorsal skull shape of all specimens were highly significantly correlated ($P < 0.001$) with longitude, biomes, ecoregions, and dominant call frequencies, while ventral skull shape of all specimens was highly significantly correlated ($P < 0.001$) with different species.

The significant correlation in skull shape between centroid size and the first principal component scores was similar for both dorsal (Fig. 3.17) and ventral skull shapes (Fig. 3.18). Although a strong linear relationship between the first relative warp and centroid size was observed across some species, it did not include all the species. A plot between centroid size and the first principal component scores of ventral skull shape showed a strong linear relationship between the first relative warp and centroid size in seven species (*N. capensis*, *N. africanus*, *N. zuluensis*, *N. rendalli*, *H. anchietae*, *P. hesperidus*, *N. schlieffenii*) where the points for each specimen plotted around the mean regression line. The points of specimens of three species (*E. hottentotus*, *S. dinganii*, *L. namibensis*) plotted some way above the mean regression line for all 16 species, the points for specimens of five species (*L. botswanae*, *M. schreibersii*, *M. tricolor*, *N. rueppellii*, *N.* cf. *melckorum*) plotted above the mean regression line, and the points for specimens of one species (*P. rusticus*) plotted below the mean regression line (*P. rusticus*). In the analysis of dorsal skull shape, the same seven species showed a strong linear relationship between the first relative warp and centroid size plotting around the mean regression line, and the same species plotted below the mean regression line as in the ventral skull shape. While five species (*E. hottentotus*, *S. dinganii*, *L. namibensis*, *M. schreibersii*, *M. tricolor*) plotted some way above the mean regression line of all 16 species, and three species (*L. botswanae*, *N. rueppellii*, *N.* cf. *melckorum*) plotted above the mean regression line. Regression coefficients calculated between centroid size and the first principal component scores of the ventral skull for all 16 species together and for each of six species separately (Table 3.5) also indicate different scaling patterns between the species, as different species have different regression slopes and elevations and different proportions of shape explained by centroid size on the first relative warp. Hence, allometric scaling appears to influence dorsal and ventral skull shape change in some but not all species, and appears to follow complex, heterogeneous and possibly non-linear models of scaling in the different species.

Although size is usually associated with the first relative warp, allometric scaling continued to be linked to dorsal and ventral skull shape change in successive relative warps, however, the species showing an allometric trend were slightly different on the different relative warps. Centroid size of the ventral skull was significantly correlated with the second ($P < 0.01$) and highly significantly correlated with the third principal component score ($P < 0.001$), but not the fourth principal component scores. A plot between centroid size and the second principal component scores of the ventral skull of all 16 species (Fig. 3.19) showed a strong linear relationship that included 13 species, whereas the position of *E. hottentotus*, *S. dinganii*, and *M. tricolor* specimens on the plot does not show the same relationship as that shared by the other species. In a plot between centroid size and the third principal component scores of the ventral skull (Fig. 3.19) 14 of the 16 species showed a strong linear relationship, but that relationship appears to exclude *E. hottentotus* and *S. dinganii*. Centroid size of the dorsal skull was highly significantly correlated with the third ($P < 0.001$) and significantly correlated with the fourth principal component scores ($P < 0.01$), but not significantly correlated with the second principal component scores of skull shape.

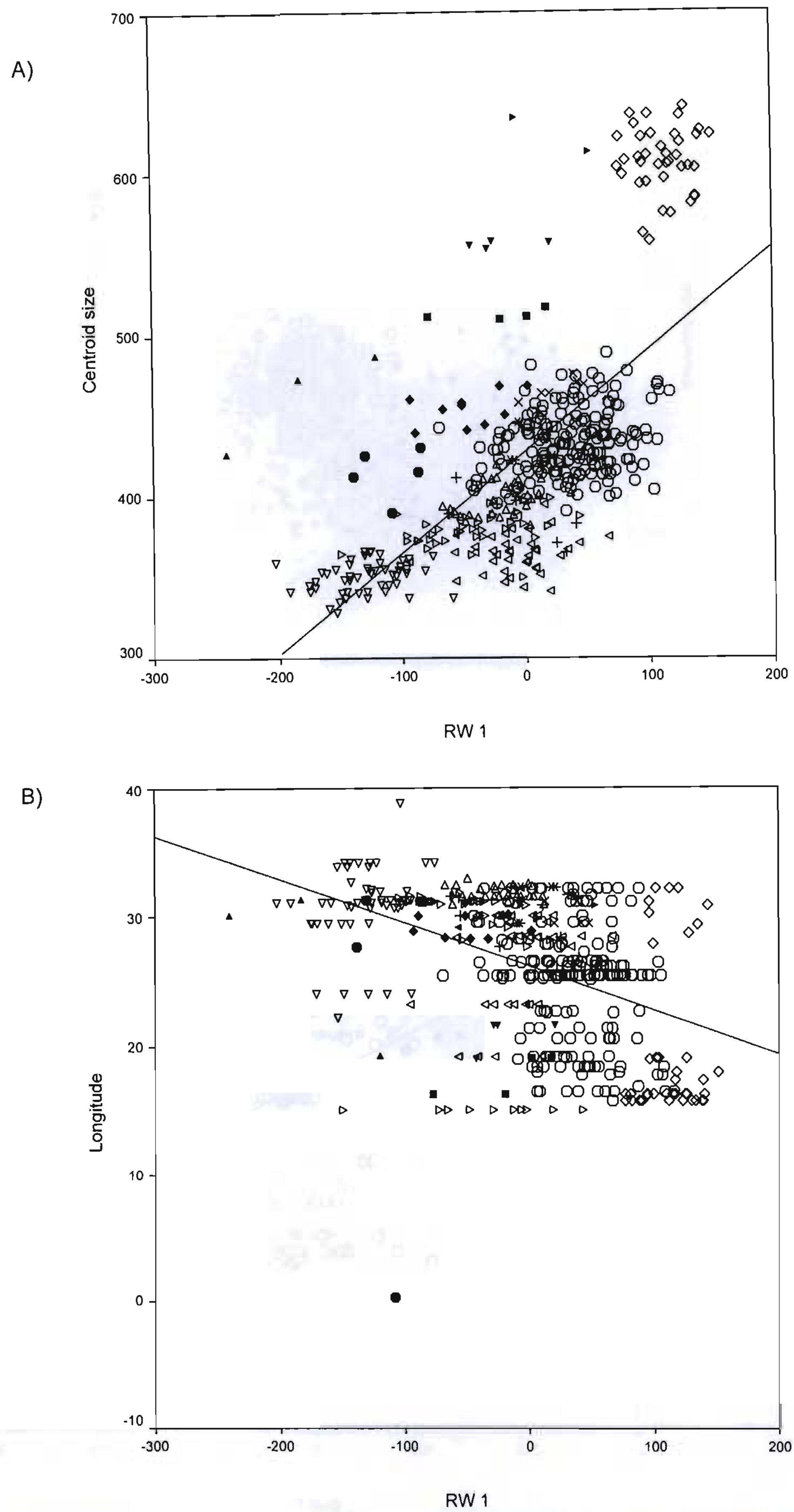


Figure 3.17 Plots of relative warp one (RW 1) with A) centroid size and B) longitude of the dorsal skull of 16 Vespertilionidae species from southern Africa. Species codes: *N. capensis* = ○, *E. hottentotus* = ◇, *P. hesperidus* = △, *N. africanus* = ▽, *P. rusticus* = ◁, *N. zuluensis* = ▷, *H. anchietae* = +, *N.* cf. *melckorum* = ×, *N. rendalli* = ∗, *N. rueppellii* = ●, *L. botswanae* = ■, *L. namibensis* = ◆, *M. schreibersii* = ▲, *M. tricolor* = ▼, *N. schlieffenii* = ◀, *S. dinganii* = ▶.

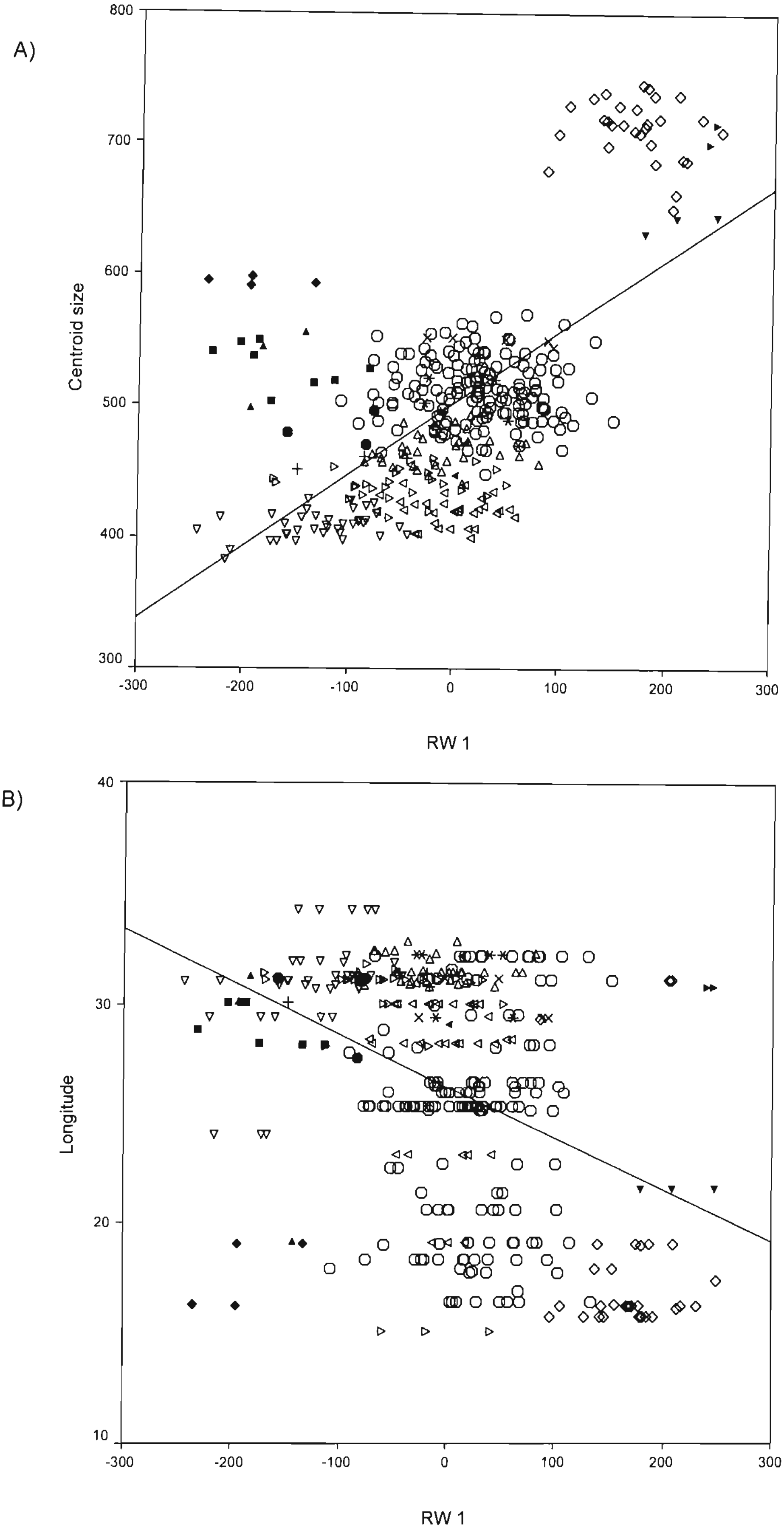


Figure 3.18 Plots of relative warp one (RW 1) with A) centroid size and B) longitude of the ventral skull of 16 Vespertilionidae species from southern Africa. Species codes: *N. capensis* = ○, *E. hottentotus* = ◇, *P. hesperidus* = △, *N. africanus* = ▽, *P. rusticus* = ◁, *N. zuluensis* = ▷, *H. anchietae* = +, *N.* cf. *melckorum* = ×, *N. rendalli* = ∗, *N. rueppellii* = ●, *L. botswanae* = ■, *L. namibensis* = ◆, *M. schreibersii* = ▲, *M. tricolor* = ▼, *N. schlieffenii* = ◀, *S. dinganii* = ▶.

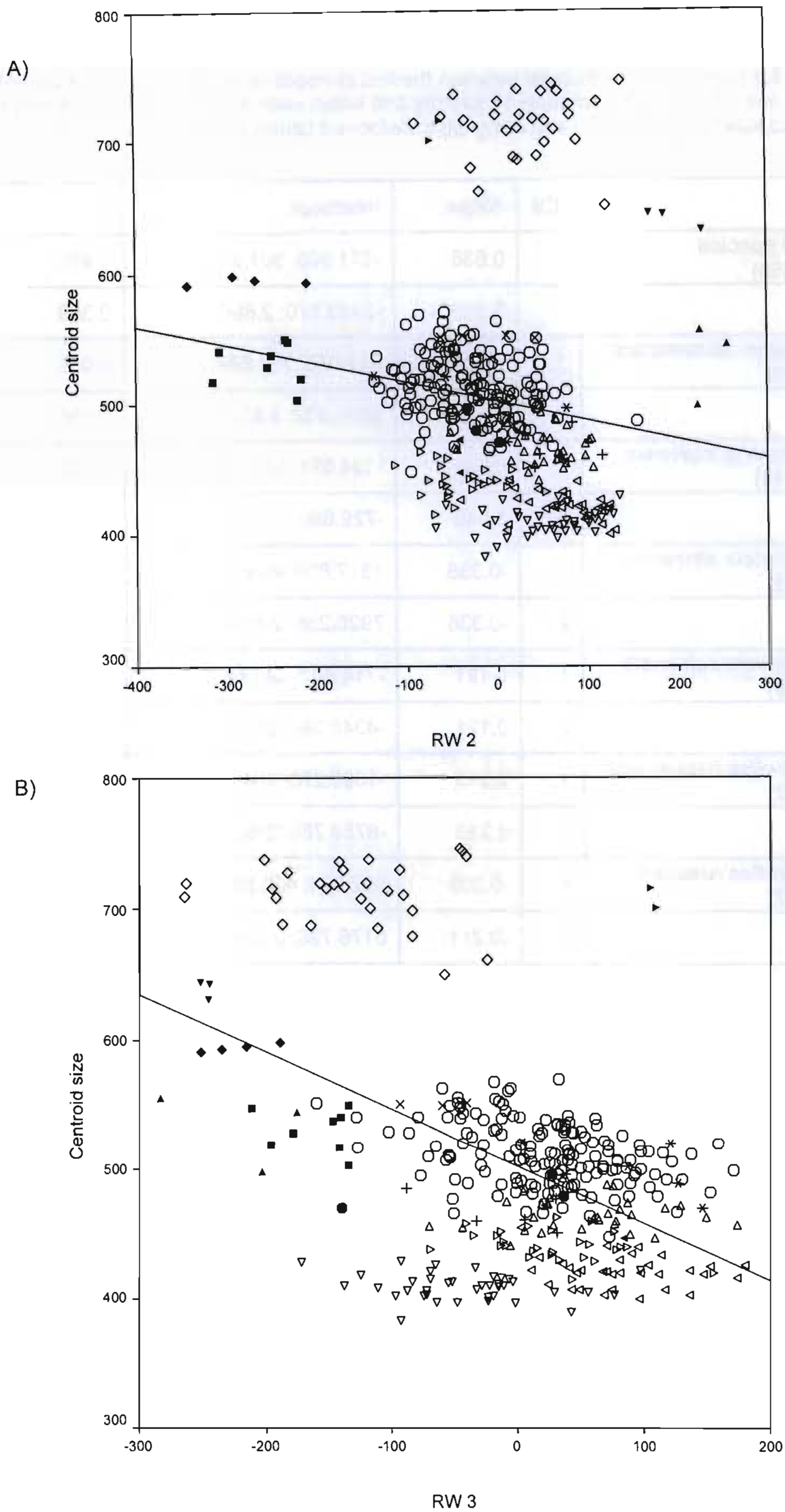


Figure 3.19 Plots of centroid size with A) relative warp two (RW 2) and B) relative warp three (RW 3) of the ventral skull of 16 Vespertilionidae species from southern Africa. Species codes: *N. capensis* = ○, *E. hottentotus* = ◇, *P. hesperidus* = △, *N. africanus* = ▽, *P. rusticus* = ◁, *N. zuluensis* = ▷, *H. anchietae* = +, *N.* cf. *melckorum* = ×, *N. rendalli* = ∗, *N. rueppellii* = ●, *L. botswanae* = ■, *L. namibensis* = ◆, *M. schreibersii* = ▲, *M. tricolor* = ▼, *N. schlieffenii* = ◀, *S. dinganii* = ▶.

Table 3.5 Regression coefficients between the first principal component scores of ventral skull shape and centroid size across all 16 species and within each of six species, using actual centroid size (CS) values (1) and using log transformed centroid sizes (2).

	CS	Slope	Intercept	r^2
All 16 species (*n* = 359)	1	0.636	-371.908: 501.908	0.405
	2	0.632	-2469.670: 2.696	0.399
***Eptesicus hottentotus* (*n* = 29)**	1	-0.236	941.055: 712.084	0.056
	2	-0.236	6084.532: 2.852	0.056
***Neoromicia capensis* (*n* = 158)**	1	0.049	-124.621: 511.726	0.002
	2	0.046	-729.690: 2.709	0.002
***Neoromicia africanus* (*n* = 39)**	1	-0.336	1317.809: 409.677	0.113
	2	-0.336	7928.236: 2.612	0.113
***Neoromicia zuluensis* (*n* = 28)**	1	0.121	-714.602: 441.542	0.015
	2	0.121	-4348.280: 2.645	0.015
***Pipistrellus hesperidus* (*n* = 32)**	1	0.210	-1098.276: 464.671	0.044
	2	0.210	-6759.286: 2.667	0.044
***Pipistrellus rusticus* (*n* = 32)**	1	-0.206	992.974: 420.988	0.043
	2	-0.211	6176.726: 2.624	0.045

A plot between centroid size and the third principal component scores of the dorsal skull (Fig. 3.20) showed the same results as in the ventral skull between centroid size and the third principal component scores. A plot between centroid size and the fourth principal component scores of dorsal skull shape (Fig. 3.20) showed the same results as in the ventral skull between centroid size and the second principal component scores of all 16 species.

Investigation of the highly significant correlation ($P < 0.001$) between the first principal component scores of dorsal (Fig. 3.17) and ventral (Fig. 3.18) skull shape and longitude, identified that more specimens of species with their localities at low longitudes were associated with negative principal component one scores and visa-versa. However, in ventral skull shape, exceptions are *S. dinganii, M. tricolor*, and two specimens of *E. hottentotus* from Pafuri (TM36879, TM38167) which plot on the more positive side of the first relative warp than other specimens from the same longitude, while *L. namibensis,* most specimens of *L. botswanae*, and various specimens of *N. africanus* from Pafuri and Sentinal Ranch in South Africa and from Zambia plot further along on the more negative side of the first relative warp than other specimens from the same longitude. Exceptions to the significant correlation in dorsal skull shape are *M. schreibersii* (DM6897) from Hella-Hella in South Africa, *N. zuluensis* (NMZ64058) from Gobabeb in Namibia, and *N. rueppellii* (MRAC16294) from Uganda which all plot further along on the more negative side of the first relative warp than other specimens from the same longitude. Although there was a highly significant correlation ($P < 0.001$) between the first principal component scores of dorsal and ventral skull shape and both biome and ecoregion, with the exception of *N. capensis*, skull shape within a species appears to be fairly consistent irrespective of the biome and ecoregion of their origin. This correlation, like that between the first principal component score and longitude, appears to be driven by species with different skull shapes (as indicated by differences at the extremes of the first relative warp) occurring, for the most part, in different biomes and ecoregions (i.e. the difference between *E. hottentotus* and *N. africanus* and *E. hottentotus* and *P. rusticus*). In dorsal skull shape individuals of most species occupied a similar area of the first relative warp irrespective of the latitude of their origin. Hence, the highly significant correlation ($P < 0.001$) in dorsal skull shape between the first principal component scores and latitude appears to be due to more specimens of *N. zuluensis* and *P. rusticus* being associated with higher latitudes and thus the more positive side of the first relative warp, while more specimens of *N. capensis* were associated with lower latitudes and thus the more negative side of the first relative warp.

Highly significant correlations ($P < 0.001$) between the dominant frequency of the call and the principal component scores of dorsal and ventral skull shape occurred on the same principal component scores of dorsal and ventral skull shape as the significant correlations between skull shape and centroid size. Larger centroid size generally correlated with lower dominant frequency of the call and visa versa. Exceptions to the correlation of dominant call frequency with skull shape and centroid size on the first principal component score of ventral skull shape are *M. tricolor, M. schreibersii, L. botswanae, S. dinganii* and *N. rueppellii*, exceptions on the second principal component score are *M. tricolor, M. schreibersii* and *L. botswanae*, and on the third principal component score are *M. tricolor, M. schreibersii* and *N. africanus*.

In plots of the first and second relative warps (Fig. 3.13), ventral skull shape differences summarised along the first relative warp explained 19.46% of shape variation. In *S. dinganii* and *E. hottentotus,* the posterior edge of the hard palate extended further beyond the intersection of the jugal onto the maxilla and posterior palatal region was broader. The maxilla region was less laterally deflected, the anterior insertion of the zygomatic arch was broader and less laterally displaced, while the posterior insertion of the zygomatic arch was also broader but more laterally deflected, as well as being closer to the widest point of the mastoid region. The occipital condyle was further back, the opening of the foramen magnum in the anterior posterior plane was narrower, and the posterior supra-occipital bone was shorter than in *N. africanus*. On the second relative warp which explained 18.01% of ventral skull shape variation, separated *L. botswanae* and *L. namibensis*, and *M. tricolor* and *M. schreibersii* from the other species. *Laephotis botswanae* and *L. namibensis* have a shorter maxilla region, a longer hard palate, and a broader and less laterally displaced anterior insertion of the zygomatic arch. The most lateral expansion of the mastoid region is further back from the posterior insertion of the zygomatic process, and the overall skull shape is narrower than in *M. schreibersii.* The third and fourth relative warps explained 13.99% and 6.67%, respectively of shape variation, and subtle shape changes associated with these relative warps together with the second relative warps separated the two species of *Laephotis* (Fig. 3.15). *Laephotis namibensis* has a narrower nasal region particularly at

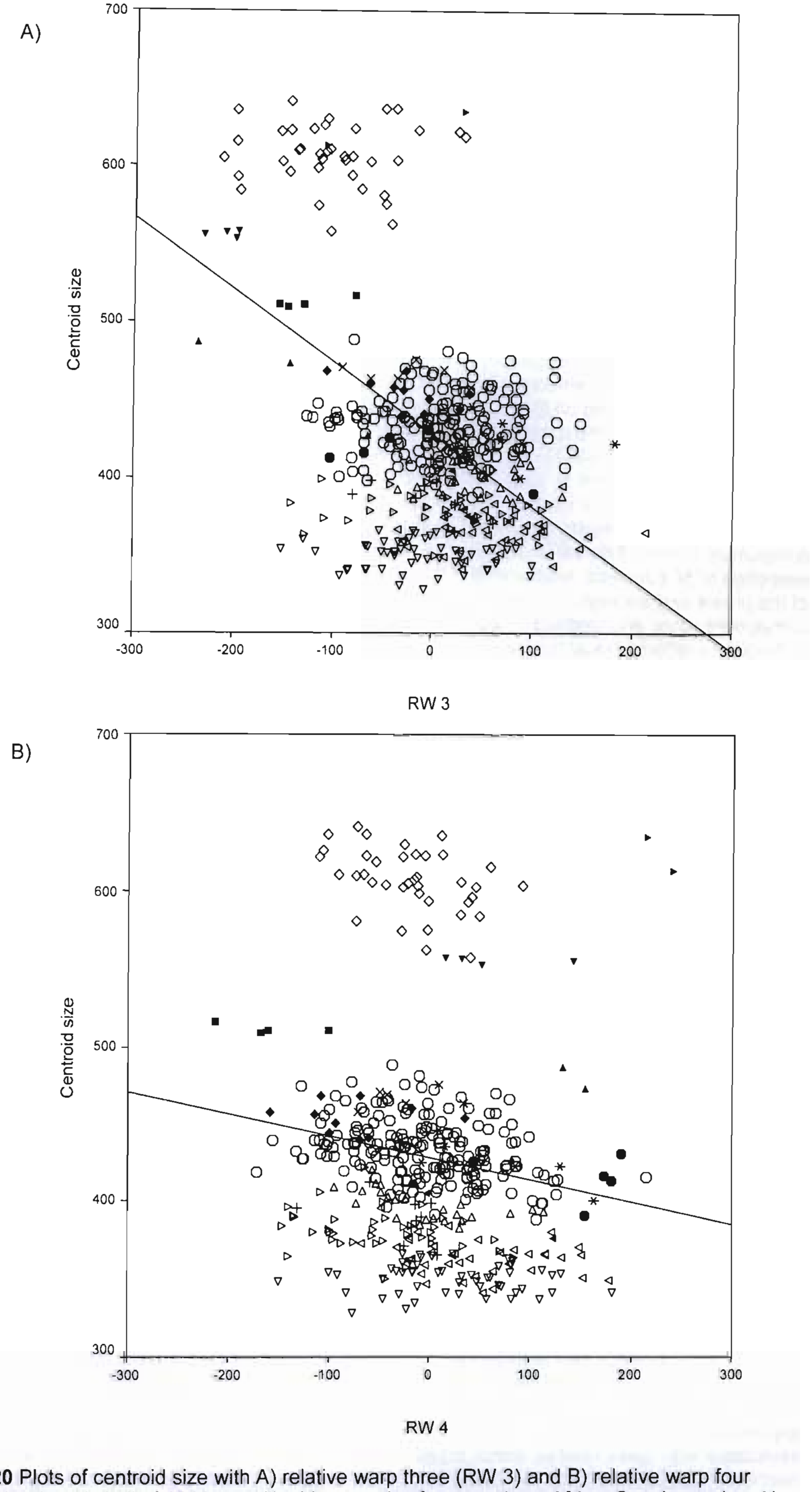


Figure 3.20 Plots of centroid size with A) relative warp three (RW 3) and B) relative warp four (RW 4) of the dorsal skull of 16 Vespertilionidae species from southern Africa. Species codes: *N. capensis* = ○, *E. hottentotus* = ◇, *P. hesperidus* = △, *N. africanus* = ▽, *P. rusticus* = ◁, *N. zuluensis* = ▷, *H. anchietae* = +, *N.* cf. *melckorum* = ×, *N. rendalli* = ∗, *N. rueppellii* = ●, *L. botswanae* = ■, *L. namibensis* = ◆, *M. schreibersii* = ▲, *M. tricolor* = ▼, *N. schlieffenii* = ◀, *S. dinganii* = ▶.

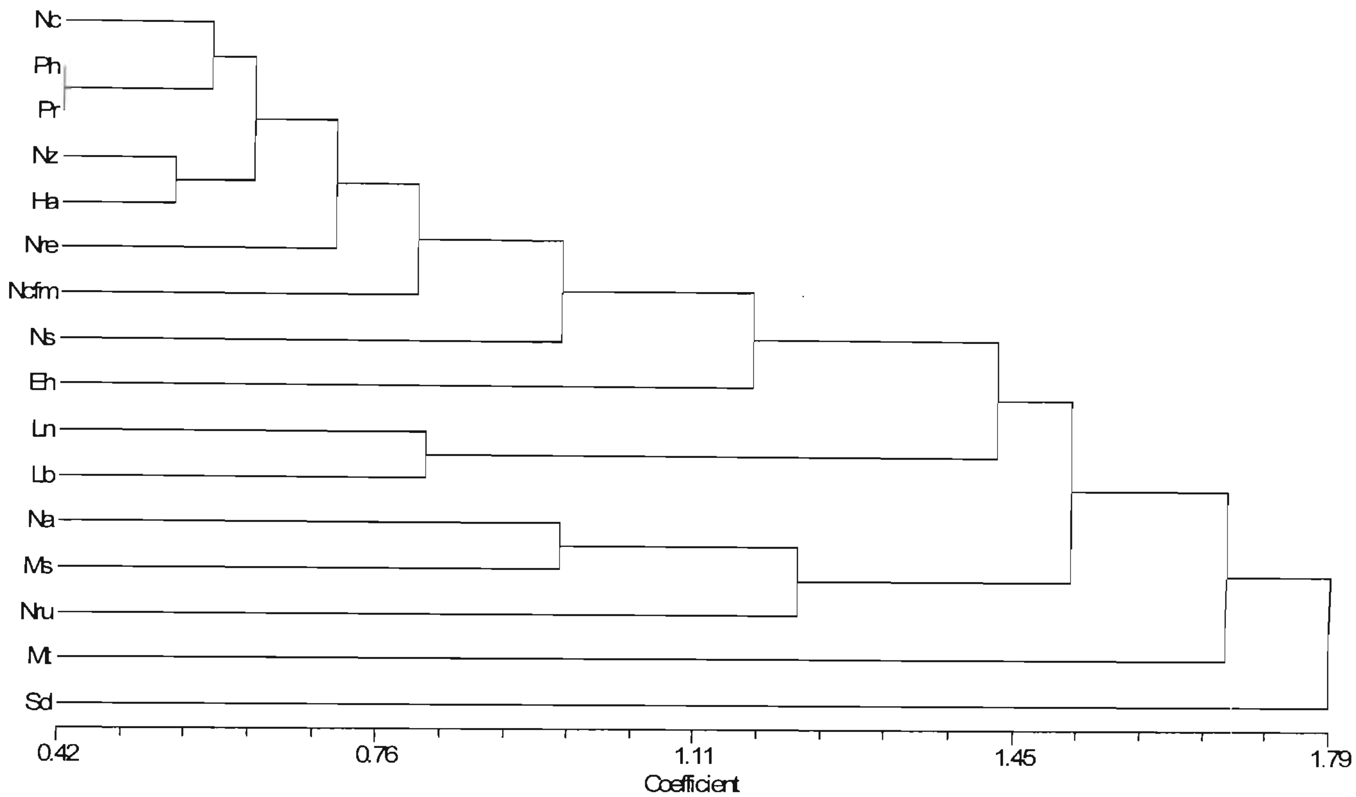
the anterior end, and shorter distances between the most lateral extension of the mastoid region and the posterior insertion of the zygomatic arch, and between the deepest indentation between the occipital condyle and the foramen magnum and the most posterior extension of the occipital condyle than in *L. botswanae*.

Although the plot of the first and second relative warps of dorsal skull shape, that explained 29.87% and 16.53% of shape variation, respectively, did not clearly distinguish between any of the 16 species the following shape differences were identifiable (Fig. 3.14). Along the first relative warp, *N. africanus* has a shallower inter-nasal opening, and a longer maxilla region in front of the anterior insertion of the zygomatic arch but a shorter maxilla and frontal region posterior to the insertion of the zygomatic arch. The posterior attachment of the zygomatic arch is narrower and more laterally displaced and also further from the widest point of the mastoid, and the posterior mid-point of the skull is further from the widest point of the mastoid than in *E. hottentotus*. Along the second relative warp, *L. botswanae* and *L. namibensis* have a narrower dorsal skull shape, a shorter snout region, and a longer distance between the widest point of the mastoid and the posterior attachment of the zygomatic arch than *M. tricolor*. The fourth relative warp that explains 10.74% of dorsal skull shape variation separates *S. dinganii* from the other taxa. In a plot of the second and fourth relative warps which separates S. *dinganii* as well as *L. botswanae* and *L. namibensis* (although both species overlap each other), thin plate splines (Fig. 3.14) indicate that in *S. dinganii,* the anterior and posterior insertions of the zygomatic arch are further back along the skull, while the deepest indentation of the inter-orbital region is further forward. In addition, the posterior insertion of the zygomatic arch is closer to the most lateral extension of the mastoid, which in turn is further from the most posterior extension of the skull than in *L. botswanae* and *L. namibensis*.

The results of multiple regression analyses between dorsal and ventral skull shape of all 16 species and centroid size were also significant (dorsal skull: Wilks lambda 0.334, $F_{(14,422)}$ = 59.971, P = 5.284E-091; ventral - Wilks lambda 0.232, $F_{(22,336)}$ = 50.542, P = 1.300E-092). The tests for common slopes indicated common slopes were sufficient for dorsal and ventral data, i.e. the species have homogenous slopes and hence the same linear model can be used for all the species (dorsal - Wilks lambda 0.582, $F_{(210,2065.7)}$ = 1.047, P = 0.312; ventral - Wilks lambda 0.423, $F_{(330,\ 3853.2)}$ = 0.837, P = 0.983). However, shape differences were significantly different between the species when size was held constant, as the slope intercepts were not homogenous (dorsal - Wilks lambda 0.017, $F_{(210,4220.2)}$ = 9.771, P = 1.929E-233; ventral - Wilks lambda 0.002, $F_{(330,4039.7)}$ = 7.772, P = 7.395E-248). Even tests for common slopes run on smaller subsets of ten (*E. hottentotus*, *N. capensis, N. rueppellii*, *N. africanus*, *N.* cf. *melckorum*, *N. rendalli*, *N. zuluensis*, *H. anchietae, P. hesperidus*, and *P. rusticus*) and eight species (*N. capensis, N. rueppellii*, *N.* cf. *melckorum*, *N. rendalli*, *N. zuluensis*, *H. anchietae, P. hesperidus*, and *P. rusticus*), gave similar results and indicated shape differences existed between species and were not only due to allometric projections of species size difference (see Appendix 3.5 for the full common slope results). This, even though in the analysis of ten species these were the same species that formed the overlapping group in the relative warp plots in which allometric scaling seems most apparent, while in the analysis of eight species, the largest and smallest of the species were removed.

As with the relative warp analyses, the UPGMA dendrograms of dorsal and ventral skull shapes of the means of the different species were similar (Fig. 3.21). Both phenograms showed the basal separation of *M. schreibersii*, *M. tricolor* (although this species formed a sister taxa with *M. schreibersii* in the phenogram of dorsal skull shape), *S. dinganii*, *L. botswanae* and *L. namibensis* (with the latter two species clustering as sister taxa), whereas thereafter the phenograms were different. In the phenogram based on dorsal skull shape, *N. rueppellii* and *N. africanus* clustered together, followed by successive inter-nested clustering of *E. hottentotus*, *N. schlieffenii*, *N.* cf. *melckorum* and *N. rendalli*, and two clusters of *P. rusticus*, *P. hesperidus* and *N. capensis*, and *N. zuluensis* and *H. anchietae*. In the phenogram based on ventral skull shape *E. hottentotus* is basal to the group of *Neoromicia*, *Pipistrellus*, *Hypsugo* and *Nycticeinops* species, in which all the species with the exception of *N.* cf. *melckorum* and *N. schlieffenii* form successively inter-nested sister taxa clusters, *N. africanus* with *H. anchietae*, *N. zuluensis* with *N. rueppellii*, *N. capensis* with N. *rendalli*, and *P. hesperidus* with *P. rusticus*. In the UPGMA of all specimens of all 16 species of ventral skull shape (dendrogram not shown), as with the relative warp analyses, only *M. tricolor*, *M. schreibersii* and *S. dinganii* clustered as separate species, while the specimens of *L. botswanae* and *L. namibensis* were mixed together in a cluster of their own. The similarity in skull shape of the remaining species was evident in the mixed clusters of

A)



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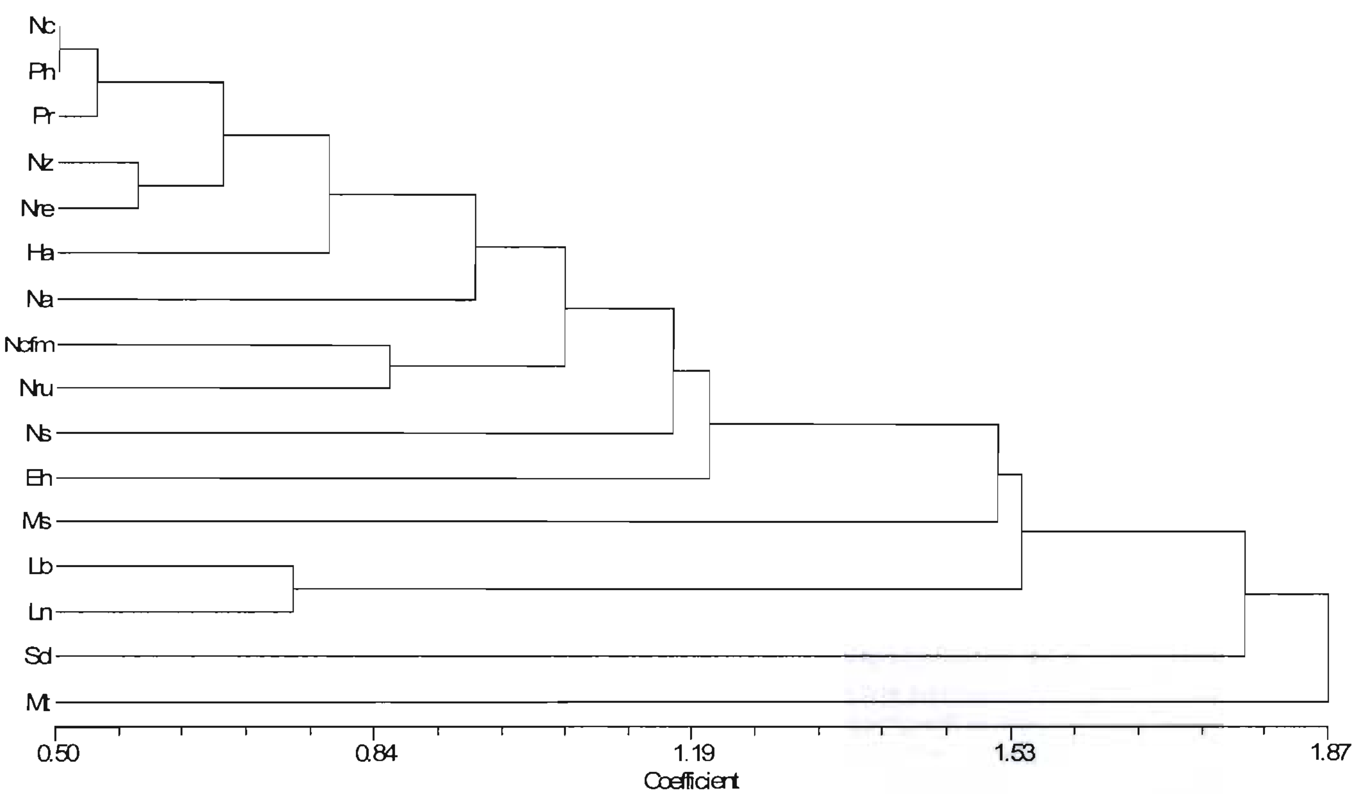


Figure 3.21 Dendrograms based on UPGMA cluster analysis of A) dorsal and B) ventral skull shape of the mean of 16 Vespertilionidae species from southern Africa, based on a clustering of a matrix of taxonomic distances computed from partial warp scores. Species codes: Eh = *E. hottentotus*, Ncfm = *N.* cf. *melckorum*, Nc = *N. capensis*, Nre = *N. rendalli*, Nru = *N. rueppellii*, Ph = *P. hesperidus*, Ha = *H. anchietae*, Nz = *N. zuluensis*, Pr = *P. rusticus*, Na = *N. africanus*, Sd = *S. dinganii*, Mt = *M. tricolor*, Ln = *L. namibensis*, Ms = *M. schreibersii*, Lb = *L. botswanae*, Ns = *N. schlieffenii*.

these species throughout the phenogram. Besides a cluster of *E. hottentotus* specimens, six other specimens of *E. hottentotus* were distributed in different clusters with *N. capensis* and *P. hesperidus*. And, while there were clusters of predominantly *N. africanus*, *P. rusticus*, *N. zuluensis*, *N. capensis* and *N.* cf. *melckorum*, all of these also included specimens of other species, and specimens of these taxa were also found throughout the phenogram clustering with different species.

The following observations were made investigating, within the UPGMA of ventral skull shape of all specimens, the position of *N. capensis* specimens that were outliers in the intra-specific analysis of ventral skull centroid size and shape. The two larger specimens of *N. capensis* from Pafuri in the Kruger National Park (TM37811 and TM34240) clustered together with 17 specimens of *N. capensis* (two of which were also outliers on centroid size, TM32547 a smaller male from Rheinvels, and TM32657 a larger female from Swartkop), one specimen of *N. zuluensis*, and all five *N.* cf. *melckorum* specimens. The other outlying specimens, including the other larger specimen of *N. capensis* from Pafuri (TM34185), were scattered throughout the phenogram.

To identify whether the species of *L. botswanae*, *L. namibensis*, *M. tricolor*, *N. schlieffenii*, *S. dinganii*, and *M. schreibersii*, which were distinguishable on dorsal and ventral skull shape (with the exception of *N. schlieffenii*), were obscuring possible differences among the overlapping group of species of *Eptesicus*, *Pipistrellus* and *Neoromicia* additional tests were run with only the species of *Eptesicus*, *Pipistrellus* and *Neoromicia* (i.e. ten species). The relative warp analysis of dorsal and ventral skull shape of all specimens did not distinguish clear and significant differences between the species. Although *E. hottentotus* and *N. africanus* plotted at either ends of the first relative warp (which explained 33.13 and 21.16% of dorsal and ventral shape variation, respectively) were almost separated, all the species formed a single cluster within which they were arranged largely by size. The correlation tests for both dorsal and ventral skull shape (see Appendix 3.3 G for full correlation test results) continued to show significant correlations between skull shape and different species, centroid size, latitude, longitude and dominant call frequency.

Further tests were run on an even more reduced set of species of *Eptesicus*, *Pipistrellus* and *Neoromicia* excluding the largest (*E. hottentotus*) and smallest (*P. africanus*) species (i.e. eight species) to identify whether size was obscuring subtle shape differences among the remaining species. Nevertheless, the relative warp analyses continued to show no difference between the species in dorsal or ventral skull shape, as the species of *Neoromicia*, *Pipistrellus* and *Eptesicus* still formed a single overlapping group. The correlation tests for both dorsal and ventral skull shape (see Appendix 3.3 H for full correlation test results) still showed significant correlations between skull shape and different species, centroid size, latitude, longitude and dominant call frequency.

3.4 DISCUSSION

The limitation of the geometric morphometric technique to capture and reconstruct form is in the placement of landmarks, hence the shapes and centroid sizes described are a reflection of the relative positions of the landmarks, which should be chosen carefully to relate to biologically meaningful points and sufficiently capture the shape of the structure of interest. The assignment of homologous landmarks to both the dorsal and ventral surface of the vesper bat skulls proved difficult due to the lack of sutures and defining features, which meant the landmarks chosen to capture dorsal and ventral skull shape were mostly placed along the edge of the skull at points of most concave or convex curvature, and hence the shapes captured for the dorsal and ventral aspects were similar. A similar result was found in an analysis of mandibles of yellow-bellied marmots (Cardini and Tongiorgi, 2003).

Since variation in intra-specific patterns of morphology may change behavior, it was useful to have tested intra-specific variation (Swartz *et al.*, 2003), albeit intra-specific tests without the affect of geographic variation, sex and tooth wear class was only tested in a single population of one species. The lack (for the most part) of significant variation in centroid size and shape between different tooth wear classes and the sexes within this population guided the decision to combine tooth wear classes and sexes within species. However, this extrapolation from one population in one species should be more widely tested in the future as sufficient specimens become available.

It is recognised that body size dictates most aspects of organismal ecology and physiology. In bats, body size influences virtually all aspects of their biology including flight behaviour, echolocation call structure, diet selection, roosting and reproductive behaviour, and physiology

(Simmons and Conway, 2003; Swartz *et al.*, 2003). Understanding patterns of structure and behaviour in relation to body size are thus central to an overall understanding of ecomorphology (Swartz *et al.*, 2003). In this analysis, centroid size of the skull was used as a measure of geometric size. Of the six species in which centroid size was analysed, four species (*N. capensis*, *N. africanus*, *N. zuluensis* and *P. hesperidus*) showed significant sexual dimorphism, while two did not (*E. hottentotus* and *P. rusticus*). In each case of significant sexual dimorphism of centroid size, females were slightly larger than males and the difference in sexually dimorphic size ranged from 2.27% to 4.24%. The percentages that the female skulls were larger than the male skulls were similar to those found in an analysis of *E. fuscus* in America where sexual differences ranged from 1.3 - 3.8% (Burnett, 1983), and in an analysis of plecotine bats where the difference was small and only exceeded 2.3% in one case, where female *Otonycteris hemprichi* were 4.4% larger than males (Bogdanowicz and Owen, 1996). Sexual dimorphism with females being larger than males has been recorded in a number of vespertilionid species occurring in North and South America (Findlay & Traut, 1970; Myers, 1978; Williams and Findlay, 1979) and Australia (Carpenter, McKean and Richards, 1978; Kitchener, Caputi & Jones, 1986; Kitchener, Jones & Caputi, 1987; Kitchener and Caputi, 1985).

Although possible reasons why vespertilionid females are larger than males were not tested in this study, various explanations have been suggested to try and explain vespertilionid sexual dimorphism. Ralls (1976) gave the following explanations to support his suggestions that larger size of the female may be an ecological response to optimising the efficiency of motherhood. A larger mother may be more able to produce a greater number of larger offspring with greater chances of survival, by providing more or better milk, and she may be better at such aspects of maternal care such as carrying or defending her baby. Williams and Findlay (1979) discounted Ralls' (1976) big mother hypothesis, suggesting the reasons were not an inherent advantage to variation in size *per se*. However, both Myers (1978) and Williams and Findlay (1979) explored more extensively Ralls' (1976) suggestions that factors associated with the female reproductive process, such as the size of the newborn, the energetic demands of pregnancy and lactation would be powerful determinants of female size. Myers (1978) suggested the advantages of larger size of the female (in relation to the extra mass that females carry during pregnancy and lactation), was a reduction in the proportionate load of the foetus, a reduction of the relative cost of producing milk, and an increase in the quantity of ingested insects a female can carry. Williams and Findlay (1979) suggested increased energy demands during pregnancy could be the primary factors in the selection of larger size in females, since larger females can maintain homoeothermy and hence the timing of the birth more efficiently, can store more fat, and have a greater array of prey available to them. Although, Williams and Findlay (1979) also considered the possibilities of differential niche utilisation, differential wing loading, and differential thermoregulation. Williams and Findlay (1979) also suggested increased weight loading of pregnant females was probably important in the selection of larger size in females but this was not supported by their data. Unlike Myers (1978) and Burnett (1983), Williams and Findlay (1979) did not find a significant correlation between the number of young per pregnancy and the degree of dimorphism. Burnett (1983) found that larger female size in *E. fuscus* correlated positively with moisture and negatively with temperature, and hence that the degree and direction of dimorphism were geographically variable. Although Williams and Findlay (1979) dismissed the wing-loading and thermoregulation hypotheses, Burnett's (1983) results encouraged further investigation of these hypotheses. Meanwhile, the causes of vespertilionid sexual dimorphism remain unresolved.

In the absence of a more suitable measure of age, tooth wear was used in this study as a relative measure of age, bearing in mind, however, the criticism that tooth wear may not only be a function of time but might also reflect differences in diet, environment, habitat and/or health (Pessoa and Dos Reis, 1991a and b). Only *E. hottentotus* showed a significant difference in dorsal and ventral skull centroid size between tooth wear classes, with specimens of tooth wear class B being significantly smaller than tooth wear classes C and D. In addition, although there was no significant difference, the dorsal and ventral skull centroid size of tooth wear class D was smaller than tooth wear class C in two out of three OTUs. Differences in the diet in *E. hottentotus* are not known for the localities sampled, but given that this difference was found across several OTUs, it suggests that in *E. hottentotus* (unlike any of the other species tested) skull centroid size increases significantly and then decreases with age. Although an increase in skull size accompanying an increase in age is not unusual, a decrease in skull size with age is more unusual. However, Kitchener and Foley (1985) recorded a decrease in post-orbital width with increasing age in a fruit bat, *Cynopterus brachyotis brachyotis*, from Bali. Even so, these results based on small sample sizes should be treated with some caution as increased samples of tooth wear classes A and B may give different results.

Significant variation in dorsal and ventral skull centroid size between different OTUs within a species occurred in three of the six species tested (*E. hottentotus*, *N. capensis*, and *P. hesperidus*), but was only highly significant in *N. capensis*. Of these three species, *N. capensis* was the only species to also show highly significant correlations between both dorsal and ventral skull centroid size and different biomes and ecoregions. In all three species, the variation in centroid size occurs across both longitude and latitude, such that centroid size generally increases southwards and the westwards (i.e. centroid size increases with increasing latitude and decreasing longitude). Of these three species, *N. capensis* was the only species to also show highly significant correlations between both dorsal and ventral skull centroid size and different biomes and ecoregions. As in the correlation with latitude and longitude, centroid size increases in the drier more southerly and westerly deserts and xeric shrublands and mediterranean forests, woodlands and shrub biomes and ecoregions with a primarily winter rainfall. And, centroid size is smaller in the more easterly and northerly occurring tropical and subtropical grasslands, savannas and shrublands, and montane grasslands and shrublands biomes and ecoregions with a primarily summer rainfall.

The most notable exception to the clinal latitudinal and longitudinal variation in centroid size in *N. capensis* were three specimens (TM34185, TM34240 and TM37811) from Kruger National Park in north-east South Africa, which have centroid sizes comparable to specimens from the most southerly and westerly localities. Since the analyses of shape were run on individual specimens, the possibility that these specimens were mis-identified was investigated in the analysis of shape (see below). In both *N. capensis* and *P. hesperidus,* the variation in centroid size is largely clinal, whereas in *E. hottentotus,* the variation in centroid size appears more as a stepped cline or the divergence of a peripheral population (Thorpe, 1983 and 1991) due to the hiatus in the distance of the smaller Pafuri-Messina OTU from the rest of the *E. hottentotus* OTUs. Whether the observed pattern in *E. hottentotus* is a true reflection of the actual pattern of variation in centroid size, given it has a patchy distribution that appears to be related to a habitat association with cliffs and crags and is poorly represented in museum collections, remains to be confirmed with additional specimens. The results also indicate that while there were significant correlations between centroid size and latitude and longitude, localities with large sample sizes show there is a considerable range in the centroid size of specimens from a single locality, as has also been shown for body size in carnivores (Rosenzweig 1968). The pattern of variation in centroid size in *E. hottentotus* does not correspond to the different subspecies described in Meester *et al.* (1986). The centroid size of specimens from localities within the range of *E. hottentotus pallidior* (Northwestern Cape and Namibia) and *E. hottentotus hottentotus* (Southern and south-western Cape) were not different. In the subspecies *E. hottentotus bensoni* (KwaZulu-Natal Drakensberg; northern Limpopo; Taung; Mozambique, Zimbabwe and Malawi), specimens from more northerly OTUs assessed (Zimbabwe and the northern parts of South Africa) were different in centroid size to specimens from more south-easterly OTUs (Lesotho and KwaZulu-Natal) within the range of *E. hottentotus bensoni*. Specimens from the more south-easterly OTUs of *E. hottentotus bensoni* (Lesotho and KwaZulu-Natal) were also similar in centroid size to the other subspecies *E. hottentotus hottentotus* and *E. hottentotus pallidior.*

According to Bergmann's (1847) rule, geographically variable homoeothermic species are usually larger in body size in cooler areas of the species range, the classic explanation for this relates to the thermoregulatory advantages associated with a lower surface to volume ratio in larger individuals (James, 1970). Another selective advantage for large size in areas of climatic seasonality is that the length of time an individual can survive without food is positively correlated with body weight (Morrison, 1960). While some studies find fairly clear evidence of this ecogeographic pattern, others indicate morphological trends result from a more complex interplay between factors, which can be further complicated by geographic variation in the extent of local, sexual and ontogenetic variation (Thorpe, 1983). This study identified a pattern of significant geographic variation in centroid size of the skull in three species that appears to follow Bergmann's rule, where with increasing winter extremes of coldness and increasing climatic variability and aridity, i.e. both increasing latitude (from north to south) and decreasing longitude (from east to west), centroid size of the skull increased.

Studies that have shown negative correlations between environmental temperature (usually associated with increasing latitude) and vespertilionid skull size following Bergmann's rule include *Scotorepens orion* and *Scotorepens sanborni* in Australia (Kitchener and Caputi, 1985), *Myotis* *daubentoni* in Europe (Bogdanowicz, 1990), *Myotis lucifugus* and *Myotis fortidens* in south-western North America (Findlay and Jones, 1967), and *Eptesicus fuscus* in North America (Burnett, 1983). Morphological clines in *Pipistrellus pipistrellus* in Great Britain were also attributed to Bergmann's rule (Stebbins, 1973), however, this was prior to the recognition of two genetic clades corresponding to two phonic types of cryptic *P. pipistrellus* (Barratt *et al.*, 1995), and no geographic variation in body size was found when the two cryptic species of *P. pipistrellus* were investigated separately, although skull morphology has not yet been tested (Barlow *et al.*, 1997). Studies of vespertilionid species that did not conform entirely to Bergmann's rule include *Pipistrellus hesperus* in North America where populations to the west of the continent followed Bergmann's rule but populations to the east of the continent did not (Findlay and Traut, 1970), as well as *Scotorepens balstoni* and *Scotorepens greyii* in Australia which became smaller with increasing winter extremes of coldness (Kitchener and Caputi, 1985). Geographic variation in size has also been correlated with inter-specific competition in several studies of bat species (Bogdanowicz, 1990), such that in areas with fewer species, there may be less competition for resources and selection would favour larger size so that species may utilise a wider range of food, whereas in species-rich areas, there is increased competition for available resources and selection would favour smaller individuals that occupy more specialised feeding niches (Grant, 1965; Heaney 1978). However, species diversity is often strongly correlated with increasing temperature and it may be that species diversity and body size are both responding independently to temperature (McNab, 1971).

The single test of intra-locality variation of dorsal and ventral skull shape in *N. capensis* from Jagersfontein in the Free State, showed no highly significant variation in skull shape due to different sex, tooth wear class or centroid size which may have confounded subsequent analyses between OTUs and other species, although the variation in dorsal and ventral skull shape was slightly significantly related to variation in centroid size and sex ($P < 0.05$). Variation in centroid size was, however, not significantly correlated with either different sex or different tooth wear class. This may indicate the use of tooth wear classes as a measure of age is flawed, or there may be indeterminate growth within tooth wear classes as was found by Pessoa and Strauss (1999) in the rodent *Proechimys albispinus*. However, this would need to be confirmed by more detailed studies with larger samples.

Intra-specific skull shape analyses of six species showed different patterns of significant correlation between changes in skull shape in relation to different factors (different OTUs, centroid size, sex, tooth wear class, latitude, longitude, biome and ecoregion) between the different species. However, only two species showed highly significant correlations. *Pipistrellus hesperidus* showed a highly significant correlation between dorsal skull shape on the second relative warp and sex. However, given the difference in sample size between males (n = 20) and females (n = 7), these results should be treated with caution as they may be different given larger sample sizes for females. Although shape variability associated with size usually occurs on the first relative warp, *Neoromicia capensis* showed highly significant correlations between dorsal skull shape on the third relative warp and centroid size, longitude, biome and ecoregion, and in ventral skull shape on the first relative warp in relation to latitude and on the second relative warp in relation to centroid size, longitude, biome and ecoregion, such that apart from a few exceptions, dorsal skull shape of *N. capensis* in southern Africa varies significantly across longitude and different biomes and ecoregions, while ventral skull shape varies significantly across longitude, latitude and different biomes and ecoregions, with allometric scaling being an underlying influence of both dorsal and ventral skull shape changes. Although multiple regression analyses identified slightly different species showing low level significant relationships between skull shape and centroid size than the correlation of centroid size with different principal component scores, both methods identified the highly significant relationship in *N. capensis*. The thin plate splines associated with the multiple regression analyses confirmed that the skull shape changes associated with change in centroid size were similar between the three species, and were consistent with cranial changes associated with allometric scaling across a variety of different mammals (Singleton, 2002).

The identification of significant patterns of skull shape and centroid size change in *N. capensis* associated with longitude, latitude, and different biomes and ecoregions is useful, given this species has been documented to show considerable variation across its extensive range which, at times, has confused the taxonomy of the species (Rosevear, 1965; Skinner and Smithers, 1990; Taylor, 2000). This probably led Roberts (1919) to erroneously describe *Eptesicus melckorum* (Rautenbach *et al.*, 1993; Kearney *et al.*, 2002) from a locality in the distribution of *N. capensis* at which point they are much larger in the cline based on latitude, longitude, and different biomes and ecoregions. Variation in skull shape and size in different biomes and ecoregions could reflect local adaptations to varying environmental conditions and hence varying prey type and availability. A similar suggestion was made to explain the strong population substructure revealed by a mitochondrial DNA analysis of *M. schreibersii* in South Africa (Miller-Butterworth *et al.* 2003), which together with wing morphological differences seemed to be associated with environmental conditions since the location of three genetic sub-populations of *M. schreibersii* corresponded to four local biomes. Miller-Butterworth *et al.* (2003) suggested this might indicate that *M. schreibersii* have adapted to local environmental conditions surrounding their roosts, which might have involved adaptation to local vegetation types, to climatic conditions and/or to regional differences in prey abundance which are closely correlated with rainfall. And, that the bats might respond to these regional differences by specialising on locally available prey, adapting their foraging strategies and/or reproductive cycles to ensure parturition coincides with the time of greatest availability of insects (Miller-Butterworth *et al.*, 2003) . Although use was made of two different scales of vegetation information at the biome and ecoregion levels, the results for each were very similar.

Inter-specific analysis of dorsal and ventral skull centroid size identified four different size groups, and of the 16 species analysed, only two species (*L. namibensis* and *M. tricolor*) showed distinct centroid size differences, whereas the other species overlapped in a large and small centroid size group. The inter-specific analysis of dorsal and ventral skull shapes captured by the landmarks were able to distinguish the majority of the additional species added to the analysis (*L. botswanae*, *L. namibensis*, *M. tricolor*, *M. schreibersii*, and *S. dinganii*), with the exception of *N. schlieffenii*. Hence, relative to each of the other species, *L. botswanae* and *L. namibensis* have narrower skulls, *M. tricolor* has a shorter cranium in the region of the mastoid, *M. schreibersii* has a longer maxillary region and the pre-orbital region is more laterally angled relative to the anterior-posterior plane of the skull, while *S. dinganii* has a skull that is longer from the region of the posterior insertion of the zygomatic arch forward, and the cranium is relatively narrow. However, the dorsal and ventral skull shapes of species in the genera *Eptesicus*, *Neoromicia*, *Hypsugo* and *Pipistrellus* (as well as *N. schlieffenii*) are similar to each another (showing morphological homoplasy) and cannot, for the most part, clearly distinguish between the different species. Although, allometric scaling (change in shape as a function of size) appears to separate large and small-bodied species, such that size increase is accompanied by positive facial allometry (characterised by increased facial prognathism) and negative neurocranial allometry. Thus, the skull of *E. hottentotus* has a broader, more forward projecting nasal region and a narrower cranial region relative to the skull of *N. africanus*. Hence, allometric size effects appear to be the major underlying influence of patterns of inter-specific skull shape variability in *E. hottentotus*, *H. anchietae*, *N. capensis*, *N.* cf. *melckorum*, *N. africanus*, *N. rendalli*, *N. zuluensis*, *N. rueppellii*, *P. hesperidus*, *P. rusticus*, and *N. schlieffenii*, and even in analyses with only these species, homoplasy and allometric effects continue to constrain species separation.

Given the extensive literature documenting similar cranial scaling patterns across varying taxonomic levels, in mammals as diverse as equids, canids, ant-eaters, carnivores, primates (Singleton, 2002), the allometric trends which appear to be a determinant of dorsal and ventral skull shape variation in *Eptesicus*, *Neoromicia*, *Hypsugo* and *Pipistrellus* reflect general patterns of mammalian cranial allometry. Allometry may be a function of evolutionary change, however such changes follow scaling rules based on mechanical principles (Swiderski, 2003). This study has shown that the pattern of allometric scaling between the different species appears to be complex and heterogeneous, and while it provides some insight into the patterns of adult inter-specific allometry, to elucidate the precise nature of the scaling relationships will require new studies including ontogenetic studies, with larger samples and possibly non-linear models.

An alternative method to the correlation of shape (i.e. relative warps) with centroid size, using multivariate analysis of covariance and hence incorporating shape variation across all the relative warps in a single analysis, gave similar results to the correlation tests. While the correlation and regression analyses of shape on individual relative warps, and in particular, the first relative warp, identified differences in allometric slope between the species, the multivariate analyses of covariance (analyzing across shape information across all relative warps) found no difference between the allometric slopes of the different species. However, when size was held constant allometrically, species shapes were significantly different, which indicated that species shape differences were not only allometric projections of species size differences. Besides the strong association of skull shape variation with centroid size and hence, allometric scaling, inter-specific dorsal and ventral skull shape variation was also significantly correlated with differences between the species, the geographic variables of latitude (dorsal skull shape only) and longitude, the environmental variables of biome and ecoregion, and the behavioural variable of dominant frequency of the call. The significant correlation of several of these variables with inter-specific skull shape over various relative warps suggests an inter-relationship between certain variables. This reflects a pitfall of correlation studies, since it is then required that functional relationships should be disentangled from the interrelated factors.

The dominant frequency of the call was not only associated with specific changes in skull shape but also skull centroid size, such that species with larger skull centroid sizes have echolocation calls with lower dominant frequencies. This corresponds with the understanding that echolocation call structure is often influenced by body size and that larger bats usually use lower frequency echolocation pulses to reduce signal attenuation over long distance because increased body size decreases maneuverability and necessitates detection of prey at greater distances (Houston *et al.*, 2004; Simmons and Conway, 2003; Swartz *et al.*, 2003). However, as the frequency of the echolocation signal decreases and the wavelength gets longer, the spatial resolution needed to detect small prey may be lost, as the echo from an insect smaller than the wavelength of an echolocation would become weak and difficult to detect due to Rayleigh scattering (Houston *et al.*, 2004). Rayleigh scattering occurs when the size of the scattering object is smaller than the wavelength of the incident echolocation and the intensity of scattered sound is inversely proportional to the wavelength (Houston *et al.*, 2004). Hence, since a bat's auditory scene is largely influenced by the frequencies that dominate a call, bats using high frequencies can detect smaller prey than bats using lower-frequency calls (Houston *et al.*, 2004; Simmons and Stein, 1980).

Kingston and Rossiter (2004) have shown in horseshoe bats that resource distribution is different for different size bats with different echolocation frequencies, and that larger species with lower frequency echolocation calls have a competitive advantage in taking larger insects. Although, the work of Aldridge and Rautenbach (1987) showed that large bat species ate insects of a broad range of sizes, and that the size of prey appeared to be correlated with the foraging habitat. Houston *et al.* (2004) also showed that some bats with long wavelength and duration echolocation calls ate smaller prey than they had predicted. However, they proposed the variability in detection performance could be accounted for by behavioral flexibility in search-signal design, which had not been incorporated into their initial predictions. Variations in echolocation between bat species thus often coincide with differences in behaviour and ecology (Denzinger *et al.*, 2004).

The significant correlation of dorsal and ventral skull shape with longitude also appears to be interrelated with centroid size. *Eptesicus hottentotus* and *N. africanus* which have distributions largely at either ends of the longitudes sampled and skull shapes at either end of the first relative warp, are also the largest and smallest species on centroid size. Longitude and centroid size also appear to be interrelated with different biomes and ecoregions, since the major pattern of biome change occurs longitudinally. However, the significant correlation of dorsal skull shape with latitude appears to be related to the distributions of species with different dorsal skull shapes on the first relative warp being more predominant at certain latitudes, as skull shape within a species on the first relative warp appears to be fairly similar across the latitudinal distributions of species.

Given that species of the genera *Eptesicus*, *Pipistrellus*, *Neoromicia*, *Hypsugo* and *Nycticeinops* share similar, allometrically constrained dorsal and ventral skull shapes it was not surprising to find that their skull shapes lacked phenetic signal and UPGMA phenograms based on dorsal and ventral skull shapes of individual specimens mix species from all these genera and hence does not reflect the relationships suggested by either GTG-chromosome banding characters (Volleth *et al.*, 2001; Kearney *et al.*, 2002) or the molecular phylogenetic study of Vespertilionidae (Hoofer and Van Den Bussche, 2003).

A few of the species distinguished by skull shape (*M. schreibersii*, *M. tricolor*, *S. dinganii*) appear to have some phenetic signal in their ventral skull shape since the UPGMA phenogram based on ventral skull shape of species means suggests a relationship for *M. schreibersii*, *M. tricolor*, *S. dinganii* (related basally through successive links to the above taxa) that is congruent with the results suggested by molecular data (Hoofer and Van Den Bussche, 2003). Hence, skull shape at the level of the newly recognized family, Miniopteridae, at the level of the subfamily Myotinae, and for the tribe Scotophilini (within the subfamily Vespertilioninae) appears to reflect phylogenetic relationships. Although distinguishable on skull shape the position of *L. botswanae* and *L. namibensis* in the UPGMA of ventral skull shape was not congruent with the molecular (Hoofer and Van Den Bussche, 2003) or bacula morphology (Kearney *et al.*, 2002) results, since these species did not form clusters with other species of the tribe Vespertilionini.

The phenogram based on ventral skull shape of species means also reflects the distinction of *E. hottentotus* and the transfer of the other species that had previously been called *Eptesicus* as was suggested by GTG-chromosome banding characters (Volleth *et al.*, 2001; Kearney *et al.*, 2002), and supported by the molecular phylogenetic study of Vespertilionidae (Hoofer and Van Den Bussche, 2003). However, the phenogram based on ventral skull shape did not support the monophyly of the species transferred from *Eptesicus* on the basis of three shared Robertsonian fusion chromosomes together with *N. africanus* into the genus *Neoromicia* (Volleth *et al.*, 2001; Kearney *et al.*, 2002), as these species clustered together with *H. anchietae* and *N. schlieffenii* in the phenogram of skull shape. Given that skull shape in the majority of these species does not reflect the suggested phylogeny, it would appear due to homoplasy in skull shape as a result of allometric scaling and other ecogeographical and bioclimatic constraints influencing skull morphology.

While the analyses based on means of OTUs and means of species summarised the results more succinctly, the analyses based on individual specimens allowed a better appreciation of the range of variation occurring within the OTUs and species, and hence, probably allowed a more realistic understanding of the intra- and inter-species relationships. It is possible that specimens of *N. capensis* which were outliers in the intra-specific analyses of skull centroid size and shape were incorrectly identified, since they plotted along with a number of other specimens together with all the specimens of *N.* cf. *melckorum* in the UPGMA of ventral skull shape of all 16 species. In the absence of a better description for *N.* cf. *melckorum*, inclusion of specimens as *N.* cf. *melckorum* in this analysis was based on the rather restrictive characteristic of their diploid chromosome number being the same as that described by Rautenbach *et al.* (1993). However, given the extent of the overlap of different species of *Eptesicus*, *Neoromicia*, *Pipistrellus, Hypsugo* and *Nycticeinops* in the relative warp analyses and the UPGMA phenograms due to the lack of phylogenetic signal in skull shape it would be unwise on the basis of this skull shape data to make any suggested taxonomic changes, other than to draw attention to these specimens whose identification requires further clarification.

In conclusion, this study has shown that dorsal and ventral skull shape as captured by the chosen landmarks indicates little within population variation in skull shape due to varying age and sex (although this was only tested on a single population), intra-specific skull shape variation is different in different species, and that although skull shape cannot be used for the inter-specific identification of the ten species of insectivorous bats from the genera *Eptesicus*, *Neoromicia*, *Hypsugo* and *Pipistrellus*, or *N. schlieffenii*, it can distinguish the species of *M. schreibersii*, *M. tricolor*, *S. dinganii*, *L. botswanae* and *L. namibensis*. The lack of concordance between skull morphology and phylogeny in the ten species of insectivorous bats from the genera *Eptesicus*, *Neoromicia*, *Hypsugo* and *Pipistrellus* and *N. schlieffenii* is due to a high degree of homoplasy (which conceals any link between skull shape and phylogeny) which appears to be the result of allometric and ecological constraints causing convergent evolution in the skull morphology, as has been shown for a number of different mammals (Milne and O'Higgens, 2002; Singleton, 2002; Viguier, 2002). Although information about the specific feeding strategies of the species is not known and hence not included in this analysis, these results concur with the findings of Ruedi and Mayer (2001) for *Myotis* that similarities in external morphology which did not correspond to phylogenetically related species, were similar due to similar feeding strategies and similar ecomorphs, as ecological similarities appear to play an important role in shaping skull morphology (Milne and O'Higgens, 2002; Viguier, 2002; Sanchez-Villagra and Williams, 1998).

Since the importance of interpreting variation in morphology in the context of well-defined phylogenies is crucial for an accurate interpretation of ecomorphology (Swartz *et al.*, 2003), future research should include molecular analyses that incorporate a more inclusive suite of vespertilionid species to provide a phylogenetic framework in which to more clearly identify influences such as diet and climate on skull shape in morphologically conserved taxa (Stadelmann *et al.*, 2004). Only with a clear understanding of the phylogenetic relationships will it be possible to try and establish to what extent morphological similarities are due to selective pressures imposed by the contemporary setting and what proportion are from shared ancestry (Swartz *et al.*, 2003). Future research may also benefit from three-dimensional techniques of shape analysis or the addition of the lateral view into the analysis (Monteiro *et al.*, 2003).

APPENDIX 3.1

Specimens examined for geometric morphometric analysis of shape and size

Acronyms: DM - Durban Natural Science Museum, Durban, South Africa; KM – Amathole Museum (formerly the Kaffrarian Museum), King Williams Town, South Africa; MRAC - Royal Museum for Central Africa, Tervuren, Belgium; NMB – National Museum, Bloemfontein, South Africa; NMBZ – National Museum, Bulawayo, Zimbabwe; TM - Transvaal Museum, Pretoria, South Africa; ZM – Iziko Museum (formerly the South African Museum), Cape Town, South Africa.

Numbers before localities identify pooled groups used in dorsal and ventral analyses, respectively. D = used in dorsal shape analysis, V = used in ventral shape analysis.

Eptesicus hottentotus

1 / -) **ZIMBABWE**: Near Nyapfunde School, Nyashato Dam (1732Aa): Female - NMBZ32571 (D), NMBZ32572 (D), NMBZ32573 (D).

2 / 1) **NAMIBIA**: Ombo Eronga Mountains (2115Da): Female - TM9480 (D, V), TM9482 (D, V), TM9484 (D, V), TM9488 (D, V), TM9489 (D). Male - TM9481 (D, V), TM9485 (D, V), TM9486 (D, V), TM9491 (D, V), TM9493 (D, V).

3 / 2) **NAMIBIA**: 70km W of Maltahohe, Zwartmodder (101) (24°54'S, 16°17'E): Female - TM37624 (D, V). Farm Kanaan (25°52'S, 16°07'E): Male - TM27418 (D, V). 3km W of Luderitz-Aus, Klein Aus (8) (26°39'S, 16°13'E): Female - TM37539 (D, V), TM37551 (D, V), TM37553 (D, V), TM37554 (D, V), TM37555 (D, V), TM37560 (D, V). Male - TM37540 (D, V), TM37552 (D, V).

4 / 3) **NAMIBIA**: 35km SSW Keetmanshoop, Rheinvels Farm (26°57'S, 17°56'E): Female - TM32566 (D, V). Male - TM32565 (D, V). Bethanie-Huns (106) (2717Ad): Female - TM32695 (D), TM37588 (D, V).

5 / 4) **SOUTH AFRICA**: LIMPOPO PROVINCE: 67km W of Messina, Shashi/Limpopo confluence, Greefswald Farm (37) (22°13'S, 29°22'E): Female - TM41421 (D, V). Kruger National Park, Pafuri, Fig Tree Camp (22°25'S, 31°11'E): Female - TM38167 (D, V). Male - TM36879 (V).

6 / -) **LESOTHO**: Kofa, Qacha's Nek, (White Hill) (3028Ab): Female - NMB8343 (D). Mount Moorosi, Quthing (3027Bb): Male - NMB8176 (D).

7 / -) **SOUTH AFRICA**: KWAZULU-NATAL PROVINCE: Ithala Game Reserve (27°30'S, 30°12'E): Male - TM31756 (D). Kloof, Kranskloof Nature Reserve (29°47'S, 30°48'E): Female - TM40017 (D).

8 / 5) **SOUTH AFRICA**: WESTERN CAPE PROVINCE: Cederberg, Kliphuis (32°08.183'S, 19°00.197'E): Female - ZM41416 (D, V). Cederberg, Algeria (32°22.472'S, 19°03.708'E): Female - ZM41419 (D, V). Male - ZM41418 (D, V), TM35150 (D, V), TM38412 (D, V).

Hypsugo anchietae

ZIMBABWE: near Gwayi River (1827Dc): Female - NMBZ31965 (D). 2km N of Chenjerai Confluence (1731Bc): Male - NMBZ32524 (D).

SOUTH AFRICA: LIMPOPO PROVINCE: Kruger National Park, Skukuza (24°59'S, 31°35'E): Male - TM39767 (D). Ellisras District, Farm Klipfontein (24°08'S, 28°18'E): Female - TM40291 (D). KWAZULU-NATAL: Ngome Forest Reserve (2731Cd): Male - TM40205 (D). Harold Johnson Nature Reserve (29°12'S, 31°25'E): Female - DM5357 (D, V), DM5364 (V). Male - DM5353 (D, V). Near Richmond, Hella-Hella (29°54'S, 30°05'E): Female - DM5362 (D, V). Near Umkomaas, Empisini Nature Reserve (30°12'S, 30°48'E): Female - DM5377 (D, V).

Neoromicia capensis

1 / 1) **ZAMBIA**: North western Zambezi, Balovale District, Barotseland, Balovale (1322Ba): Female - KM2204 (D, V), KM2219 (D), KM2221 (D, V), KM2222 (D, V). Male - KM2193 (D).

2 / 2) **ZIMBABWE**: Harare, Thornpark (1731Ca): Female - NMZ58828 (D, V). Male - NMBZ58818 (D, V), NMBZ58823 (D), TM34844 (D, V).

3 / -) **ZIMBABWE**: Near Gwayi River, Volunteer Farms (1827Dc): Female - NMBZ31989 (D), NMZ31991 (D).

4 / 3) **ZIMBABWE**: Sengwa Research Station (1828Aa): Female - TM34970 (D, V). Male - TM34864 (D, V), TM34972 (D), TM34975 (D), TM34889 (V).

5 / 4) **BOTSWANA**: Nthane (2126Ac): Male - NMBZ64079 (D, V), NMBZ64082 (D, V), NMBZ64083 (D), NMBZ64098 (D, V), NMBZ64100 (D, V), NMBZ64102 (D, V), NMBZ64103 (D, V), NMBZ64105 (D).

APPENDIX 3.1 continued

6 / 5) **NAMIBIA**: Okahandja, Quickborn, Okaland (21°09'S, 17°05'E): Female - TM3381 (D, V). Omaruru, Okombake (21°22'S, 15°24'E): Female - TM9476 (D). Windhoek, Liebig's Ranch (2216DB): Female - TM8308 (D, V).

7 / 6) **NAMIBIA**: Omaheke, Gobabis District, Sandfontein (468) (2219Ac): Female - KM2123 (D), KM2124 (D), KM2127 (D), KM2135 (D), KM2138 (D), KM2140 (D), KM2144 (D), KM2146 (D).

8 / 7) **SOUTH AFRICA**: NORTHERN CAPE PROVINCE: Kalahari-Gemsbok National Park, 6km SE of Nossob, Marie Se Gat (2520Da): Female - TM35583 (D, V), TM35585 (D, V), TM35589 (D, V), TM35592 (D, V). Male - TM35594 (D, V), TM35596 (D, V), TM35598 (D, V), TM35600 (D, V), TM35602 (D, V).

9 / 8) **NAMIBIA**: 35km SSW of Keetmanshoop, Farm Rheinvels (26°57'S, 17°56'E): Male - TM32547 (D, V), TM32567 (D, V). Oranjemund, Swartkop, Diamond area number 1 (28°33'S 16°25'E): Female - TM32657 (D, V), TM32658 (D, V), TM32659 (D, V), TM32682 (D), TM32683 (D, V), TM32684 (D, V), TM32685 (D, V), TM32686 (D, V), TM32687 (D, V).

10 / 9) **SOUTH AFRICA**: LIMPOPO PROVINCE: Kruger National Park, Pafuri, Anthrax Camp (22°25'S, 31°11'E): Female - TM37811 (D, V). Kruger National Park, Pafuri (22°25'S, 31°18'E): Male - TM37823 (V). Kruger National Park, Levuvhu Hippo Pool (22°26'S, 31°11'E): Female - TM34185 (D, V), TM34240 (D, V).

11 / 9) **SOUTH AFRICA**: MPUMALANGA PROVINCE: Kruger National Park, Skukuza, Rhenosterkoppies (25°08'S, 31°37'E): Female - TM37297 (D, V). Male - TM37299 (D), TM37301 (D).

12 / 10) **SOUTH AFRICA**: NORTH WEST PROVINCE: 13 km W of Ventersdorp, Farm Ratsegaai (204) (26°22'S, 26°32'E): Female - TM27767 (D), TM27768 (D, V), TM27769 (D), TM27772 (D, V), TM27775 (D, V), TM27776 (D), TM27778 (D, V), TM27779 (D, V), TM27781 (D, V), TM27782 (D, V), TM27783 (D, V). Male - TM27752 (V), TM27773 (D, V).

13 / 11) **SOUTH AFRICA**: NORTH WEST PROVINCE: 25km NNE of Bloemhof-Christiana, Farm Welgedaan (292) (27°41'S, 25°14'E): Female - TM20833 (D, V), TM20842 (D, V), TM20844 (D, V), TM20846 (D, V). Male - TM20848 (V).

14 / 12) **SOUTH AFRICA**: FREE STATE PROVINCE: Middelwater (750), Hoopstad (2725Cb): Female - NMB7804 (D), NMB7806 (D, V). Male - NMB7802 (D), NMB7805 (D), NMB7807 (D), NMB7810 (V).

15 / 12) **SOUTH AFRICA**: FREE STATE PROVINCE: Florisbad (686), Brandfort (2826Cc): Female - NMB7751 (D, V), NMB7752 (D, V), NMB7765 (D, V), NMB7766 (D), NMB7768 (D, V), TM17042 (D, V), TM17044 (D, V), TM17046 (D, V). Male - NMB7762 (D, V), NMB7763 (D, V), NMB7764 (D), NMB7767 (D, V), NMB7769 (D, V).

16 / 13) **SOUTH AFRICA**: FREE STATE PROVINCE: Alma, Clocolan (2925Ca): TM7847. Free State, Disused Mine, Jagersfontein Common (2925Cb): Female - NMB7581 (D, V), NMB7593 (D, V), NMB 7602 (V), NMB7609 (D), NMB7611 (D, V), NMB7618 (D), NMB7621 (V), NMB7634 (D, V), NMB7639 (D, V), NMB7682 (D, V), NMB7688 (D), NMB7694 (D, V), NMB7699 (D). Male - NMB7578 (D), NMB7584 (D), NMB7585 (D, V), NMB7594 (V), NMB7595 (D, V), NMB7600 (D, V), NMB7601 (D, V), NMB7603 (D, V), NMB7604 (D, V), NMB7605 (D, V), NMB7617 (D, V), NMB7619 (D), NMB7625 (D), NMB7629 (D), NMB7633 (D, V), NMB7635 (D), NMB7636 (D, V), NMB7642 (D), NMB7643 (D, V), NMB7646 (D, V), NMB7647 (D), NMB7675 (D, V), NMB7677 (D, V), NMB7679 (D, V), NMB7680 (V), NMB7681 (V), NMB7683 (D), NMB7684 (D, V), NMB7685 (D), NMB7686 (D), NMB7689 (D, V), NMB7691 (D, V), NMB7692 (V), NMB7693 (V), NMB7695 (V), NMB7697 (D, V), NMB7698 (D).

17 / 14) **LESOTHO**: Botsoela, Mafeteng (Malealea) (2927Dc): Male - NMB8657 (D). Marakabei, Maseru (2928Ca): Female - NMB7270 (V). Male - NMB7354 (D, V). Mt Moorosi, Quthing (3027Bb): Female - NMB8225 (D), NMB8226 (D). Male - NMB8223 (D), NMB8224 (D), NMB8227 (D), NMB8228 (V), NMB8229 (V).

18 / 15) **SOUTH AFRICA**: KWAZULU-NATAL PROVINCE: Mkuze Game Reserve (27°47'S, 32°12'E): Female - DM5371 (V), TM35270 (V), TM35311 (D), TM35313 (D, V), TM35314 (D), TM35322 (V), TM35323 (V). Male - DM5380 (D, V), DM5400 (D, V), TM35246 (D, V), TM35247 (D, V), TM35249 (D, V), TM35309 (D, V), TM35310 (D, V), TM35324 (D, V), TM35326 (D).

19 / 16) **SOUTH AFRICA**: KWAZULU-NATAL PROVINCE: 45km N of Himeville, Loteni Nature Reserve (29°27'S, 29°32'E): Female - DM1909 (V), DM1910 (V), DM1911 (D), DM1941 (V). Male - DM1912 (D), DM1944 (D), DM1945 (D), DM1946 (D), DM1947 (D), DM1948 (D).

APPENDIX 3.1 continued

Mooi River District (29°13'S, 29°59'E): Female - NMD818 (D), NMD819 (D). 10km W of Weenan, Weenan Game Reserve (2830Cc): Male - DM2319 (V).

20 / 17) **SOUTH AFRICA**: NORTHERN CAPE PROVINCE: 28km SSE of Springbok, Narap Farm (29°53'S, 17°45'E): Female - TM28002 (D, V), TM28003 (D, V), TM28004 (D, V).

21 / 18) **SOUTH AFRICA**: WESTERN CAPE PROVINCE: 9km NW of Beaufort West, Karoo National Park (32°20'S, 22°33'E): Female - TM29512 (D, V), TM29513 (D, V), TM29613 (D).

22 / 18) **SOUTH AFRICA**: WESTERN CAPE PROVINCE: Riversdale, Stilbaai (34°22'S, 21°25'E): Female - TM8970 (D), TM8971 (D, V), TM8972 (D), TM8973 (D, V), TM8975 (D, V).

23 / 19) **SOUTH AFRICA**: WESTERN CAPE PROVINCE: Cederberg, Kliphuis (32°08.183'S, 19°00.197'E): Male - ZM41457 (D, V). Cederberg, Algeria (32°22.472'S, 19°03.708'E): Male - ZM41452 (D, V).

24 / 19) **SOUTH AFRICA**: WESTERN CAPE PROVINCE: Kersefontein Farm (32°54'S, 18°20'E): Female - DM7204 (D, V), DM7200 (D, V), DM7199 (D, V), DM7207 (D, V), DM7208 (D, V), DM7205 (D, V), DM7206 (D, V), DM7192 (D, V), DM7193 (D, V), TM2281 (D, V). Male - DM5630 (D, V), TM2280 (D), TM2284 (D).

Neoromicia cf. *melckorum*

ZIMBABWE: Mana Pools (1529Cb): Female - TM41860 (D, V), TM41861 (D, V), TM41862 (D, V). **SOUTH AFRICA**: LIMPOPO PROVINCE: Kruger National Park, Pafuri, Fig tree Forest (22°25'S, 31°15'E): Female - TM37680 (D, V), TM38843 (D, V). Kruger National Park, Pafuri, Old Picnic Site (22°25'S, 31°18'E): Male - TM39506 (D).

Neoromicia africanus

1 / 1) **ZAMBIA**: Kabompo Boma (1324Ca): Female - NMBZ10105 (D). Male - NMBZ10000 (D, V), NMBZ10006 (D, V), NMZ10020 (D, V), NMBZ10058 (D).

2 / 2) **MALAWI**: Nkhota-kota District, W. Lake Malawi, Nkhota-kota (1234Cd): Female - KM11732 (D, V), KM11737 (D, V), KM11741 (D, V), KM11742 (D), KM11745 (D, V). Male - KM11743 (D), KM11744 (D, V).

3 / 3) **BOTSWANA**: Sepopa (1822Ca): Male - NMBZ64001 (D). **ZIMBABWE**: E. Highlands, 15km SE Juliesdale, Chingamwe Estate, ZTA Cottage (18°27'S, 32°45'E): Male - DM5366 (D). Sentinel Ranch, Limpopo River (2229Ba): Female - NMBZ10106 (D), NMBZ29585 (V), NMBZ29588 (D, V), NMBZ29601 (D, V), NMBZ29602 (D), NMBZ29609 (D, V). Male - NMBZ29600 (D), NMBZ29607 (D), NMBZ29608 (V).

4 / -) **MOZAMBIQUE**: Estatuane (2632Ac): Female - NMBZ64007 (D). Mount Gorongoza (1834Ac): Female - NMBZ64013 (D), NMZ64014 (D), NMBZ64016 (D). 20 M WSW of Nampula, Nabaunama River (1538Db): Male - NMBZ64000 (D).

5 / 4) **SOUTH AFRICA**: LIMPOPO PROVINCE: Kruger National Park, Pafuri, Picnic Site, Mockford's Garden and Fig Tree Forest (22°25'S, 31°18'E): Female - TM41731 (D, V), TM37907 (D, V), TM38523 (D, V), TM38607 (D, V), TM38608 (D, V), TM38610 (D, V). Male - TM38604 (D), TM38605 (D, V).

6 / 5) **SWAZILAND**: 10km N of Simunye (26°07'S, 31°57'E): Male - DM5879 (D, V), DM5880 (D, V). **SOUTH AFRICA**: KWAZULU-NATAL PROVINCE: Jozini Dam Wall (27°25'S, 32°04'E): Male - DM5367 (D, V).

6 / 6) **SOUTH AFRICA**: KWAZULU-NATAL PROVINCE: Ithala Game Reserve, Squaredarvel (27°32'30.0"S, 31°22'23.0"E): Male - DM5900 (D, V). Ithala Game Reserve, Craigadam (27°31'S, 31°21'E): Male - DM5901 (D, V).

7 / 6) **SOUTH AFRICA**: KWAZULU-NATAL: Hluhluwe Game Reserve (28°05'S, 32°02E'): NMD1408 (D, V), NMD1409 (V). Bonamanzi Game Reserve (28°06'S, 32°18'E): Female - DM5405 (D, V).

7 / 7) **SOUTH AFRICA**: KWAZULU-NATAL: Entumeni, Vuma Farm (2831Cd): Female - DM4551 (D, V), DM4552 (D), DM4554 (D, V), DM4556 (D, V). Male - DM4553 (V).

8 / 8) **SOUTH AFRICA**: KWAZULU-NATAL: Yellowwood Park, Stainbank Nature Reserve (29°54'S, 30°56'E): Male - DM5869 (D, V), DM5870 (D, V), DM5871 (D, V).

9 / 9) **SOUTH AFRICA**: KWAZULU-NATAL: Near Umkomaas, Empisini Nature Reserve (30°12'E, 30°48'S): Female - DM5373 (D, V). Renishaw, Old Community Health Hall (30°17'S, 30°44'E): Male - DM5365 (D, V), DM5402 (D, V), DM5404 (D, V).

APPENDIX 3.1 continued

Neoromicia rendalli
ZIMBABWE: Mana Pools National Park (1529Cb): Female -TM41859 (D, V). Male - TM41858 (D, V).
SOUTH AFRICA: KwaZulu-Natal, Bonamanzi Game Reserve (28°06'S, 32°18'E): Female - DM5878 (D, V). Male - DM5361 (D, V), DM5370 (D, V), DM5877 (D, V).

Pipistrellus rueppellii
UGANDA: Entebbe (00°14'N, 32°17'E): Female - MRAC16294 (D).
ZIMBABWE: near Gwayi River, Volunteer Farm (1827Dc): Male - NMBZ31995 (D, V).
SOUTH AFRICA: Limpopo, Kruger National Park, Pafuri, Fig Tree Forest (22°25'50"S, 31°11'50"E): Female - TM36934 (D, V). Limpopo, Kruger National Park, Pafuri, Levuvhu River (22°25'S, 31°18'E): Male - TM37074 (D, V). Limpopo, Kruger National Park, Pafuri, New Fig Forest (22°25'S, 31°18'E): Male - TM37908 (D).

Neoromicia zuluensis
1 / 1) **NAMIBIA**: Gobabeb, Namibia Desert Research Station (23°33'S, 15°03'E): Female - NMBZ64058 (D), NMBZ64061 (D), NMBZ64063 (D), NMBZ64064 (D, V), NMBZ64065 (D), NMBZ64067 (D), NMBZ64069 (D), NMBZ64070 (D, V), TM27592 (D), TM27593 (D, V).
2 / 2) **SOUTH AFRICA**: LIMPOPO PROVINCE: Messina, 67km W of the Shashi and Limpopo Confluence, Greefswald Farm (37) (22°13'S, 29°22'E): Female - TM41408 (D, V). Messina Nature Reserve (22°23'S, 30°04'E): Female - DM5359 (D, V), DM5375 (D, V).
3 / 3) **SOUTH AFRICA**: LIMPOPO PROVINCE: Kruger National Park, Pafuri, Fig Tree and Anthrax Camps (22°25'S, 31°11'E): Female - TM36759 (D, V), TM36846 (D, V), TM37436 (V), TM37863 (D, V). Male - TM37017 (D, V), TM38169 (D, V). Kruger National Park, Pafuri, Fig tree Forest and Culling Camp (22 °25'S, 31 °15'E): Male - TM37678 (V), TM37938 (D, V). Kruger National Park, Pafuri, Old Picnic Site and New Fig Forest (22°25'S, 31°18'E): Female -TM36631 (V). Male - TM37905 (D).
3 / 4) **SOUTH AFRICA**: LIMPOPO PROVINCE: Kruger National Park, Levuvhu River, Fig Tree Camp, Hippo Pools and Simuwana Ranger's post (22°26'S, 31°11'E): Female - TM30534 (D, V), TM34213 (D, V), TM36118 (D), TM36426 (V). Kruger National Park, Shashanga Windmill (22°40'S, 30°59'E): Male - TM30672 (D, V), Female - TM30673 (D, V).
4 / 5) **SOUTH AFRICA**: LIMPOPO PROVINCE: Waterberg, 65km N of Vaalwater, Lapalala Wilderness Area (2824Aa): Female - TM39792 (D, V), TM39795 (D, V).
5 / 6) **SOUTH AFRICA**: MPUMALANGA PROVINCE: Kruger National Park, 12km E of Phalaborwa Gate, Erfplaas Windmill (23°57'S, 31°07'E): Female - TM36572 (D, V). Male - TM36574 (D, V). Kruger National Park, 2km E of Letaba and Olifants Confluence, Lebombo Ironwood Forest (23°59'S, 31°50'E): Male - TM39697 (D, V). Kruger National Park, 1.5km NW of Skukuza, dense woodland of western reservoir (24°59'S, 31°35'E): Female - TM39760 (D). Female – TM39760 (V). Male - TM39761 (D). Leydsdorp, Sheila Farm (10) (24°04'S, 31°09'E): Male - TM6457 (D, V). Kruger National Park, 2km SE of Roodewal Camp (24°08'S, 31°36'E): Male - TM39684 (D). Acornhoek, 11km N of Newington (24°45'S, 31°25'E): Female - TM17293 (D, V).
6 / -) **ZIMBABWE**: Near Gwayi River, Volunteer Farms (1827Dc): Female - NMBZ31973 (D), NMBZ31988 (D). Umfuli River, Frog Mine (1729Dd): Female - NMBZ58889 (D). Sohwe River, Mavhuradonha (1630Db): Female - NMBZ82881 (D).

Pipistrellus hesperidus
1 / 1) **SOUTH AFRICA**: KWAZULU-NATAL PROVINCE: Ndumu Game Reserve (26°53'S, 32°15'E): Male - TM35184 (D, V), TM35209 (D, V). Kosi Lake, Department of Health Camp (26°57'30"S, 32°49'30"E): Male – TM40455 (V), TM40457 (D, V).
2 / 2) **SOUTH AFRICA**: KWAZULU-NATAL PROVINCE: 70km NE of Vryheid-Ngome, Ngome Forest Reserve (27°50'S, 31°24'E): Male - TM39135 (D, V), TM39854 (D, V).
3 / 3) **SOUTH AFRICA**: KWAZULU-NATAL PROVINCE: Hluhluwe Game Reserve, Research Camp (28°04'S, 32°02'E): Male - TM44396 (D), TM44399 (D, V). St Lucia, False Bay (27°48'S, 32°23'E): Male - DM2269 (D). St Lucia, Ipheva Campsite, (28°21'S, 32°25'E): Female - DM6895 (D, V). Male - DM1063 (D), DM1064 (V), DM6896 (D, V). 6km NNE of Mtubatuba, Dukuduku Forest (28°22'S, 32°21'E): Male - TM40410 (D, V).
4 / 4). **SOUTH AFRICA**: KWAZULU-NATAL PROVINCE: Eshowe, Dlinza Forest (28°53.991'S,

APPENDIX 3.1 continued

31°27.007'E): Female - DM5352 (D, V), DM5363 (D, V), DM5372 (D, V), DM5393 (D, V), DM5406 (D, V). Male - DM5356 (D, V), DM5360 (D, V), DM5386 (D, V), DM5397 (D, V). Mtunzini, Twin Streams Farm (28°57'S, 31°30'E): Male - DM5872 (D, V). Harold Johnson Nature Reserve (29°07'S, 31°15'E): Male - DM5369 (D).

5 / 5) **SOUTH AFRICA**: KWAZULU-NATAL PROVINCE: Mount Edgecombe (29°42'S, 31°04'E): Male - DM7143 (D, V). Kranskloof Nature Reserve, Bridle Road Picnic Site (29°46'S, 30°49'E): Male - DM5876 (D, V). Cowies Hill (29°50'S, 30°53'E): Male - DM7201 (D, V). Durban, North Park Nature Reserve (29°52'S, 30°45'E): Female - DM5382 (V). Male - DM5403 (V). South Africa: Durban, Pigeon Valley Park (29°51'S, 30°59'E): Male - DM5384 (V), DM5385 (V). Durban, 108 Bowen Avenue (29°52'S, 30°59'E): Female - DM6893 (D, V). Yellowwood Park, 18 Dove Crescent (29°54'S, 30°56'E): Female - DM5388 (V). Yellowwood Park, Stainbank Nature Reserve (29°54'S, 30°56'E): Male - DM5868 (V).

Pipistrellus rusticus

1 / 1) **NAMIBIA**: Kano Vlei (1919Ac): Female - KM1890 (D, V), KM1891 (D, V). Male - KM1893 (D), KM1894 (D, V).

2 / 2) **BOTSWANA**: Four Rivers Camp, Okavango River (19°03'S, 23°10'E): Female - NMBZ54104 (D), NMBZ54107 (D, V), NMBZ54108 (D, V), NMBZ54109 (D, V), NMBZ63995 (D), NMBZ63997 (D), NMBZ63998 (D), NMBZ63999 (D, V). Male - NMBZ54106 (D, V), NMBZ54218 (D, V).

3 / 3) **ZIMBABWE**: Sentinel Ranch, Limpopo River (2229Ab): Female - NMBZ9896 (D), NMBZ9901 (D, V). **SOUTH AFRICA**: LIMPOPO PROVINCE: Messina Nature Reserve (22°23'S, 30°04'E): Female - DM5394 (D, V), DM5395 (D, V), DM5399 (D, V), DM5407 (D, V), DM5865 (D, V). Male - DM5318 (D, V), DM5379 (D, V), DM5389 (D, V), DM5390 (D, V), DM5391 (D, V).

4 / 4) **SOUTH AFRICA**: LIMPOPO PROVINCE: Waterberg-Ellisras, 30km NE of Vaalwater, Klipfontein Farm (24°08'S, 28°18'E): Female - TM39813 (D, V), TM39815 (D, V), TM39880 (D, V), TM39884 (D, V), TM39886 (D, V), TM39891 (D, V), TM39894 (V). Male - TM39882 (D, V), TM39889 (D, V).

5 / 5) **SOUTH AFRICA**: LIMPOPO PROVINCE: 8km E of Warmbaths, Rissik Private Nature Reserve (24°53'S, 28°27'E): Female - TM20654 (D). Male - TM20648 (D), TM20650 (D, V), TM20652 (D, V), TM20654 (V).

Laephotis botswanae

ZIMBABWE: Eastern Matopos, Lunare Valley (2028Db): Male - NMBZ29992 (D, V). Eastern Matopos, Mtshavezi Valley (2028Db): Female - NMBZ29592 (D). Sengwa (18°10'S, 28°13'E): Female - NMBZ63202 (V). Male - NMZ63201 (D). Que-Que, Rhodesdale, Gem Tree Ranch (1830Cc): Male - NMBZ58131 (D).

BOTSWANA: Kurunxaraga (1922Db): Male - NMBZ59310 (D, V).

SOUTH AFRICA: LIMPOPO PROVINCE: Punda Maria, Mahogany Drive, Witsand Dam (22°41'S, 31°02'E): Male - TM38123 (D, V). Ellisras District, 30 km NE of Vaalwater, Farm Klipfontein, (24°08'S, 28°18'E): Male - TM39946 (D, V). KWAZULU-NATAL PROVINCE: Near Richmond, Hella-Hella (29°54'S, 30°05'E): Female - DM6898 (D, V). Male - DM5351 (D, V), DM6899 (D, V).

Laephotis namibensis

NAMIBIA: Klein Aus 8, 3 km W Aus, Luderitz (2028Db): Male - TM37547 (D, V). Zwartmodder 101, 70 km W Maltahohe (24°54'S, 16°17'E): Male - TM37608 (D, V).

SOUTH AFRICA: WESTERN CAPE PROVINCE: Cederberg, Algeria Campsite (32°22.472'S, 19°03.708'E): Male - ZM41415 (D, V), ZM41417 (D, V).

Myotis tricolor

SOUTH AFRICA: KWAZULU-NATAL PROVINCE: Ithala Game Reserve (27°31'S, 31°22'E): Female - DM5895 (D, V), DM5896 (D, V), DM5897 (D, V). WESTERN CAPE PROVINCE: Cederberg, Algeria Campsite (32°22.472'S, 19°03.708'E): Male - ZM41451 (D).

Nycticeinops schlieffenii

BOTSWANA: Tuli Block, Nitani (2229Aa): Male – TM47494 (D, V).

SOUTH AFRICA: KWAZULU-NATAL PROVINCE: Mkuze Game Reserve (27°47'S, 32°12'E):

APPENDIX 3.1 continued

Male - DM5401 (D, V).

Scotophilus dinganii
SOUTH AFRICA: KWAZULU-NATAL PROVINCE: Kranskloof Nature Reserve (29°46'S, 30°49'E): Male - DM5874 (D, V), DM5875 (D, V).

Miniopterus schreibersii
SOUTH AFRICA: WESTERN CAPE PROVINCE: Cederberg, Kliphuis (32°08.183'S, 19°00.197'E): Male - ZM41459 (D, V). KWAZULU-NATAL PROVINCE: Ithala Game Reserve (27°31'S, 31°22'E): Female - DM5898 (D, V). Hella-Hella (29°54'S, 30°05'E): Female - DM6897 (D, V).

APPENDIX 3.2

Description of landmark positions on southern African vespertilionid dorsal and ventral skull surfaces

Landmarks on the dorsal surface of the skull were placed in the following positions:
1. Centre of posterior curvature of inter-nasal opening; 2. deepest indentation of the premaxilla between last incisor and canine; 3. most lateral extension at canine; 4. intersection of maxilla and anterior edge of the jugal; 5. deepest indentation in the orbital region i.e. point of narrowest inter-orbital width; 6. intersection of squamosal and anterior edge of zygomatic process; 7. deepest angle formed by the posterior edge of the zygomatic process close to the intersection with the squamosal; 8. most lateral extension of mastoid region; and 9. mid-point of skull along posterior edge.

Landmarks on the ventral surface of the skull were placed in the following positions:
1. Centre of posterior curvature of anterior hard palate; 2. deepest indentation of premaxilla be-tween last incisor and canine; 3. deepest angle at intersection of maxilla and anterior edge of the jugal; 4. deepest angle at intersection of maxilla and posterior edge of jugal; 5. deepest angle at intersection of squamosal and anterior edge of zygomatic process; 6. deepest angle at posterior edge of zygomatic process at intersection with squamosal; 7. most lateral extension of mastoid region; 8. most posterior extension of occipital condyle; 9. deepest indentation point between oc-cipital condyle and foramen magnum; 10. most lateral angle of the foramen magnum; 11. centre of posterior curvature of occipital at foramen magnum (posterior-most point of foramen magnum); 12. centre of anterior curvature of occipital at foramen magnum (anterior-most point of foramen magnum); and 13. centre of anterior curvature of posterior hard palate.

APPENDIX 3.3 (A-H)

Results of correlation tests

Non-parametric Spearman r_s and parametric Pearson r values together with probabilities, and percentage contributions to the total shape variation by the different relative warps.

A)

Between the first four principal component scores (PCS) of dorsal and ventral skull shape of *Neoromicia capensis* specimens from a single locality (Jagersfontein, Free State) in southern Africa and centroid size (CS), sex, and tooth wear class (TW). % = variance explained by each principal component axis. * denotes significance at $P < 0.05$.

		PCS1	PCS2	PCS3	PCS4
Dorsal view	%	23.83%	19.68%	13.70%	9.90%
CS	r	-0.326; 0.035 *	-0.362; 0.019 *	0.059; 0.711	-0.088; 0.578
Sex	r_s	-0.065; 0.684	-0.168; 0.289	-0.020; 0.899	-0.369; 0.016 *
	r	-0.062; 0.697	-0.193; 0.220	-0.006; 0.970	-0.383; 0.012 *
TW	r_s	0.144; 0.364	0.294; 0.059	0.041; 0.795	0.137; 0.386
	r	0.179; 0.256	0.298; 0.056	0.049; 0.757	0.144; 0.362
Ventral view	%	17.88%	16.26%	10.54%	9.13%
CS	r	-0.036; 0.835	-0.387; 0.022 *	-0.177; 0.309	0.069; 0.693
Sex	r_s	0.071; 0.684	-0.201; 0.248	-0.123; 0.482	0.252; 0.143
	r	0.120; 0.493	-0.230; 0.184	-0.150; 0.389	0.256; 0.137
TW	r_s	0.005; 0.977	0.135; 0.440	0.291; 0.090	0.156; 0.370
	r	0.031; 0.862	0.200; 0.250	0.293; 0.087	0.107; 0.542

APPENDIX 3.3 B)

Between the first four principal component scores (PCS) of dorsal skull shape of all specimens within the following species, *Eptesicus hottentotus*, *Neoromicia capensis*, *N. africanus*, *N. zuluensis*, *Pipistrellus hesperidus*, and *P. rusticus* and different OTUs from southern Africa, centroid size (CS), sex, tooth wear class (TW), latitude (Lat), longitude (Long), biome (B), and ecoregion (E). % = variance explained by each principal component axis. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Dorsal		PCS1	PCS2	PCS3	PCS4
Eptesicus hottentotus					
	%	22.37%	18.66%	14.08%	9.75%
OTU	r_s	0.500; 0.001 **	-0.020; 0.903	0.024; 0.888	0.183; 0.272
	r	0.532; 0.001 **	0.107; 0.522	0.076; 0.649	0.158; 0.344
CS	r	0.173; 0.299	-0.083; 0.619	-0.118; 0.481	-0.008:0.963
Sex	r_s	0.099; 0.556	-0.331; 0.042 *	-0.159; 0.339	-0.210; 0.206
	r	0.034; 0.837	-0.356; 0.028 *	-0.171; 0.306	-0.258; 0.118
TW	r_s	0.199; 0.231	-0.223; 0.178	-0.040; 0.813	-0.121; 0.468
	r	0.197; 0.237	-0.139; 0.405	-0.067; 0.690	-0.220; 0.185
Lat	r_s	-0.391; 0.015 *	0.140; 0.402	0.045; 0.790	-0.201; 0.227
	r	-0.426; 0.008 **	0.150; 0.367	0.037; 0.824	-0.183; 0.272
Long	r_s	0.334; 0.040 *	0.022; 0.895	0.070; 0.675	-0.037; 0.824
	r	0.184; 0.268	0.147; 0.380	0.017; 0.918	-0.305; 0.062
B	r_s	-0.325; 0.046 *	-0.284; 0.084	-0.078; 0.642	0.276; 0.093
	r	-0.216; 0.192	-0.134; 0.421	0.162; 0.332	0.328; 0.044 *
E	r_s	-0.414; 0.010 *	-0.052; 0.756	0.060; 0.720	0.024; 0.885
	r	-0.226; 0.172	-0.136; 0.417	0.158; 0.342	0.328; 0.045 *

APPENDIX 3.3 B) continued

Dorsal view		PCS1	PCS2	PCS3	PCS4
Neoromicia capensis					
	%	19.08%	15.08%	14.40%	10.64%
OTU	r_s	-0.046; 0.524	0.015; 0.832	0.018; 0.804	-0.173; 0.016 *
	r	-0.025; 0.734	0.032; 0.664	0.063; 0.389	-0.173; 0.017 *
CS	r	0.025; 0.728	-0.072; 0.320	-0.355; 4.6E-06 ***	0.045; 0.533
Sex	r_s	0.172; 0.018 *	-0.049; 0.500	0.207; 0.004 **	0.042; 0.565
	r	0.180; 0.013 *	-0.025; 0.729	0.198; 0.006 **	0.056; 0.443
TW	r_s	0.040; 0.583	0.107; 0.141	-0.099; 0.175	0.003; 0.972
	r	0.031; 0.674	0.109; 0.132	-0.096; 0.188	-0.015; 0.842
Lat	r_s	0.008; 0.909	0.033; 0.652	-0.166; 0.021 *	0.153; 0.034 *
	r	-0.008; 0.913	0.017; 0.811	-0.151; 0.037 *	0.122; 0.091
Long	r_s	-0.065; 0.374	0.090; 0.216	-0.320; 6.40E-06 ***	-0.035; 0.631
	r	-0.046; 0.530	0.093; 0.202	-0.248; 0.001 **	-0.065; 0.369
B	r_s	0.036; 0.616	-0.120; 0.098	0.312; 1.10E-05 ***	-0.084; 0.251
	r	0.047; 0.514	-0.081; 0.264	0.283; 7.36E-05 ***	-0.116; 0.109
E	r_s	0.095; 0.192	-0.146; 0.044 *	0.355; 1.00E-06 ***	-0.025; 0.726
	r	0.051; 0.487	-0.084; 0.247	0.287; 5.61E-05 ***	-0.112; 0.124

APPENDIX 3.3 B) continued

Dorsal view		PCS1	PCS2	PCS3	PCS4
Neoromicia africanus					
	%	22.00%	15.20%	14.38%	12.90%
OTU	r_s	0.105; 0.461	0.449; 0.001 **	-0.116; 0.413	-0.132; 0.352
	r	0.111; 0.435	0.441; 0.001 **	-0.107; 0.452	-0.146; 0.301
CS	r	0.166; 0.239	0.276; 0.048 *	-0.013; 0.925	-0.037; 0.795
Sex	r_s	0.185; 0.190	0.015; 0.914	0.167; 0.238	0.241; 0.085
	r	0.243; 0.082	-0.002; 0.990	0.107; 0.405	0.237; 0.090
TW	r_s	0.361; 0.009 **	0.023; 0.872	0.072; 0.610	-0.017; 0.904
	r	0.361; 0.009 **	0.025; 0.862	0.034; 0.808	0.012; 0.932
Lat	r_s	-0.145; 0.307	-0.365; 0.008 **	0.074; 0.603	0.193; 0.169
	r	-0.165; 0.243	-0.336; 0.015 *	0.081; 0.566	0.191; 0.175
Long	r_s	-0.015; 0.918	0.292; 0.035 *	-0.076; 0.590	0.182; 0.198
	r	0.073; 0.608	0.285; 0.041 *	-0.135; 0.339	0.199; 0.401
B	r_s	-0.115; 0.418	-0.169; 0.232	0.005; 0.972	-0.013; 0.929
	r	-0.089; 0.530	-0.290; 0.037 *	0.024; 0.865	0.014; 0.921
E	r_s	-0.079; 0.575	-0.168; 0.234	0.103; 0.467	-0.074; 0.604
	r	-0.089; 0.532	-0.297; 0.033 *	0.029; 0.836	0.011; 0.941

APPENDIX 3.3 B) continued

Dorsal view		PCS1	PCS2	PCS3	PCS4
Neoromicia africanus					
	%	22.00%	15.20%	14.38%	12.90%
OTU	r_s	0.105; 0.461	0.449; 0.001 **	-0.116; 0.413	-0.132; 0.352
	r	0.111; 0.435	0.441; 0.001 **	-0.107; 0.452	-0.146; 0.301
CS	r	0.166; 0.239	0.276; 0.048 *	-0.013; 0.925	-0.037; 0.795
Sex	r_s	0.185; 0.190	0.015; 0.914	0.167; 0.238	0.241; 0.085
	r	0.243; 0.082	-0.002; 0.990	0.107; 0.405	0.237; 0.090
TW	r_s	0.361; 0.009 **	0.023; 0.872	0.072; 0.610	-0.017; 0.904
	r	0.361; 0.009 **	0.025; 0.862	0.034; 0.808	0.012; 0.932
Lat	r_s	-0.145; 0.307	-0.365; 0.008 **	0.074; 0.603	0.193; 0.169
	r	-0.165; 0.243	-0.336; 0.015 *	0.081; 0.566	0.191; 0.175
Long	r_s	-0.015; 0.918	0.292; 0.035 *	-0.076; 0.590	0.182; 0.198
	r	0.073; 0.608	0.285; 0.041 *	-0.135; 0.339	0.199; 0.401
B	r_s	-0.115; 0.418	-0.169; 0.232	0.005; 0.972	-0.013; 0.929
	r	-0.089; 0.530	-0.290; 0.037 *	0.024; 0.865	0.014; 0.921
E	r_s	-0.079; 0.575	-0.168; 0.234	0.103; 0.467	-0.074; 0.604
	r	-0.089; 0.532	-0.297; 0.033 *	0.029; 0.836	0.011; 0.941

APPENDIX 3.3 B) continued

Dorsal view		PCS1	PCS2	PCS3	PCS4
Pipistrellus hesperidus					
	%	20.17%	16.98%	15.62%	10.48%
OTU	r_s	0.244; 0.221	-0.044; 0.827	-0.012; 0.952	0.223; 0.264
	r	0.132; 0.512	-0.076; 0.707	-0.006; 0.978	0.242; 0.224
CS	r	0.134; 0.506	0.538; 0.004 **	-0.304; 0.124	-0.205; 0.304
Sex	r_s	0.239; 0.230	0.629; 4.37E-04 ***	-0.109; 0.590	-0.022; 0.914
	r	0.205; 0.306	0.554; 0.003 **	-0.082; 0.683	-0.095; 0.637
TW	r_s	-0.196; 0.327	0.326; 0.097	0.006; 0.975	0.078; 0.701
	r	-0.248; 0.212	0.312; 0.113	0.059; 0.769	0.046; 0.819
Lat	r_s	-0.243; 0.221	-0.092; 0.646	0.089; 0.658	0.154; 0.442
	r	-0.102; 0.612	-0.255; 0.199	0.121; 0.546	0.178; 0.374
Long	r_s	-0.251; 0.207	-0.217; 0.278	0.124; 0.537	0.016; 0.936
	r	-0.200; 0.318	-0.214; 0.284	0.107; 0.596	0.066; 0.745
B	r_s	0.185; 0.356	0.273; 0.168	-0.141; 0.484	0.182; 0.363
	r	0.200; 0.318	0.295; 0.135	-0.099; 0.624	0.146; 0.469
E	r_s	0.155; 0.440	0.262; 0.187	-0.218; 0.274	0.148; 0.461
	r	0.201; 0.316	0.295; 0.135	-0.100; 0.620	0.145; 0.470

APPENDIX 3.3 B) continued

Dorsal view		PCS1	PCS2	PCS3	PCS4
Pipistrellus rusticus					
	%	23.62%	16.67%	11.52%	10.76%
OTU	r_s	0.140; 0.402	-0.308; 0.060	-0.170; 0.309	-0.405; 0.012 *
	r	-0.067; 0.690	-0.307; 0.061	-0.126; 0.449	-0.412; 0.010 *
CS	r	0.204; 0.219	-0.238; 0.150	-0.067; 0.687	-0.091; 0.586
Sex	r_s	-0.025; 0.882	0.000; 1.000	-0.229; 0.167	-0.139; 0.404
	r	-0.007; 0.965	-0.002; 0.990	-0.307; 0.061	-0.169; 0.311
TW	r_s	-0.091; 0.588	-0.089; 0.595	0.065; 0.699	0.523; 0.001 **
	r	-0.054; 0.747	-0.108; 0.518	0.014; 0.932	0.478; 0.002 **
Lat	r_s	-0.183; 0.272	0.304; 0.063	0.129; 0.441	0.439; 0.006 **
	r	-0.137; 0.411	0.325; 0.046 *	0.048; 0.775	0.461; 0.004 **
Long	r_s	-0.059; 0.724	-0.283; 0.085	0.188; 0.258	-0.185; 0.265
	r	-0.046; 0.783	-0.306; 0.062	0.124; 0.458	-0.324; 0.047 *
B	r_s	-0.240; 0.147	0.285; 0.083	-0.003; 0.987	0.364; 0.025 *
	r	-0.226; 0.172	0.281; 0.087	-0.062; 0.710	0.363; 0.025 *
E	r_s	-0.198; 0.235	0.108; 0.520	-0.070; 0.675	0.220; 0.185
	r	-0.226; 0.172	0.271; 0.099	-0.067; 0.691	0.357; 0.028

APPENDIX 3.3 C)

Results of correlation tests between the first four principal component scores (PCS) of ventral skull shape of all specimens within the following species, *E. hottentotus*, *N. capensis*, *N. africanus*, *N. zuluensis*, *P. hesperidus*, and *P. rusticus* and different OTUs from southern Africa, centroid size (CS), sex, tooth-wear class (TW), latitude (Lat), longitude (Long), biome (B), and ecoregion. % = variance explained by each principal component axis. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Ventral view		**PCS1**	**PCS2**	**PCS3**	**PCS4**
Eptesicus hottentotus					
	%	22.77%	16.62%	9.75%	6.55%
OTU	r_s	0.569; 0.001 **	0.066; 0.733	0.498; 0.006 **	-0.214; 0.264
	r	0.526; 0.003 **	0.138; 0.475	0.566; 0.001 **	-0.075; 0.699
CS	r	-0.236; 0.217	0.134; 0.487	0.016; 0.936	-0.043; 0.824
Sex	r_s	-0.092; 0.635	0.226; 0.239	-0.209; 0.276	-0.042; 0.829
	r	-0.127; 0.510	0.220; 0.251	-0.221; 0.250	-0.104; 0.590
TW	r_s	-0.257; 0.179	0.168; 0.383	0.131; 0.499	-0.234; 0.221
	r	-0.300; 0.113	0.209; 0.277	0.118; 0.541	-0.231; 0.228
Lat	r_s	-0.511; 0.005 **	-0.011; 0.956	-0.264; 0.166	0.434; 0.019 *
	r	-0.515; 0.004 **	-0.059; 0.760	-0.265; 0.164	0.364; 0.052
Long	r_s	0.570; 0.001 **	0.082; 0.671	0.468; 0.011 *	-0.121; 0.531
	r	0.223; 0.245	0.155; 0.421	0.425; 0.022 *	0.161; 0.404
B	r_s	-0.385; 0.039 *	-0.152; 0.430	-0.565; 0.001 **	-0.098; 0.612
	r	-0.230; 0.230	-0.300; 0.114	-0.358; 0.057	-0.095; 0.626
E	r_s	-0.568; 0.001 **	-0.156; 0.419	-0.402; 0.031 *	0.272; 0.154
	r	-0.243; 0.203	-0.296; 0.119	-0.377; 0.044 *	-0.096; 0.622

APPENDIX 3.3 C) continued

Ventral view		PCS1	PCS2	PCS3	PCS4
Neoromicia capensis					
	%	17.52%	11.94%	9.99%	8.21%
OTU	r_s	-0.185; 0.020 *	-0.121; 0.131	-0.139; 0.082	-0.016; 0.843
	r	-0.148; 0.063	-0.087; 0.277	-0.177; 0.026 *	-0.019; 0.813
CS	r	0.049; 0.542	-0.355; 4.87E-06 ***	-0.064; 0.422	-0.161; 0.043 *
Sex	r_s	0.167; 0.036 *	-0.094; 0.238	0.058; 0.467	0.188; 0.018 *
	r	0.188; 0.018 *	-0.102; 0.204	0.071; 0.378	0.174; 0.029 *
TW	r_s	0.040; 0.615	-0.022; 0.785	-0.039; 0.626	-0.119; 0.138
	r	0.027; 0.739	0.053; 0.506	-0.006; 0.941	-0.122; 0.128
Lat	r_s	0.293; 1.92E-04 ***	0.169; 0.033 *	0.137; 0.086	0.191; 0.016 *
	r	0.187; 0.018 *	0.098; 0.219	0.168; 0.035 *	0.196; 0.014 *
Long	r_s	0.051; 0.528	0.317; 4.97E-05 ***	-0.034; 0.674	0.088; 0.271
	r	0.038; 0.636	0.268; 0.001 **	-0.081; 0.314	0.109; 0.174
B	r_s	-0.209; 0.008 **	-0.246; 0.002 **	0.022; 0.779	-0.192; 0.016 *
	r	-0.219; 0.006 **	-0.237; 0.003 **	-3.81E-04; 0.996	-0.179; 0.025 *
E	r_s	-0.196; 0.014 *	-0.278; 4.09E-04 ***	0.025; 0.758	-0.272; 0.001 **
	r	-0.219; 0.006 **	-0.239; 0.002 **	0.005; 0.949	-0.185; 0.020 *

APPENDIX 3.3 C) continued

Ventral view		PCS1	PCS2	PCS3	PCS4
Neoromicia africanus					
	%	17.15%	15.62%	10.41%	8.82%
OTU	r_s	-0.394; 0.013 *	-0.258; 0.112	-0.303; 0.060	0.169; 0.305
	r	-0.383; 0.016 *	-0.232; 0.155	-0.255; 0.117	0.176; 0.284
CS	r	-0.336; 0.037 *	0.051; 0.758	0.120; 0.468	-0.009; 0.955
Sex	r_s	0.210; 0.200	0.128; 0.439	0.068; 0.679	0.105; 0.525
	r	0.148; 0.368	0.075; 0.650	0.069; 0.675	0.085; 0.606
TW	r_s	-0.240; 0.142	-0.090; 0.587	-0.089; 0.591	0.070; 0.673
	r	-0.186; 0.257	-0.126; 0.445	-0.104; 0.530	0.043; 0.795
Lat	r_s	0.345; 0.032 *	0.273; 0.093	0.354; 0.027 *	-0.130; 0.430
	r	0.299; 0.065	0.185; 0.260	0.302; 0.062	-0.102; 0.536
Long	r_s	-0.417; 0.008 **	-0.001; 0.997	0.102; 0.538	0.152; 0.355
	r	-0.317; 0.049*	0.017; 0.918	0.136; 0.409	0.217; 0.185
B	r_s	0.212; 0.195	-0.034; 0.837	-0.248; 0.128	-0.109; 0.509
	r	0.236; 0.148	0.009; 0.958	-0.165; 0.315	0.042; 0.801
E	r_s	0.199; 0.224	0.001; 0.994	-0.239; 0.143	0.094; 0.570
	r	0.241; 0.140	0.012; 0.941	-0.164; 0.941	0.039; 0.814

APPENDIX 3.3 C) continued

Ventral view		PCS1	PCS2	PCS3	PCS4
Neoromicia zuluensis					
	%	20.13%	15.89%	10.82%	9.15%
OTU	r_s	-0.493; 0.008 **	-0.504; 0.006 **	-0.199; 0.309	0.096; 0.627
	r	-0.557; 0.002 **	-0.489; 0.008 **	-0.181; 0.356	0.040; 0.841
CS	r	0.212; 0.539	-0.142; 0.472	0.058; 0.768	0.199; 0.309
Sex	r_s	0.323; 0.094	-0.010; 0.961	0.098; 0.620	0.108; 0.586
	r	0.296; 0.126	-0.001; 0.994	0.124; 0.530	0.086; 0.663
TW	r_s	0.178; 0.365	0.151; 0.443	-0.124; 0.530	0.130; 0.511
	r	0.228; 0.244	0.186; 0.344	0.003; 0.988	0.175; 0.373
Lat	r_s	0.498; 0.007 **	0.156; 0.427	0.169; 0.390	-0.318; 0.099
	r	0.480; 0.010 *	-0.043; 0.827	0.063; 0.749	-0.170; 0.388
Long	r_s	-0.395; 0.037 *	-0.340; 0.076	-0.270; 0.164	-0.019; 0.924
	r	-0.208; 0.288	0.526; 0.004 **	0.068; 0.731	0.237; 0.225
B	r_s	0.211; 0.280	0.375; 0.050	0.030; 0.879	0.134; 0.495
	r	0.234; 0.231	0.449; 0.017	0.059; 0.765	0.156; 0.429
E	r_s	0.025; 0.899	0.350; 0.068	-0.034; 0.862	0.172; 0.381
	r	0.227; 0.246	0.458; 0.014	0.057; 0.773	0.165; 0.402

APPENDIX 3.3 C) continued

Ventral view		PCS1	PCS2	PCS3	PCS4
Pipistrellus hesperidus					
	%	18.98%	13.94%	13.13%	9.21%
OTU	r_s	-0.002; 0.992	-0.506; 0.003 **	0.131; 0.474	-0.146; 0.427
	r	0.131; 0.474	-0.463; 0.008 **	0.048; 0.792	-0.112; 0.540
CS	r	0.210; 0.248	-0.167; 0.360	0.062; 0.736	-0.421; 0.016 *
Sex	r_s	0.526; 0.002 **	0.088; 0.633	0.372; 0.036 *	-0.051; 0.781
	r	0.525; 0.002 **	0.113; 0.536	0.288; 0.110	-0.033; 0.856
TW	r_s	0.014; 0.938	-0.094; 0.607	-0.153; 0.402	0.421; 0.017 *
	r	0.063; 0.734	-0.139; 0.450	-0.240; 0.185	0.383; 0.031 *
Lat	r_s	-0.023; 0.899	0.466; 0.007 **	-0.125; 0.496	0.170; 0.353
	r	-0.076; 0.678	0.478; 0.006 **	0.003; 0.985	0.123; 0.503
Long	r_s	0.198; 0.277	0.435; 0.013 *	-0.138; 0.452	0.129; 0.483
	r	0.115; 0.532	0.432; 0.013 *	-0.192; 0.293	0.097; 0.599
B	r_s	0.224; 0.217	-0.030; 0.871	0.253; 0.163	-0.293; 0.104
	r	0.217; 0.234	-0.031; 0.866	0.204; 0.264	-0.343; 0.054
E	r_s	0.358; 0.044 *	0.017; 0.928	0.304; 0.090	-0.301; 0.095
	r	0.219; 0.228	-0.030; 0.869	0.205; 0.260	-0.344; 0.054

APPENDIX 3.3 C) continued

Ventral view		PCS1	PCS2	PCS3	PCS4
Pipistrellus rusticus					
	%	18.38%	11.53%	10.55%	10.35%
OTU	r_s	-0.261; 0.148	-0.233; 0.199	-0.415; 0.018 *	-0.114; 0.535
	r	-0.303; 0.092	-0.117; 0.523	-0.415; 0.018 *	-0.090; 0.624
CS	*r*	-0.206; 0.257	-0.015; 0.936	-0.101; 0.582	0.109; 0.554
Sex	r_s	-0.238; 0.190	0.252; 0.165	0.315; 0.079	-0.077; 0.676
	r	-0.220; 0.227	0.297; 0.099	0.253; 0.163	-0.056; 0.760
TW	r_s	0.044; 0.813	0.574; 0.001 **	-0.023; 0.901	0.280; 0.120
	r	0.042; 0.821	0.545; 0.001 **	-0.031; 0.866	0.153; 0.404
Lat	r_s	0.178; 0.331	0.244; 0.178	0.429; 0.014 *	0.121; 0.511
	r	0.261; 0.149	0.209; 0.250	0.395; 0.025 *	0.093; 0.612
Long	r_s	-0.296; 0.100	-0.057; 0.759	-0.097; 0.599	0.117; 0.524
	r	-0.365; 0.040 *	-0.149; 0.416	-0.215; 0.237	0.104; 0.573
B	r_s	0.052; 0.777	0.234; 0.197	0.165; 0.368	0.104; 0.571
	r	0.077; 0.676	0.232; 0.201	0.180; 0.325	0.131; 0.476
E	r_s	-0.191; 0.294	0.137; 0.455	0.126; 0.490	0.076; 0.681
	r	0.063; 0.733	0.230; 0.206	0.181; 0.321	0.131; 0.474

APPENDIX 3.3 D)

Results of correlation tests between the first four principal component scores (PCS) of dorsal and ventral skull shape of the OTU means within *N. capensis* and different OTUs, centroid size (CS), latitude (Lat), longitude (Long), biome (B) and ecoregion (E). % = variance explained by each principal component axis.

Dorsal view		**PCS1**	**PCS2**	**PCS3**	**PCS4**
Neoromicia capensis	%	32.47%	20.43%	13.81%	10.40%
OTU	r_s	0.111; 0.605	-0.041; 0.850	-0.399; 0.053	-0.056; 0.796
	r	0.127; 0.554	-0.080; 0.711	-0.433; 0.035	-0.020; 0.926
CS	r	0.606; 0.002 **	-0.360; 0.084	-0.230; 0.279	-0.184; 0.390
Lat	r_s	-0.209; 0.327	0.023; 0.916	0.354; 0.090	0.064; 0.767
	r	-0.200; 0.348	0.065; 0.764	0.417; 0.043 *	-0.028; 0.898
Long	r_s	-0.517; 0.010 *	0.274; 0.195	0.028; 0.897	-0.026; 0.904
	r	-0.458; 0.025 *	0.275; 0.194	0.043; 0.843	0.004; 0.984
B	r_s	0.565; 0.004 **	-0.198; 0.354	0.016; 0.940	-0.140; 0.514
	r	0.543; 0.006 **	-0.168; 0.431	-0.142; 0.509	-0.160; 0.456
E	r_s	0.626; 0.001 **	-0.212; 0.319	0.023; 0.916	-0.059; 0.786
	r	0.552; 0.005	-0.175; 0.414	-0.128; 0.550	-0.155; 0.470
Ventral view					
Neoromicia capensis	%	28.84%	18.32%	10.38%	8.60%
OTU	r_s	-0.058; 0.814	-0.361; 0.128	-0.477; 0.039 *	-0.291; 0.226
	r	0.015; 0.952	-0.373; 0.115	-0.445; 0.056	-0.320; 0.182
CS	r	-0.446; 0.056	-0.393; 0.096	-0.203; 0.405	-0.305; 0.204
Lat	r_s	-0.025; 0.920	0.588; 0.008 **	0.381; 0.108	0.251; 0.300
	r	-0.038; 0.876	0.457; 0.049 *	0.305; 0.204	0.238; 0.327
Long	r_s	0.088; 0.721	0.158; 0.519	0.016; 0.949	0.005; 0.983
	r	0.266; 0.271	0.119; 0.628	0.011; 0.964	0.054; 0.826
B	r_s	0.157; 0.520	-0.230; 0.343	-0.218; 0.369	-0.340; 0.155
	r	0.079; 0.748	-0.220; 0.365	-0.217; 0.373	-0.466; 0.044 *
E	r_s	-0.119; 0.626	-0.381; 0.107	-0.184; 0.451	0.049; 0.843
	r	-0.163; 0.504	-0.336; 0.159	-0.194; 0.425	-0.179; 0.463

APPENDIX 3.3 E)

Results of correlation tests between the first four principal component scores (PCS) of dorsal and ventral skull shape of all specimens of 16 vespertilionid species from southern Africa, and different species (Sp), centroid size (CS), latitude (Lat), longitude (Long), biome (B), ecoregion (E) and dominant frequency of the call (for 11 species only) (Call). % = variance explained by each principal component axis. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

		PCS1	PCS2	PCS3	PCS4
Dorsal view		29.87%	16.53%	12.05%	10.74%
Sp	r_s	-0.556; 1.00E-06 ***	0.198; 2.93E-05 ***	-0.042; 0.386	0.032; 0.504
	r	-0.443; 0.00E-17 ***	0.321; 6.66E-16 ***	-0.130; 0.006 **	0.090; 0.059
CS	*r*	0.661; 0.00E-17 ***	-0.039; 0.411	-0.486; 0.00E-17 ***	-0.148; 0.002 **
Lat	r_s	-0.236; 1.00E-06 ***	0.091; 0.058	0.064; 0.182	0.151; 0.002 **
	r	-0.266; 1.71E-08 ***	0.089; 0.063	0.091; 0.058	0.169; 3.98E-04 ***
Long	r_s	-0.478; 1.00E-06 ***	-0.008; 0.866	0.105; 0.028 *	0.177; 1.94E-04 ***
	r	-0.445; 0.00E-17 ***	0.003; 0.955	0.161; 0.001 **	0.164; 0.001 **
B	r_s	0.473; 1.00E-06 ***	-0.072; 0.133	-0.204; 1.68E-04 ***	-0.229; 1.36E-06 ***
	r	0.400; 0.00E-17 ***	-0.054; 0.257	-0.194; 4.26E-05 ***	-0.212; 7.95E-06 ***
E	r_s	0.472; 1.00E-06 ***	-0.072; 0.133	-0.174; 2.49E-04 ***	-0.259; 1.00-06 ***
	r	-0.014; 0.766	1.18E-04; 1.000	0.039; 0.417	0.071; 0.136
Call	r_s	-0.748; 1.00E-06 ***	-0.034; 0.509	0.209; 1.00E-06 ***	0.268; 1.00E-06 ***
	r	-0.809; 0.00E-17 ***	-0.080; 0.122	0.149; 0.004 **	0.186; 3.08E-04 ***
Ventral view		19.46%	18.01%	13.99%	6.67%
Sp	r_s	-0.406; 1.00E-06 ***	0.225; 1.75E-05 ***	-0.109; 0.038 *	-0.249; 1.75E-06 ***
	r	-0.304; 3.91E-13 ***	-0.053; 0.321	-0.248; 1.99E-06 ***	-0.230; 1.05E-05 ***
CS	*r*	0.636; 0.00E-17 ***	-0.150; 0.004 **	-0.489; 0.00E-17 ***	-0.059; 0.263
Lat	r_s	0.031; 0.555	0.054; 0.306	0.041; 0.439	0.018; 0.729
	r	-0.070; 0.185	0.048; 0.362	0.028; 0.591	0.010; 0.850
Long	r_s	-0.355; 1.00E-06 ***	0.183; 0.001 **	0.182; 0.001 **	-0.044; 0.403
	r	-0.376; 1.58E-13 ***	0.144; 0.006 **	0.275; 1.16E-07 ***	-0.047; 0.373
B	r_s	0.315; 1.00E-06 ***	-0.218; 3.03E-05 ***	-0.196; 1.91E-04 ***	0.049; 0.358
	r	0.265; 3.31E-07 ***	-0.175; 0.001 **	-0.180; 0.001 **	0.062; 0.244
E	r_s	0.316; 1.00E-06 ***	-0.212; 5.14E-05 ***	-0.198; 1.56E-04 ***	0.032; 0.549
	r	0.266; 3.02E-07 ***	-0.176; 0.001 **	-0.180; 0.001 **	0.061; 0.253
Call	r_s	-0.580; 1.00E-06 ***	0.469; 1.00E-06 ***	0.235; 2.95E-05 ***	0.005; 0.935
	r	-0.617; 0.00E-17 ***	0.376; 6.80E-12 ***	0.081; 0.152	0.097; 0.087

APPENDIX 3.3 F)

Results of correlation tests between the first four principal component scores (PCS) of dorsal and ventral skull shape of the means of each of 16 vespertilionid species from southern Africa, and centroid size (CS), latitude (Lat), longitude (Long), dominant frequency of the call (for 11 species only) (Call), and different species (Sp). % = variance explained by each principal component axis. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

		PCS1	PCS2	PCS3	PCS4
Dorsal view		36.09%	23.64%	18.44%	12.75%
Sp	r_s	0.185; 0.492	-0.185; 0.492	0.456; 0.076	-0.394; 0.131
	r	-0.081; 0.765	-0.151; 0.576	0.484; 0.058	-0.435; 0.092
CS	r	4.55E-04; 0.999	0.408; 0.116	-0.193; 0.473	-0.889; 4.10E-06 ***
Lat	r_s	0.029; 0.914	-0.009; 0.974	0.138; 0.610	0.641; 0.007 **
	r	0.077; 0.776	-0.191; 0.478	0.207; 0.441	0.578; 0.019 *
Long	r_s	0.012; 0.966	0171; 0.528	0.529; 0.035 *	0.362; 0.169
	r	0.050; 0.854	0.141; 0.603	0.600; 0.014 *	0.370; 0.158
Call	r_s	-0.629; 0.038 *	-0.228; 0.501	0.027; 0.936	0.588; 0.057
	r	-0.412; 0.208	-0.304; 0.307	0.082; 0.812	0.497; 0.120
Ventral view		34.64%	33.51%	16.48%	7.12%
Sp	r_s	-0.276; 0.300	0.003; 0.991	0.247; 0.356	-0.288; 0.279
	r	-0.114; 0.675	-0.005; 0.985	0.298; 0.261	-0.327; 0.216
CS	r	-0.057; 0.834	0.367; 0.162	0.720; 0.002 **	-0.205; 0.445
Lat	r_s	-0.138; 0.610	-0.074; 0.787	-0.274; 0.305	0.015; 0.957
	r	-0.161; 0.552	-0.051; 0.851	-0.254; 0.342	0.047; 0.863
Long	r_s	-0.059; 0.829	0.135; 0.617	-0.394; 0.131	0.012; 0.966
	r	-0.132; 0.626	0.122; 0.653	-0.698; 0.003 **	-0.165; 0.540
Call	r_s	0.446; 0.169	0.009; 0.979	-0.515; 0.105	0.187; 0.582
	r	0.346; 0.297	-0.133; 0.697	-0.274; 0.414	0.324; 0.332

APPENDIX 3.3 G)

Results of correlation tests between the first four principal component scores (PCS) of dorsal and ventral skull shape of all specimens of 10 vesper species from southern Africa (*E. hottentotus*, *N. capensis*, *N. rueppellii*, *N. africanus*, *N.* cf. *melckorum*, *N. rendalli*, *N. zuluensis*, *H. anchietae*, *P. hesperidus*, and *P. rusticus*), and centroid size (CS), latitude (Lat), longitude (Long), dominant frequency of the call (for 6 species only) (Call), and different species (Sp). % = variance explained by each principal component axis. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

		PCS1	PCS2	PCS3	PCS4
Dorsal view		33.13%	12.44%	12.02%	9.68%
Sp	r_s	-0.547; 1.00E-06 ***	0.189; 1.09E-04 ***	0.009; 0.855	0.129; 0.009 **
	r	-0.504; 0.00E-17 ***	0.257; 1.21E-07 ***	0.069; 0.163	0.116; 0.019 *
CS	r	0.740; 0.00E-17 ***	-0.241; 7.61E-07 ***	-0.372; 5.20E-15 ***	0.070; 0.154
Lat	r_s	-0.260; 1.00E-06 ***	0.212; 1.40E-05 ***	0.000; 1.00	-0.036; 0.463
	r	-0.292; 1.49E-09 ***	0.232; 1.97E--6 ***	0.026; 0.595	-0.076; 0.124
Long	r_s	-0.497; 1.00E-06 ***	0.183; 1.82E-04 ***	0.057; 0.250	-0.066; 0.179
	r	-0.468; 0.00E-17 ***	0.157; 0.001 **	0.103; 0.037 *	-0.044; 0.373
Call	r_s	-0.830; 1.00E-06 ***	0.285; 1.00E-06 ***	0.217; 4.24E-05 ***	-0.044; 0.415
	r	-0.881; 0.00E-17 ***	0.247; 2.81E-06 ***	0.049; 0.358	-0.055; 0.303
Ventral view		21.16%	14.11%	10.55%	7.54%
Sp	r_s	-0.486; 1.00E-06 ***	0.208; 1.18E-04 ***	-0.086; 0.115	0.324; 1.00E-06 ***
	r	-0.406; 8.70E-15 ***	0.067; 0.222	-0.091; 0.097	0.354; 2.28E-11 ***
CS	r	0.801; 0.00E-17 ***	0.316; 2.95E-09 ***	-0.072; 0.188	-0.231; 1.77E-05 ***
Lat	r_s	-0.038; 0.492	0.029; 0.598	-0.059; 0.279	0.153; 0.005 **
	r	-0.101; 0.064	0.048; 0.381	-0.064; 0.240	0.179; 0.001 **
Long	r_s	-0.492; 1.00E-06 ***	-0.053; 0.336	0.039; 0.472	0.166; 0.002 **
	r	-0.548; 0.00E-17 ***	-0.166; 0.002 **	0.061; 0.262	0.177; 0.001 **
Call	r_s	-0.801; 1.00E-06 ***	0.088; 0.134	0.024; 0.685	0.334; 1.00E-06 ***
	r	-0.785; 0.00E-17 ***	0.119; 0.043	-0.205; 4.12E-04 ***	0.207; 3.54E-04 ***

APPENDIX 3.3 H)

Results of correlation tests between the first four principal component scores (PCS) of dorsal and ventral skull shape of all specimens of 8 vesper species from southern Africa (*N. capensis, N. rueppellii, N.* cf. *melckorum, N. rendalli, N. zuluensis, H. anchietae, P. hesperidus*, and *P. rusticus)* and centroid size (CS), latitude (Lat), longitude (Long), dominant frequency of the call (for 4 species only) (Call), and different species (Sp). % = variance explained by each principal component axis. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

		PCS1	PCS2	PCS3	PCS4
Dorsal view		19.10%	15.96%	12.75%	11.32%
Sp	r_s	-0.626; 1.00E-06 ***	0.148; 0.008 **	-0.038; 0.502	0.012; 0.832
	r	-0.598; 0.00E-17 ***	0.223; 5.60E-05 ***	-0.076; 0.175	-0.018; 0.751
CS	r	0.513; 0.00E-17 ***	-0.177; 0.001 **	0.273; 6.80E-07 ***	-0.035; 0.533
Lat	r_s	-0.266; 1.27E-06 ***	0.174; 0.002 **	-0.153; 0.006 **	0.074; 0.187
	r	-0.260; 2.25E-06 ***	0.193; 4.85E-04 ***	-0.190; 0.001 **	0.056; 0.320
Long	r_s	-0.355; 1.00E-06 ***	0.133; 0.017 *	-0.142; 0.011 *	0.004; 0.942
	r	-0.263; 1.78E-06 ***	0.105; 0.061	-0.083; 0.135	-0.004; 0.947
Call	r_s	-0.543; 1.00E-06 ***	0.217; 4.03E-04 ***	-0.230; 1.83E-04 ***	0.224; 2.63E-04 ***
	r	-0.520; 0.00E-17 ***	0.197; 0.001 **	-0.227; 2.17E-04 ***	0.233; 1.44E-04 ***
Ventral view		17.00%	11.70%	10.27%	8.84%
Sp	r_s	-0.392; 1.00E-06 ***	-0.259; 1.75E-05 ***	-0.140; 0.021 *	-0.397; 1.00E-06 ***
	r	-0.302; 4.55E-07 ***	-0.291; 1.22E-06 ***	-0.188; 0.002 **	-0.372; 3.02E-10 ***
CS	r	0.473; 1.80E-15 ***	0.084; 0.169	-0.089; 0.147	0.480; 5.00E-15 ***
Lat	r_s	0.008; 0.897	0.112; 0.066	-0.072; 0.242	-0.321; 1.00E-06 ***
	r	-0.021; 0.737	0.092; 0.133	-0.118; 0.054	-0.273; 5.39E-06 ***
Long	r_s	-0.238; 7.93E-05 ***	-0.099; 0.106	0.018; 0.772	-0.275; 4.56E-06 ***
	r	-0.244; 5.29E-05 ***	-0.129; 0.035 *	0.036; 0.561	-0.284; 2.28E-06 ***
Call	r_s	-0.610; 1.00E-06 ***	0.040; 0.554	-0.143; 0.032	-0.427; 1.00E-06 ***
	r	-0.599; 0.00E-17 ***	0.045; 0.504	-0.115; 0.085	-0.437; 6.64E-12 ***

APPENDIX 3.4

Results of multivariate multiple regression analyses within vespertilionid species from southern Africa

Between dorsal and ventral skull shape and centroid size in *Eptesicus hottentotus*, *Neoromicia capensis*, *N. africanus*, *N. zuluensis*, *Pipistrellus hesperidus*, and *P. rusticus* from southern Africa. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Dorsal view	**Wilks lambda**	***F*-value**	**df**	**Significance**
Eptesicus hottentotus	0.691	5.624	14, 176	6.17E-09 ***
Neoromicia capensis	0.327	3.382	14, 23	0.005 **
Neoromicia africanus	0.664	1.340	14, 37	0.232
Neoromicia zuluensis	0.498	1.800	14, 25	0.097
Pipistrellus hesperidus	0.179	3.931	14, 12	0.012 *
Pipistrellus rusticus	0.713	0.661	14, 23	0.787
Ventral view				
Eptesicus hottentotus	0.152	1.526	22, 6	0.314
Neoromicia capensis	0.681	2.882	22, 135	9.592E-05 ***
Neoromicia africanus	0.249	2.194	22, 16	0.056
Neoromicia zuluensis	0.175	1.070	22, 5	0.522
Pipistrellus hesperidus	0.106	3.441	22, 9	0.030 *
Pipistrellus rusticus	0.282	1.040	22, 9	0.504

APPENDIX 3.5

Results of tests for multivariate multiple regression analysis between vespertilionid species from southern Africa

Between dorsal and ventral skull shape and centroid size (RA), and tests for common slopes giving the results of the allometric slopes (AS) and the slopes when size was held allometrically constant (SC) for 16 vespertilionid species from southern Africa (*S. dinganii, M. tricolor, L. namibensis, M. schreibersii, L. botswanae, N. schlieffenii, N. capensis, N. rueppellii, N. africanus, N.* cf. *melckorum, N. rendalli, N. zuluensis, H. anchietae, P. hesperidus*, and *P. rusticus*), 10 species (*E. hottentotus, N. capensis, N. rueppellii, N. africanus, N.* cf. *melckorum, N. rendalli, N. zuluensis, H. anchietae, P. hesperidus*, and *P. rusticus*) and 8 species (*N. capensis, N. rueppellii, N.* cf. *melckorum, N. rendalli, N. zuluensis, H. anchietae, P. hesperidus*, and *P. rusticus*). *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Dorsal view	**Wilks lambda**	***F*-value**	**df**	**Significance**
16 species				
RA	0.334	59.971	14, 422	5.284E-091 ***
AS	0.582	1.047	210, 2065.7	0.312
SC	0.017	9.771	210, 4220.2	1.929E-233 ***
10 species				
RA	0.306	64.250	14, 397.0	1.005E-092 ***
AS	0.678	1.207	126, 2909.5	0.061
SC	0.078	9.368	126, 2978.3	1.062E-138 ***
8 species				
RA	0.5324	19.257	14, 307.0	2.177E-034 ***
AS	0.6747	1.220	98, 1862	0.075
SC	0.156	6.651	98, 1906.3	1.799E-068 ***
Ventral view				
16 species				
RA	0.232	50.542	22, 336	1.300E-092 ***
AS	0.423	0.837	330, 3853.2	0.983
SC	0.002	7.772	330, 4039.7	7.395E-248 ***
10 species				
RA	0.218	51.245	22, 314	3.780E-090 ***
AS	0.561	0.900	198, 2495.6	0.832
SC	0.023	6.945	198, 2570.9	2.088E-132 ***
8 species				
RA	0.378	18.430	22, 246	2.932E-040 ***
AS	0.551	0.946	154, 1565.8	0.665
SC	0.1064	4.157	154, 1612.8	4.691E-048 ***

CHAPTER 4

CRANIOMETRIC MEASUREMENT SELECTION

4.1 INTRODUCTION

Prior to a traditional morphometric analysis of southern African vesper bats from the genera *Eptesicus, Hypsugo, Neoromicia* and *Pipistrellus,* univariate and multivariate statistical procedures were used, following the suggested methods of Chimimba and Dippenaar (1995). These analyses were implemented to select a set of statistically problem-free morphometric measurements, so as to reduce redundancy and yet reflect the three-dimensional shape of the skull in a pattern consistent with the concept of morphological integration (Olson and Miller, 1958; Cheverud, 1982).

4.2 MATERIAL AND METHODS

Thirty-one undamaged specimens of *Neoromicia africanus* (22 females and 9 males) from Kruger National Park in South Africa were used in the core analysis of measurement selection (see Appendix 4.1 for details of the specimens used). Specimens from three other taxa of similar size and relatively difficult to distinguish, were used to provide measurement weightings on the first three principal components of an R-mode PCA indicating which measurements were most important in distinguishing between species: 17 *Neoromicia capensis* (eight females and nine males) from Nossob; 14 *N. zuluensis* (nine females and five males) from Kruger National Park; and 30 *Pipistrellus hesperidus* (12 females and 18 males) from KwaZulu-Natal (Appendix 1).

An initial set of 52 cranial measurements (Fig. 4.1 and Appendix 4.2) were recorded from each specimen. The measurements chosen were previously used in other morphometric studies of bat crania, some of which were on other vesper bat species (de Paz, 1994; Kitchener & Caputi, 1985; Kitchener *et al.*, 1986; Kitchener *et al.*, 1987; Kitchener *et al.*, 1993a; Kitchener *et al.*, 1993b; Rautenbach, 1986; Schlitter & Aggundey, 1986; Tidemann *et al.*, 1981). The measurements were chosen to encompass qualitative characters used in keys to describe each species (Koopman, 1966; Meester *et al.*, 1986). Of these, 13 measurements were recorded to the nearest 0.01mm using Mitutuyo digital calipers, the remaining 39 measurements were recorded (rounding off values to the second decimal place) using a Kyowa stereo microscope with an ocular micrometer.

Data were screened to detect outliers using univariate statistics (mean, standard deviation and observed range) and principal component analysis (PCA). The data were also tested for skewness (g_1), kurtosis (g_2), normality (Kolmogorov-Smirnov Dmax test) (Zar, 1996) and measurement error using the sum of squared deviations from a model II ANOVA following Yezerinac *et al.* (1992). Statistically problematic measurements were removed if they showed significance in one or more test at the $P < 0.01$ level, if significance in two or more tests was at the $P < 0.05$ probability level, or measurement error was greater than 10%.

The remaining statistically problem-free measurements were subjected to a Q-mode PCA . This was followed by a Ward's (1963) cluster analysis based on a Euclidean distance matrix calculated from projected eigenvector scores of principal components (using the same number of principal components as that of variables). Measurements were then chosen from phenotypic sets (Cheverud, 1982) using the same criteria as Chimimba and Dippenaar (1995). These were: relative weightings of measurements on the first three principal components of an R-mode PCA of four taxa (*N. africanus, N. capensis, N. zuluensis*, and *P. hesperidus*); coefficients of variation, using Haldane's (1955) correction; measurement error, based on three repeated sets of measurements recorded for 36 *Neoromicia africanus* (22 females and 14 males) from Kruger National Park (see Appendix 4.1); and how often the measurement was missing data due to damage. The statistical packages NTSYS-pc, version 2.01h (Rohlf, 1997), SPSS 9.0.1 (SPSS Inc., 1999), and STATISTICA 5.5 (StatSoft, Inc., 2000) were used for the analyses.

4.3 RESULTS AND DISCUSSION

Table 4.1 lists basic statistics and results of the tests for normality and measurement error for the 31 *N. africanus* analysed. The following 23 statistically problematic measurements were rejected following the criteria outlined in the materials and methods section: PPL, ROSTH, LAS, WOUI2, WIUI2, WOUI3, WUI2, WUI3, WUM1, WUM3, LUPM2, LUM3, LLTR, LMTR, DENTT, LCON, CLCON, LPM2W, LPM4W, LM3W, LPM2L, LPM4L, and LM3L. Two measurements of incisor height (HUI2 and HUI3) were removed as they varied in some taxa due to tooth wear. Two measurements of the minute second upper premolar (WIUPM2 and WUPM2) were removed to accommodate those taxa lacking this tooth. The remaining 25 measurements

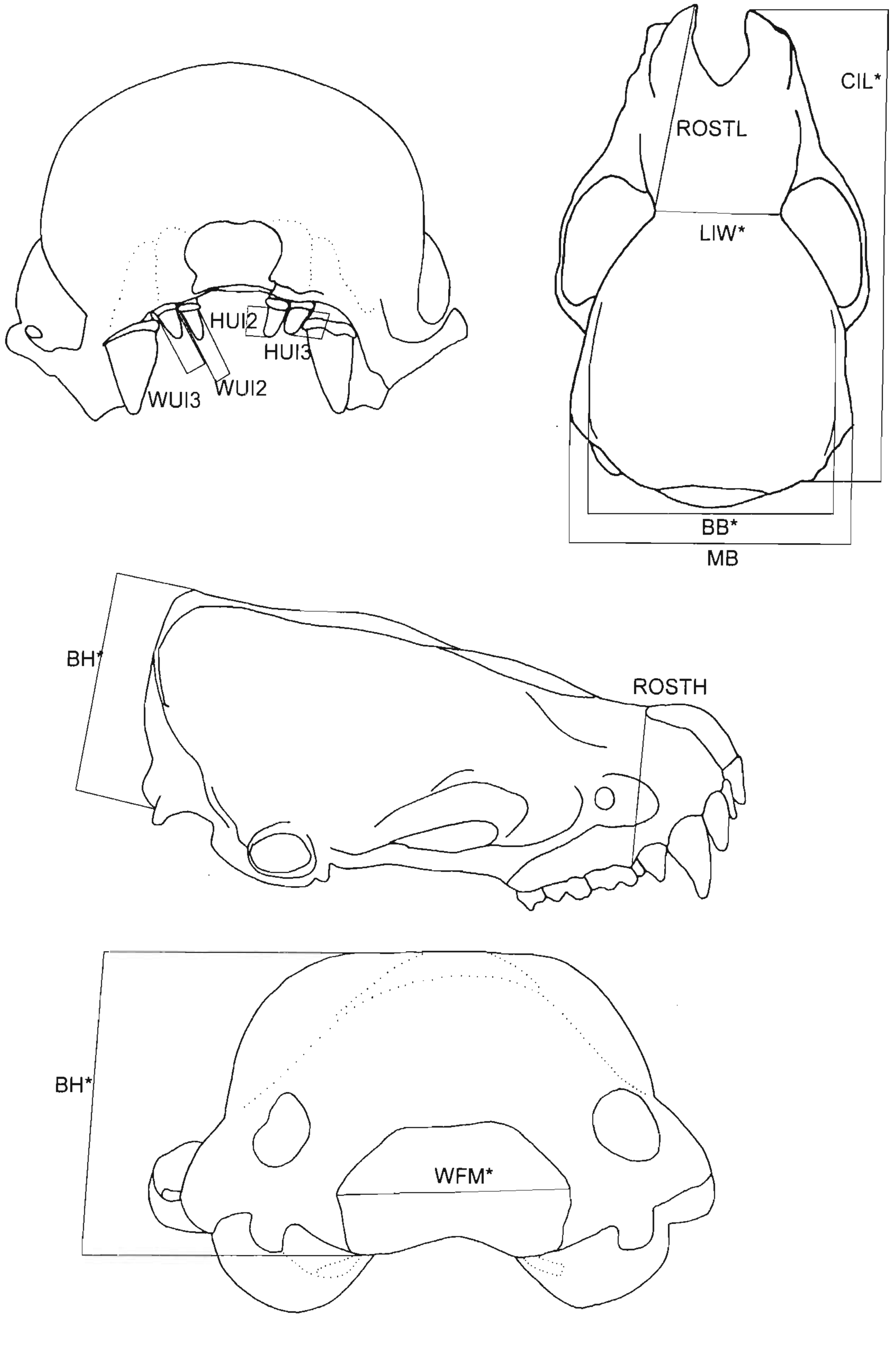


Figure 4.1 A) Views of a *Neoromicia* skull showing measurements which were used in traditional morphometric analyses. See Appendix 4.2 for full names and descriptions of measurements. * indicates measurement chosen for use in subsequent morphometric analyses.

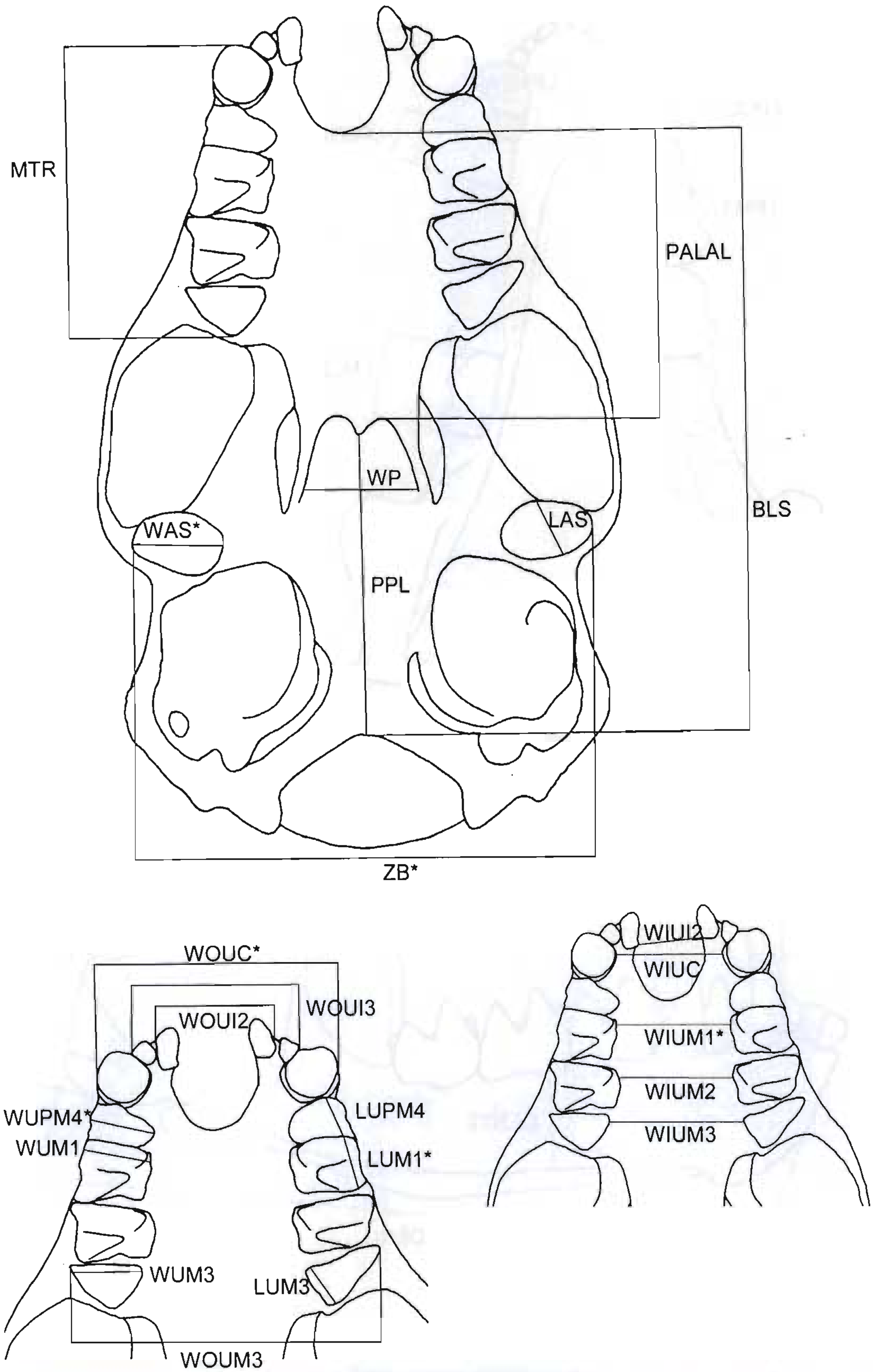


Figure 4.1 B) Views of a *Neoromicia* skull showing measurements which were used in traditional morphometric analyses. See Appendix 4.2 for full names and descriptions of measurements. * indicates measurement chosen for use in subsequent morphometric analyses.

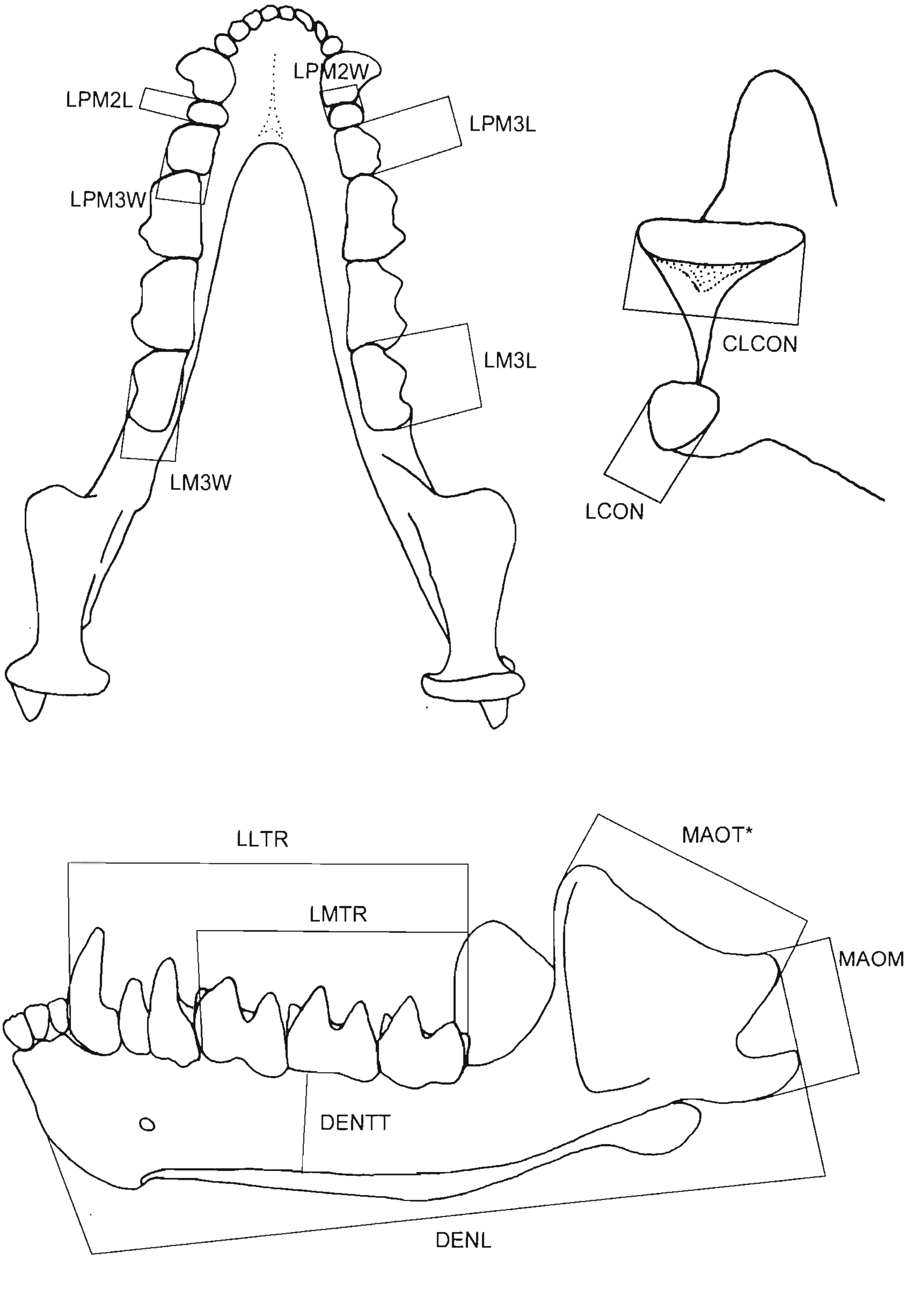


Figure 4.1 C) Views of a *Neoromicia* mandible showing measurements which were used in traditional morphometric analyses. See Appendix 4.2 for full names and descriptions of measurements.* indicates measurement chosen for use in subsequent morphometric analyses.

Table 4.1. Basic statistics (mean, standard deviation, and range) and results of tests of normality (Kolmogorov-Smirnov, skewness and kurtosis) of 52 measurements from 31 *Neoromicia. africanus* and % ME from 36 *N. africanus* from Kruger National Park. * = $P > 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. SD = standard deviation; Min. = minimum; Max. = maximum; K-S = Kolmogorov-Smirnov; Skew = skewness.

	Mean	SD	Min.	Max.	K-S	Skew	Kurtosis	%ME
CIL	11.08	0.35	10.25	11.93	0.065	0.033	0.542	0.89
BLS	8.65	0.33	7.98	9.23	0.119	0.015	-0.763	2.34
BH	4.21	0.20	3.82	4.66	0.106	0.516	-0.051	5.39
ZB	6.40	0.22	5.99	6.81	0.077	0.002	-0.902	2.33
BB	6.14	0.16	5.82	6.44	0.122	-0.049	-0.612	1.73
MB	6.79	0.20	6.37	7.12	0.114	-0.352	-0.719	1.26
POW	3.44	0.11	3.22	3.65	0.101	0.039	-0.67	0.20
MTR	3.96	0.18	3.65	4.39	0.103	0.321	0.029	0.14
ROSTL	4.76	0.20	4.37	5.25	0.081	0.199	0.201	0.22
PPL	4.63	0.19	4.33	5.26	0.144	1.308**	3.299*	7.65
PALAL	4.22	0.24	3.81	4.72	0.096	0.293	-0.737	5.55
WFM	3.13	0.13	2.90	3.39	0.152	-0.155	-0.809	3.63
ROSTH	3.04	0.15	2.59	3.28	0.168*	-1.011*	2.05*	5.45
LAS	1.12	0.08	0.92	1.27	0.198**	-0.631	-0.085	6.79
WP	1.61	0.09	1.48	1.78	0.147	0.114	-0.877	2.25
WAS	1.22	0.10	1.02	1.43	0.132	-0.051	-0.588	6.11
WOUI2	1.64	0.10	1.53	1.93	0.195**	1.133*	1.463	15.50
WIUI2	0.98	0.07	0.87	1.12	0.211**	0.583	-0.141	24.04
WOUI3	2.29	0.13	2.14	2.60	0.199**	1.006*	0.388	1.87
WIUC	2.02	0.10	1.78	2.24	0.132	-0.024	0.184	4.52
WOUC	3.47	0.18	2.90	3.82	0.135	-0.644	2.054*	3.25
WIUPM2	2.52	0.13	2.24	2.75	0.115	-0.354	0.098	0.83
WIUM1	2.34	0.10	2.14	2.60	0.132	0.327	0.143	1.99
WIUM2	2.34	0.10	2.14	2.49	0.125	0.026	-0.709	1.67
WIUM3	2.49	0.10	2.29	2.75	0.155	0.614	0.542	1.00
WOUM3	4.76	0.20	4.38	5.19	0.124	0.243	0.082	0.82

Table 4.1. Continued.

	Mean	SD	Min.	Max.	K-S	Skew	Kurtosis	%ME
WUI2	0.31	0.03	0.24	0.34	0.223***	-0.299	-1.034	5.53
WUI2	0.35	0.03	0.27	0.44	0.291***	0.598	2.116*	6.35
HUI2	0.45	0.06	0.34	0.61	0.113	0.332	0.232	2.39
HUI3	0.48	0.06	0.37	0.64	0.158*	0.747	0.358	0.97
WUPM2	0.32	0.04	0.27	0.41	0.177*	0.401	-0.357	4.51
WUPM4	0.70	0.09	0.54	0.88	0.157	0.343	-0.471	2.11
WUM1	0.95	0.07	0.85	1.12	0.198**	0.754	-0.187	2.29
WUM3	1.12	0.07	0.98	1.22	0.133	-0.267	-0.646	37.50
LUPM2	0.35	0.04	0.24	0.41	0.267***	-0.753	1.766	10.05
LUPM4	0.65	0.07	0.54	0.78	0.136	0.181	-0.979	8.39
LUM1	1.05	0.06	0.92	1.15	0.165*	-0.389	-0.271	2.00
LUM3	0.67	0.04	0.58	0.71	0.228***	-0.527	0.055	3.90
DENL	8.10	0.33	7.43	8.75	0.080	0.1	-0.486	1.13
LLTR	4.32	0.18	3.97	4.78	0.183**	0.767	1.563	1.81
LMTR	2.80	0.12	2.65	3.05	0.224***	0.672	0.42	5.62
MAOT	2.457	0.10	2.29	2.65	0.132	0.309	-0.358	1.30
DENTT	0.80	0.08	0.71	1.02	0.178*	0.895*	0.763	3.58
MAOM	1.49	0.13	1.27	1.78	0.106	0.043	-0.442	1.40
LCON	0.33	0.10	0.15	0.56	0.176*	0.336	0.137	11.40
CLCON	0.94	0.08	0.81	1.07	0.193**	-0.096	-1.149	2.19
LPM2W	0.42	0.03	0.37	0.47	0.312***	0.403	0.204	9.57
LPM4W	0.48	0.03	0.41	0.54	0.196**	0.214	-0.637	12.24
LM3W	0.68	0.04	0.61	0.78	0.199**	0.336	-0.119	4.35
LPM2L	0.49	0.03	0.41	0.54	0.244***	-0.566	0.234	3.63
LPM4L	0.61	0.05	0.51	0.75	0.199**	0.417	0.932	3.35
LM3L	0.92	0.06	0.78	1.05	0.205**	-0.223	0.264	2.20

(CIL, BLS, BH, ZB, BB, MB, POW, MTR, ROSTL, PALAL, WFM, WP, WAS, WIUC, WOUC, WIUM1, WIUM2, WIUM3, WOUM3, WUPM4, LUPM4, LUM1, DENL, MAOT, MAOM) were subjected to a Ward's cluster analysis. Twelve phenotypic sets were identified in the phenogram (Fig. 4.2) and one measurement was chosen from each set based on the criteria described in the materials and methods section to give a final set of twelve measurements: CIL, BH, ZB, BB, POW, WFM, WAS, WOUC, WIUM1, WUPM4, LUM1, MAOT. Thus 12 statistically problem-free and redundancy-reduced cranial measurements were selected, from an initial set of 52 measurements, for analysis in subsequent morphometric analyses.

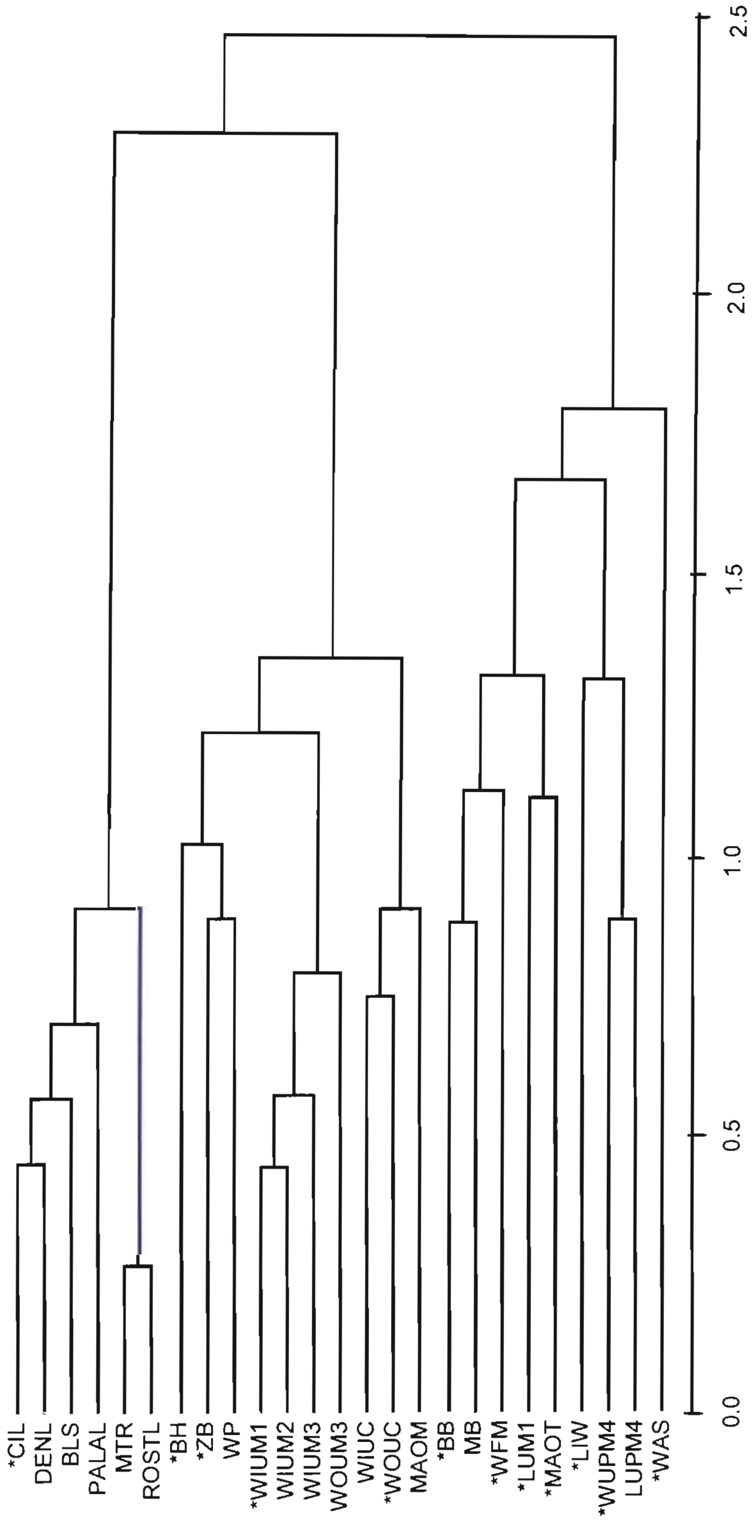


Figure 4.2 Phenogram based on Ward's (1963) hierarchical clustering of Euclidian distances between 25 craniometric variables in 25-dimensional principal component space, computed from single standardized data for 31 *Neoromicia africanus* from the Kruger National Park in South Africa. See Appendix 4.2 for explanation of measurement abbreviations.

APPENDIX 4.1

Specimens examined for measurement selection

Acronyms: DM - Durban Natural Science Museum, South Africa; TM - Transvaal Museum, Pretoria, South Africa. F = female, M = male.

1) **Specimens used in measurement selection analysis** (* denotes specimens also used to calculate measurement error):

Neoromicia nanus: **SOUTH AFRICA**: LIMPOPO PROVINCE: Kruger National Park, Old Bridge over Nwanedzi River(2431BD): TM39621* (M). Kruger National Park, Pafuri, Anthrax Camp (2231AC): TM36647* (F). Kruger National Park, Pafuri, Culling Camp(2231AD): TM37841* (F); TM37842 (F). Kruger National Park, Pafuri, Fig Tree Camp (2231AC): TM36709 (M); TM39463* (F). Kruger National Park, Pafuri, New Fig Tree Forest (2231AD): TM37856 (F); TM37857* (F). Kruger National Park, Pafuri, Mockford's Garden (2231AD): TM37849* (M); TM38607* (F); TM38608* (F); TM38609* (F); TM38610* (F); TM38612* (F); TM39465* (F); TM39466* (F); TM39467* (M). Kruger National Park, Pafuri, Old Picnic Site, (2231AD): TM37816 (F); TM37817* (F); TM37818 (F); TM37820* (F); TM37919 (F). Kruger National Park, Satara Rest Camp (2431BD): TM39642* (M); TM39643* (M). Kruger National Park, Shingwedzi Camp (2331AB): TM38319* (F); TM38322* (F). Kruger National Park, Skukuza Staff Village(2431DC): TM42126* (M); TM42127* (F); TM42129* (F). Kruger National Park, Pafuri, Picnic Site (2231AD): TM41731* (M). Kruger National Park, Pafuri, Fig Tree Forest (2231AD): TM38604* (M).

Neoromicia capensis: **SOUTH AFRICA**: NORTHERN CAPE PROVINCE: Kalahari Gemsbok National Park, Marie se Gat (2520DA): TM35584 (F); TM35585 (F); TM35586 (F); TM35587 (F); TM35588 (F); TM35589 (F); TM35591 (F); TM35592 (F); TM35593 (M); TM35594 (M); TM35595 (M); TM35596 (M); TM35597 (M); TM35598 (M); TM35599 (M); TM35600 (M); TM35602 (M).

Neoromicia zuluensis: **SOUTH AFRICA**: LIMPOPO PROVINCE: Kruger National Park, 4 km W of the bridge, Levuvhu Hippo Pool (2231AC): TM30534 (F); TM34213 (F). Kruger National Park, Pafuri, Anthrax Camp (2231AC): TM37863 (F); TM36846 (F). Kruger National Park, Pafuri, Culling Camp (2231AD): TM37938 (M). Kruger National Park, Pafuri, Fig Tree Camp, (2231AC): TM37436 (F); TM36759 (F); TM37001 (F); TM37017 (M). Kruger National Park, Pafuri, Fig Tree Forest, 4.8 km downstream (2231AD): TM37678 (M). Kruger National Park, Pafuri, Old Picnic Site (2231AD): TM36631 (F). Kruger National Park, 12 km E Phalaborwa Gate, Erfplaas Windmill (2331CC): TM36572 (F). Kruger National Park, 2 km SE Roodewal Private Camp (2431BA): TM39684 (M). Kruger National Park, Shashanga Windmill (2230DB): TM30672 (M).

Pipistrellus hesperidus: **SOUTH AFRICA**: KWAZULU-NATAL: St Lucia, Ipheva Camp (2832AD): DM1063 (M); DM1064 (M); DM6895 (F); DM6896 (M). Dukuduku Forest (2832AD): TM40406 (F); TM30126 (M); TM40410 (M). Eshowe, Dlinza Forest (2831CD): DM5352 (F); DM5356 (M); DM5360 (M); DM5363 (F); DM5372 (F); DM5374 (F); DM5386 (M); DM5393 (F); DM5397 (M); DM5406 (F). Mtunzini, Twin Streams Farm (2831DC): DM5872 (M). Mtunzini, Umlalazi Nature Reserve (2831DC): TM30126 (M). Harold Johnson Nature Reserve (2931AB): DM5369 (M). Mount Edgecombe, SASEX (2931CA): DM7143 (M). Durban, 108 Bowen Avenue, (2930DD): DM6893 (F). Durban, Cowies Hill (2930DD): DM7201 (M). Durban, Kranskloof Nature Reserve (2930DD): DM5876 (M); TM40014 (M); TM40015 (F). Durban, North Park Nature Reserve (2930DD): DM5382 FB; DM5403 (M). Durban, Pigeon Valley Park (2930DD): DM5384 (M). Durban, Stainbank Nature Reserve (2930DD): DM5868 (M). Durban, Malvern (2930DD): TM1085 (F).

APPENDIX 4.1 continued

2) Additional specimens used in the calculation of measurement error (but not used in analysis of measurement choice due to missing measurements):

Neoromicia nanus: **SOUTH AFRICA**: LIMPOPO PROVINCE: Pafuri, New Fig Tree Camp (2231AC): TM37907 (F). Pafuri, Mockford's Garden (2231AD): TM38523 (F); TM38611 (M). Pafuri, Old Picnic Site at Levuvhu (2231AD): TM43862 (F); TM43863 (M). Pafuri, Shingwedzi Camp (2331AB): TM38317 (F); TM38318 (F); TM38320 (M); TM38321 (M). Pafuri, Levuvhu River, Fig Tree Camp (2231AC): TM36120 (M). Pafuri, Fig Tree Forest (2231AD): TM38605 (M).

APPENDIX 4.2

Description of 52 cranial measurements used in character selection

* = characters important in previous morphometric studies, including studies of other vesper species (de Paz, 1994; Kitchener & Caputi, 1985; Kitchener *et al.*, 1986; Kitchener *et al.*, 1987; Kitchener *et al.*, 1993a; Kitchener *et al.*, 1993b; Rautenbach, 1986; Schlitter & Aggundey, 1986; Tidemann *et al.*, 1981).
+ = measurement of qualitative characters used in keys to describe the species (Koopman ; Meester *et al.*,1986).

Cranial measurements recorded under the microscope using calipers:
1) * Condyloincisor length (CIL) - from posterior-most part of occipital to anterior-most point of the incisors.
2) * Basilar length of the skull (BLS) - from posterior edge basioccipital to anterior edge of palate.
3) *+ Height of braincase (BH) - behind bullae.
4) * "Zygomatic breadth" (ZB) - since the zygomatic arches were usually broken, this measurement was modified to measure the width at the point of the squamosal attachment, hence measuring the width at the widest outside edges of the mandibular fossa.
5) *+ Breadth braincase (BB) - widest region of the braincase.
6) Breadth at mastoids (MB) - greatest breadth at mastoid processes.
7) * Least inter-orbital width (LIW) - width at the most constricted part of skull.
8) * Maxillary tooth row (MTR) - length from anterior alveolar border of canine to posterior alveolar border of M^3.
9) + Rostral length (ROSTL) - from anterior edge of I^1 to posterior edge of M^3 (in both cases where tooth and skull meet).
10) + Post-palatal length (PPL) - most anterior point of posterior palate edge to most anterior mid-point of basioccipital.
11) *+ Palatal length (PALAL) - from posterior border of hard palate to anterior border of premaxillary bone.
12) * Greatest width of foramen magnum (WFM).
13) Rostral height (ROSTH) - maximum height from between M^1 and highest point of nasals.

Cranial measurements recorded with a microscope and ocular micrometer:
14) Length of mandibular fossa / articular surface (LAS).
15) Width of pterygoids, at the most parallel region (WP).
16) Width of mandibular fossa / articular surface (WAS).
17) Outer breadth of upper first incisors (WOUI2) - width from outside edges at the level of the cingulum.
18) Width at inner upper first incisors (WIUI2) - width between inner edges of upper first incisors, just above the cingulum.
19) Outer breadth of upper second incisors (WOUI3) - width from outside surfaces.
20) Inner width between upper canines (WIUC) - width between inner edges of the cingula.
21) + Width between upper canines (WOUC) - from outside surfaces at level of the cingulum.
22) Width at inner upper second premolars (WIUPM2) - width between inner edges of the cingula.
23) *+ Width at inner upper first molars (WIUM1) - width between inner edges of the cingula.
24) * Width at inner upper second molars (WIUM2) - width between inner edges of the cingula.
25) *+ Width at inner upper third molars (WIUM3) - width between inner edges of the cingula.
26) + Width between upper third molars (WOUM3) - from outside surfaces at level of the cingulum.
27) + Width of I^2 (WUI2) - measuring just above the cingulum.
28) + Width of I^3 (WUI3) - measuring just above the cingulum.
29) + Height of I^2 (HUI2) - from cingulum to top edge.
30) + Height of I^3 (HUI3) - from cingulum to top edge.
31) + Width of PM^2 ($WUPM^2$) - greatest lateral-medial width of tooth.
32) Width of PM^4 ($WUPM^4$) - greatest lateral-medial width of tooth.
33) Width of M^1 (WUM1) - greatest lateral-medial width of tooth.
34) Width of M^3 (WUM3) - greatest lateral-medial width of tooth.
35) + Length of PM^2 ($LUPM^2$) - longest anterior-posterior length.
36) Length of PM^4 ($LUPM^4$) - longest anterior-posterior length.
37) Length of M^1 (LUM1) - longest anterior-posterior length.

APPENDIX 4.2 continued

38) Length of M^3 (LUM3) - longest anterior-posterior length.

Dentary measurement recorded under the microscope using calipers:
39) Dentary length (DENL) - from mid-point of mandibular condyle to anterior-most point of dentary.

Dentary measurements recorded with a microscope and ocular micrometer:
40) Lower tooth row (LLTR) - length from posterior cingulum of M_3 to anterior cingulum of C_1.
41) Length of lower molar tooth row (LMTR) - greatest length from posterior cingulum of M_3 to anterior cingulum of M_1.
42) Moment arm of temporal (MAOT) - length from outside edge of condyle to outside edge of coronoid process.
43) Dentary thickness (DENTT) - width of dentary from base of protoconid of M_2 to edge of mandible.
44) Moment arm of masseter (MAOM) - length from middle of outside edge of condyle to outside edge of angular process.
45) Length of condyle (LCON) - largest medial-lateral length of condyle surface.
46) Length of condylar process condyle (CLCON) - largest medial-lateral length.
47) + PM_2 width (LPM2W) - greatest lateral-medial width of tooth.
48) + PM_4 width (LPM4W) - greatest lateral-medial width of tooth.
49) M_3 width (LM3W) - greatest lateral-medial width of tooth.
50) + PM_2 length (LPM2L) - longest anterior-posterior length.
51) + PM_4 length (LPM4L) - longest anterior-posterior length.
52) M_3 length (LM3L) - longest anterior-posterior length.

CHAPTER 5

ANALYSIS OF SEXUAL DIMORPHISM AND TOOTH WEAR CLASS VARIATION IN TRADITIONAL CRANIAL MEASUREMENTS

5.1 INTRODUCTION

Intra-population variation in cranial and external body measurements has been recorded for many mammal groups and is thought to be a function of differences in sex, age, season, cohort, and individuals (see references in Chimimba and Dippenaar, 1994; Bronner, 1996a). However, since variations due to season, cohort and individual are more difficult to assess, especially in small mammals which are notorious for small data sets that hardly ever meet the required adequate sample sizes, most analyses concentrate on variation due to sex and age. Intra-population or non-geographic variation due to sex and age may be sufficiently marked as to obscure patterns of geographic and inter-specific variation (Leamy, 1983; Plavcan, 2002; Straney, 1978; Thorpe, 1983). Therefore, it is advisable to identify whether different sexes and tooth wear classes should be treated together or separately, prior to analyses of geographic and inter-specific variation .

As discussed in the chapter on shape morphometrics (Chapter 3) sexual dimorphism, with females being larger than males, has been recorded in a number of vespertilionid bat species occurring in North and South America (Burnett, 1983; Findlay & Traut, 1970; Myers, 1978; Williams and Findlay, 1979), Europe (Bogdanowicz and Owen, 1996) and Australia (Carpenter *et al.*, 1978; Kitchener *et al.*, 1986; Kitchener *et al.* 1987; Kitchener and Caputi, 1985). On the other hand, Willig and Hollander (1995) did not find sexual dimorphism in *Eptesicus furinalis* and *Myotis riparia* from north-eastern Brazil based on 12 cranial characters. However, only the studies of Williams and Findlay (1979) and Willig and Hollander (1995) assessed intra-population variation, since Willig and Hollander (1995) noted that systematists frequently consider sexual dimorphism as if it were a species specific attribute rather than a population level phenomenon. Although Burnett (1983) assessed sexual dimorphism in *Eptesicus fuscus* from the means of measurements for 93 different geographic localities, he acknowledged that this may not be representative of the entire range of the species and hence also assessed sexual dimorphism in 13 diverse localities and subspecies. Burnett (1983) then found considerable variation in the characters that were dimorphic as well as some variation in the direction of the dimorphism, given a few cases where males were larger than females. Willig and Hollander (1995) also analysed sexual dimorphism across different populations of the same species, but found no sexual dimorphism in either one of the two populations of *Myotis riparia* they tested. Neither of these studies, however, included variation due to age.

In chapter 3, the only test of intra-population variation, performed in a single population of *N. capensis* from Jagersfontein in the Free State Province of South Africa found no significant variation in centroid size (used as a measure of geometric size) and shape between different sexes and tooth wear classes (used as a relative measure of age). However, in analyses of sexual dimorphism and tooth wear class variation across different localities of six species, significant sexual dimorphism of centroid size of the skull (with females being slightly larger than males) was identified in four species (*N. capensis*, *N. africanus*, *N. zuluensis* and *P. hesperidus*). Similarly, significant variation between tooth wear classes was identified in one species (*E. hottentotus*) such that skull centroid size increased significantly and then decreased with tooth wear class. Aside from this pattern of variation, with increasing tooth wear is also expected that assuming the arbitrary measure of tooth wear reflected age, the variation in size across the tooth wear classes would be an increase in size with increasing age / tooth wear. Another possibility, albeit rarely documented, would be a decrease in size with increasing age / wear, as was found in the fruit bat, *Cynopterus brachyotis brachyotis* from Bali (Kitchener and Foley, 1985).

No other study has evaluated intra-population variation due to sexual dimorphism and variation due to age in vespertilionid bat species occurring in southern Africa. However, an analysis of the horseshoe bat, *Rhinolophus denti* from Koegelbeen Cave in the Northern Cape Province of South Africa found significant sexual dimorphism in three cranial and two external characters, and significant variation between the tooth wear classes in two cranial characters (Rautenbach, 1986). Furthermore, an analysis of the slit-faced bat *Nycteris thebaica* at Mlawula Nature Reserve in Swaziland, found significant sexual dimorphism with females being heavier and having longer forearms than males (Monadjem, 2001).

Thus, the aims of this chapter were as follows:

1. To examine (as far as possible given the limitation of small sample sizes from single localities), the nature and extent of variation in traditional cranial and external body

morphometric measurements due to intra-population sexual dimorphism and tooth wear class variation (used as an arbitrary measure of age) within nine different species of vespertilionid bats of the genera *Eptesicus, Hypsugo, Neoromicia* and *Pipistrellus* from southern Africa.

2. To assess intra-population sexual dimorphism and tooth wear class variation across different parts of the species distribution range by assessing variation in cranial measurements within three species (*E. hottentotus*, *N. africanus* and *N. capensis*) and variation in external body measurements within three species (*N. africanus, N. rueppellii*, and *N. capensis)*.
3. On the basis of the results, to decide whether the sexes and different tooth wear classes of the different species should be pooled for geographic and inter-specific analyses.

5.2 MATERIAL AND METHODS

Analyses of cranial and external measurements were made of nine vespertilionid bat species occurring in southern Africa (*E. hottentotus*, *H. anchietae*, *N. capensis*, *N.* cf. *melckorum*, *N. africanus*, *N. rueppellii*, *N. zuluensis*, *P. hesperidus* and *P. rusticus*). Appendix 1 provides details of the specimens used in this analysis, together with locality numbers to allow identification of the locality for each individual in the multivariate analyses. Of the species of *Eptesicus*, *Neoromicia* and *Pipistrellus*, only *N. rendalli* was excluded because sample sizes were too small. Although specimen numbers from single localities were usually small in almost all the species, the wide geographic coverage of specimens of certain species allowed more than one analysis per species. This provided an opportunity to identify intra-specific differences in non-geographic sexual dimorphism and tooth wear class variation across different geographic areas. Hence, there were two different analyses each for *E. hottentotus* and *N. rueppellii*, three different analyses for *N. africanus* and six different analyses for *N. capensis*. Although specimens from southern Africa were the primary focus of the study, two additional data suites of external measurements of *N. africanus* from Malawi and of *N. rueppellii* from Zambia were included.

As with museum collections of most small mammals, the majority of the species were represented by small samples from single localities, and although the aim of this section was to assess intra-population or non-geographic variation, small sample sizes meant specimens were pooled from more than one locality. Given the finding of Miller-Butterworth *et al.* (2003) that genetic structure in *Miniopterus schreibersii natalensis* was correlated with local biomes, specimens from different localities were pooled so as to minimise geographic variation and to sample from a single biome only. For southern Africa, the vegetation biomes of Rutherford and Westfall (1994) were following using the GIS shape file "SA Biomes (Rutherford)" available at the South African National Biodiversity Institute (SANBI) website http://www.plantzafrica.com/vegetation/vegmain.htm. For other areas in Africa, the biomes of Olsen and Dinerstein (1998) and Olsen *et al.* (2001) were followed using the shape file data available at the World Wildlife Fund (WWF) Global 200 Ecoregions website http://worldwildlife.org/science/data/terreco.cfm. Pooling data from different localities is usually considered a dubious practice in analyses of intra-population variation since it potentially introduces geographic variation into the analyses (Dippenaar and Rautenbach, 1986; Thorpe, 1976). However, awareness of this caveat and screening results for any variation due to difference in locality, allows the assessment of greater numbers of species and geographic areas.

Twelve cranial measurements chosen in the previous section on measurement selection (Chapter 4) were measured on each of the specimens to the nearest 0.01mm using Mitutuyo digital calipers, or a Kyowa stereo microscope with an ocular micrometer rounding off values to the second decimal place. The measurements were:

1. Condylo-incisor skull length (CIL);
2. Braincase height (BH);
3. Zygomatic breadth (ZB);
4. Braincase breadth (BB);
5. Least inter-orbital width (LIW);
6. Greatest width of foramen magnum (WFM);
7. Greatest width of mandibular fossa / articular surface (WAS);
8. Width across outer surfaces of the upper canine teeth, measured at the level of the cingulum (WOUC);
9. Width between inner surfaces of the upper first molar teeth, measured at the level of the cingulum (WIUM1);

10. Width of upper fourth premolar tooth (WUPM4);
11. Length of upper first molar tooth (LUM1); and
12. Moment arm of temporal: length between the condylar and the coronoid processes of the mandible (MAOT).

Where possible, five external body measurements were transcribed from specimen records:

1. Total body length (TOT) or head and body length (HB);
2. Tail length (T);
3. Hind foot length (HFL);
4. Forearm length (FAL); and
5. Ear length (E).

Hind foot (HF), forearm (FA) and tail lengths (TL) were also recorded from dried skins to compensate for instances where these measurements were missing from the specimens records. However, given the shrinkage associated with dried skins, the dried skin measurements were kept separate from measurements taken from the specimen records. The following four additional body measurements were also measured directly from dry skins to the nearest 0.01mm using Mitutuyo digital calipers:

1. Tibia length (TIB);
2. Length of third metacarpal (TMETA);
3. Tragus length from ear notch to the tip of the tragus (TRL); and
4. Tragus breadth at widest part just below tip (TRB).

The same specimens were not always represented in both cranial and external measurement data suites, since some specimens included in the analyses of external measurements were not included in the analyses of 12 cranial measurements due to broken skulls resulting in missing measurements (See Appendix 5.1).

In the absence of known-age specimens, an arbitrary relative measure of age was assessed, in which specimens were assigned to one of four tooth wear classes (adapted from Rautenbach, 1986) based on the degree of erosion pattern on molar teeth (see Appendix 5.2). Thus, age was measured under the assumption that older specimens have more tooth wear than younger specimens. However, as was mentioned in the chapter on shape morphometrics (Chapter 3), tooth wear may not only be a function of time but may also reflect differences in diet, environment, habitat and or health (Pessoa and Dos Reis, 1991a and b).

Given the problem of accurate species identification for many of the nine species investigated using the existing identification keys, discriminant function analysis (DFA) and PCA were run for each species combining specimens of "known" identity based on chromosome and/ or bacula information (Kearney *et al.*, 2002) with specimens identified using external morphological characters to identify misidentified specimens. Nine specimens were re-assigned species identification based on these DFA and PCA analyses (see Appendix 5.3). PCA was also used to screen the data for outliers. Measurements causing specimens to be outliers were either resolved or specimens were removed from further analyses.

Due to specimens missing cranial and/or external measurements, cranial and external measurements were analysed as separate data suites. Univariate analyses included the computation of summary statistics (arithmetic mean, standard deviation, coefficient of variation, and minimum and maximum values); skewedness (g_1) and kurtosis (g_2) statistics (Appendix 5.4); Model III (for unequal cell numbers) one-way analyses of variance (ANOVA) of sex and tooth wear class (which considering a two-tailed test between means gives equivalent results to those of a *t* test (Zar, 1996)); and when specimen numbers allowed, two-way ANOVAs of sex, tooth wear class and their interaction. Significant results of different tooth wear classes were followed by *a posteriori* Tukey multiple comparison tests to identify maximally non-significant subsets (Zar, 1996). Levene's test (see SPSS 9.0.1, 1999) was used to test the assumption of homogeneity of group variances for the ANOVA, and the Kolmogorov-Smirnov D-statistic (Zar, 1996) was used to test deviations from normality. For those measurements that showed significant non-normality and homogeneity and thus violated the assumptions of ANOVA, additional non-parametric Kruskal-Wallis tests were run to assess variation between sexes and tooth wear classes (Appendix 5.5). Unless otherwise stated in the results, the majority of the Kruskal-Wallis tests did not find any differences to the results obtained in the ANOVA tests.

Multivariate analysis of standardised measurements included the following tests:

1. One-way multivariate analyses of variance (MANOVA) of sex and tooth wear class;
2. Two-way MANOVAs of sex, tooth wear classes and their interactions when sample size allowed;

3. PCAs of among measurement correlation matrices;
4. Unweighted pair-group arithmetic average cluster analyses (UPGMA) based on distance matrices; and
5. Multi-group DFA.

Box's M test was used to test the assumption of homogeneity of group covariance matrices in MANOVA. However, no tests were computed because there were fewer than two non-singular cell covariance matrices, despite a process of measurement selection that was supposed to reduce the degree of inter-correlation between measurements. This was also a problem in the analyses by Bronner (1995) and Kearney (1993). MANOVAs were still computed even when the assumptions were not tested. Since external measurements were often missing, the number of specimens used in the ANOVA calculations varied, and the number of specimens and measurements used in the MANOVAs was usually fewer than the total number of specimens and measurements (see Table 5.1). A choice was made between measurements taken from specimen records and those measured from dry specimens based on which allowed more specimens to be incorporated in the MANOVA analyses.

The statistical analyses were run using the statistical packages of SPSS 9.0.1 (SPSS Inc., 1999) and NTSYS-pc, version 2.01h (Rohlf, 1997).

5.3 RESULTS

5.3.1 Species by species analysis

5.3.1.1 *Eptesicus hottentotus* – South Africa, Western Cape Province

5.3.1.1.1 Cranial measurements

These analyses were based on eight specimens from two localities in the Fynbos biome of the Western Cape (Fig. 5.1). Since the number of specimens was less than the number of variables, only one-way univariate tests were performed. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendix 5.6 A1 and A2. Three (25%) measurements, braincase height (BH), and breadth (BB), and width between the inner surfaces of the upper first molar teeth (WIUM1) were significantly sexually dimorphic in the one-way ANOVA tests with females being 3.28 to 6.41% larger than males (Table 5.2). One (8.3%) measurement, length of the first upper molar (LUM1), was significantly different between the tooth wear classes (Table 5.2). The post-hoc Tukey test identified two overlapping subsets of tooth wear classes D and C, and tooth wear classes C and B, with B being 11.30% larger than D in the length of the upper first molar tooth (LUM1) (Table 5.2). This is contrary to the assumption of increasing growth with increasing age, and suggests that the length of the upper first molar was affected by wear on the tooth and was thus an artefact of the ageing method used.

5.3.1.2 *Eptesicus hottentotus* – Namibia

5.3.1.2.1 Cranial measurements

These analyses were based on 19 specimens from five different localities in Namibia (Fig. 5.1) occurring in three different biomes: Desert, Nama-Karoo and Savanna. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendix 6 B1 and B2. No measurements were significantly sexually dimorphic in the two-way ANOVA but three (25%) measurements, braincase height (BH) and breadth (BB), and width of the articular surface (WAS) differed significantly between tooth wear classes, and one (8.3%) measurement, moment arm of the temporal (MAOT), showed a significant interaction between sexes and tooth wear classes (Table 5.3). Post-hoc Tukey tests identified the following subsets in braincase height (BH) and width of the articular surface (WAS): B was separated from C and D; and in braincase breadth (BB) there were two overlapping subsets of B and C and C and D, that separated the smaller tooth wear class B from the larger tooth wear class D. The relative differences of the significantly different measurements ranged from 4.50 to 8.11% (5.3). A two-way MANOVA found no significant sexual dimorphism (Wilks = 0.021, $F_{(2:12)}$ = 7.815, P = 0.119) but did find a significant variation between tooth wear classes (Wilks = 3.10E-06, $F_{(4,24)}$ = 94.496, P = 2.39E-04), and in the interaction of sex and tooth wear class (Wilks = 2.46E-04, $F_{(6,7)}$ = 10.470, P = 0.017).

The phenogram (Fig. 5.2) showed no distinct clustering of similar sexes, tooth wear classes or localities. However, the PCA (Fig. 5.2) showed that although there was considerable overlap between the sexes along the first principal component analysis which explained 36.4% of the variation, females were larger than males. Within males, more so than in the females, tooth wear class B specimens were smaller than tooth wear class C and D specimens on the first principal

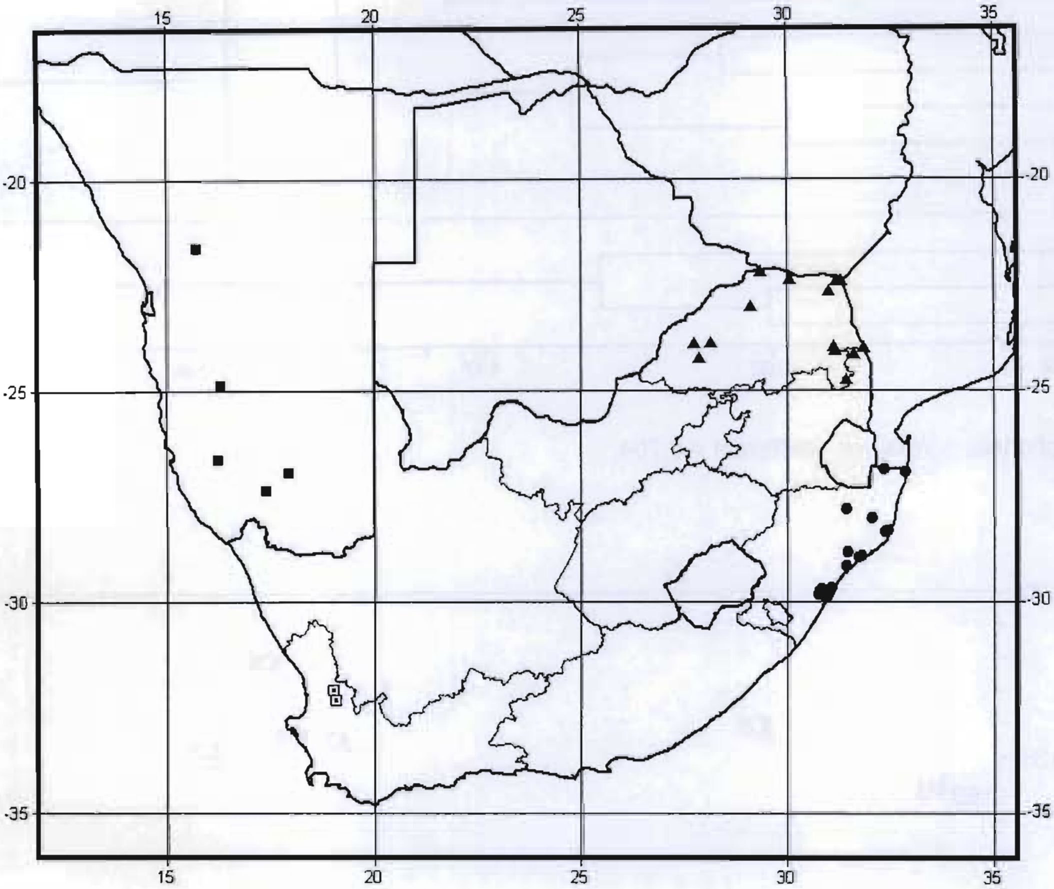
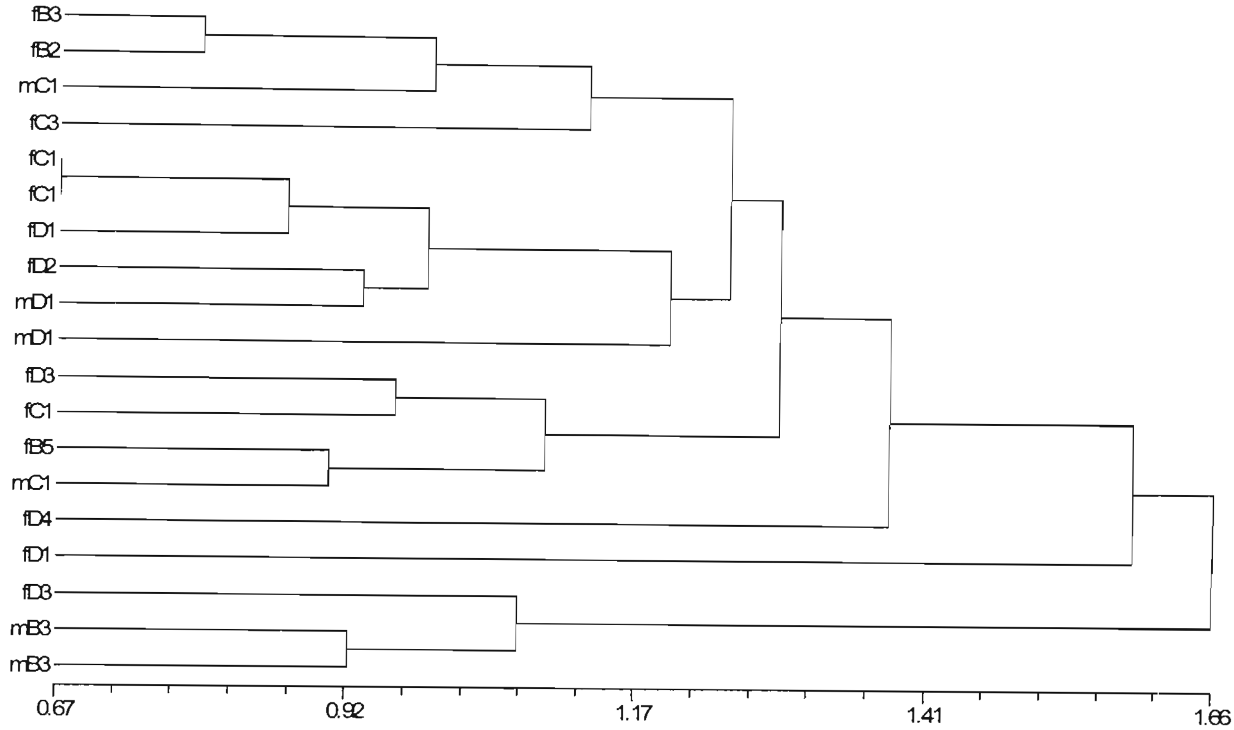


Figure 5.1 Map showing the distribution of specimens of *Eptesicus hottentotus*, *Neoromicia zuluensis* and *Pipistrellus hesperidus* from southern Africa used in the statistical analyses of cranial measurements. [*E. hottentotus* from Namibia = filled square, from the Western Cape Province of South Africa = open dotted square; *N. zuluensis* from Limpopo and Mpumalanga Provinces in South Africa = filled triangle; and *P. hesperidus* from KwaZulu-Natal in South Africa = filled circle.]

A)



Cophenetic correlation coefficient = 0.704.

B)

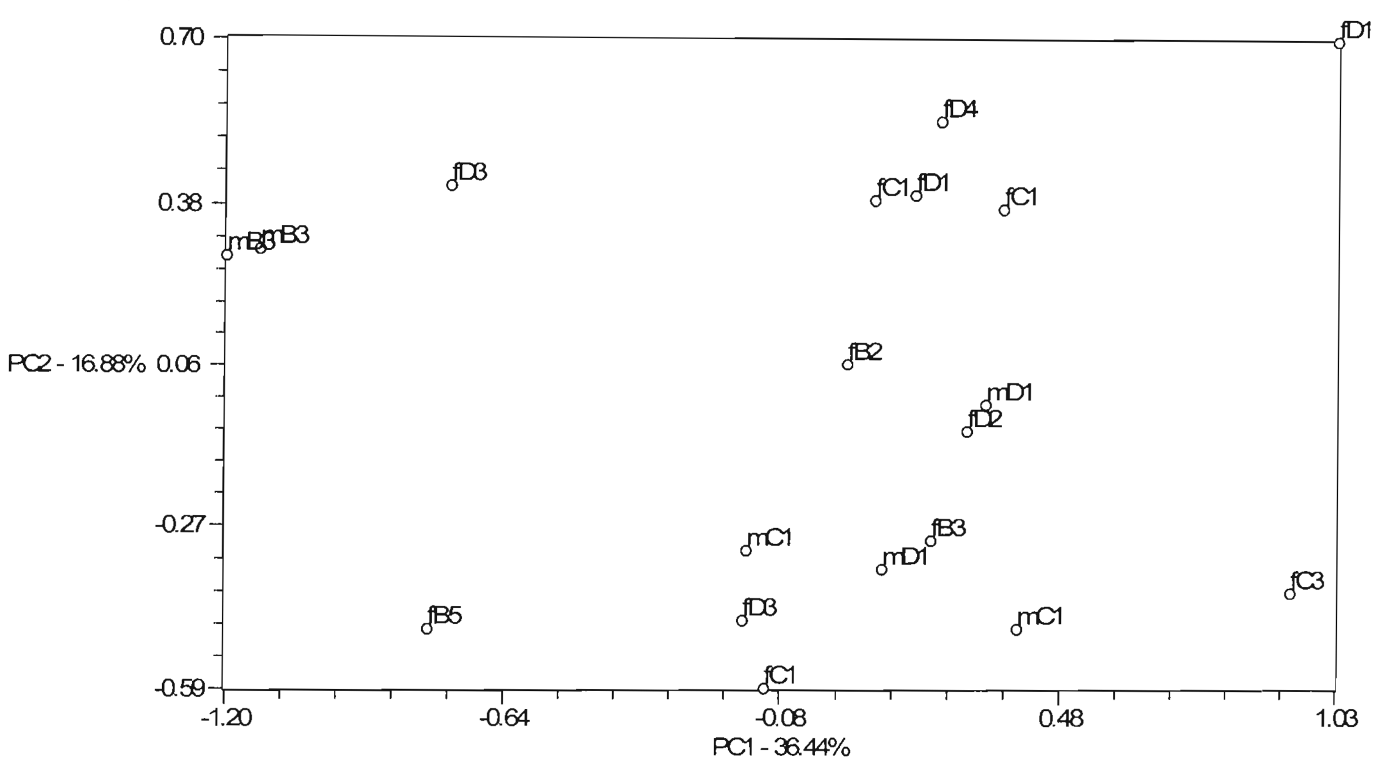


Figure 5.2 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of first two principal components of 12 cranial measurements of *Eptesicus hottentotus* from five localities in Namibia. The sex (male = m, female = f), tooth wear class (B, C, or D) and locality code (1-5, see Appendix 5.1 for locality data) of individuals are indicated.

Table 5.1 Summary of specimen numbers used in each vespertilionid species group of cranial and/or external measurements analysed for sexual dimorphism and/ or tooth wear class variation, including the number of localities pooled (# loc.) and the total number of specimens (#) in each group of cranial and external measurements ($\#^1$ = univariate analyses; $\#^2$ = multivariate analyses), as well as the number in each sex (females = F, males =M) and in each of four tooth wear classes (A, B, C, D).

Species	Area	Cranial				External				
		# loc.	#	F:M	A:B:C:D	# loc.	$\#^1$	F:M	A:B:C:D	$\#^2$
Eptesicus hottentotus	South Africa, W. Cape	2	8	3:5	-:2:3:3	-	-	-	-	-
E. hottentotus	Namibia	5	19	13:6	-:5:6:8	6	15	11:4	-:3:2:10	11
Hypsugo anchietae	Southern Africa	8	10	5:5	3:4:2:1	6	9	6:3	3:5:-:1	-
Neoromicia capensis	Namibia & South Africa	3	23	9:14	6:7:4:6	-	-	-	-	-
N. capensis	South Africa, W. Cape	4	24	17:7	3:6:8:7	-	-	-	-	-
N. capensis	South Africa, Free State, Grass-land	4	25	14:11	4:11:8:2	2	19	10:9	1:9:7:2	18
N. capensis	South Africa, Free State, Nama-Karoo	2	45	10:35	3:3:27:12	1	56	14:42	7:4:28:15	51
N. capensis	Zimbabwe	4	21	10:11	4:4:11:2	-	-	-	-	-
N. capensis	South Africa, E. Cape	-	-	-	-	1	21	12:9	2:8:3:4	19
N. cf. melckorum	South Africa & Zimbabwe	9	17	9:8	6:3:7:1	8	15	8:7	6:3:5:1	12
N. africanus	South Africa, Limpopo, Pafuri area	8	29	21:8	12:8:9:-	-	-	-	-	-
N. africanus	South Africa & Swaziland	12	35	12:23	3:8:16:8	14	40	17:23	4:3:19:7	29
N. africanus	Malawi	-	-	-	-	3	34	27:7	Females only: 1:5:8:5	14
N. rueppellii	Southern Africa	7	7	2:5	2:4:1:-	11	17	6:11	7:4:3:-	8
N. rueppellii	Zambia	-	-	-	-	1	17	8:9	-	16
N. zuluensis	South Africa, Limpopo & Mpuma-langa	20	36	20:16	6:10:12:8	13	16	6:10	-	14
Pipistrellus hesperidus	South Africa, KwaZulu-Natal	20	43	16:27	12:21:10:-	18	33	14:19	11:13:3:-	23
P. rusticus	South Africa & Zimbabwe	6	35	22:13	15:15:5:-	3	24	11:13	7:11:2:-	16

Table 5.2 Results of Levene's homogeneity and one-way ANOVA tests for sexual dimorphism (Sex) and tooth wear class (TW) variation in cranial measurements of *Eptesicus hottentotus* from two localities in the Western Cape Province of South Africa, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, P = significance of F values. * and ** denote significance at $P < 0.05$ and $P < 0.01$ respectively. SS = sum of squares.

Levene's		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Sex	*F*	2.392	0.999	0.201	3.460	1.968	0.429	0.143	1.877	0.002	7.259	1.362	3.032
	df	1,6	1,6	1,6	1,6	1,6	1,6	1,6	1,6	1,6	1,6	1,6	1,6
	P	0.173	0.506	0.669	0.112	0.210	0.537	0.718	0.220	0.969	0.036 *	0.287	0.132
TW	*F*	17.791	1.143	3.429	1.862	0.601	2.729	10.127	1.451	1.188	3.686	1.250	0.181
	df	2,5	2,5	2,5	2,5	2,5	2,5	2,5	2,5	2,5	2,5	2,5	2,5
	P	0.005 *	0.390	0.115	0.249	0.584	0.158	0.017 *	0.319	0.378	0.104	0.363	0.839
1-way ANOVA													
Sex	SS	0.782	0.299	0.328	0.188	0.054	0.153	0.058	0.100	0.115	0.006	0.000	0.261
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	4.574	6.153	2.859	24.383	1.845	4.745	2.274	4.168	9.701	0.190	0.027	3.912
	P	0.076	0.048 *	0.142	0.003 **	0.223	0.072	0.182	0.087	0.021 *	0.678	0.875	0.095
	%	-	5.81	-	3.28	-	-	-	-	6.41	-	-	-
TW	SS	0.405	0.133	0.265	5.104E-03	1.760E-02	4.075E-02	2.936E-02	0.112	2.213E-02	1.417E-02	7.494E-02	9.543E-02
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	0.721	0.729	0.883	0.056	0.207	0.332	0.401	2.138	0.337	0.180	6.113	0.421
	P	0.531	0.528	0.469	0.946	0.820	0.732	0.689	0.213	0.729	0.840	0.045 *	0.678
	%	-	-	-	-	-	-	-	-	-	-	11.30	-

Table 5.3 Results of Levene's homogeneity and two-way ANOVA tests for sexual dimorphism (Sex) and tooth wear class variation (TW) in cranial measurements of *Eptesicus hottentotus* from five localities in Namibia, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, *P* = significance of *F* values, *, ** and *** denote significance at *P* < 0.05, *P* < 0.01, and *P* < 0.001 respectively. SS = sum of squares.

Levene's		**CIL**	**BH**	**ZB**	**BB**	**LIW**	**WFM**	**WAS**	**WOUC**	**WIUM1**	**WUPM4**	**LUM1**	**MAOT**
	F	1.221	1.007	1.122	1.346	1.038	1.377	1.374	0.777	1.434	1.431	1.016	1.851
	df	5,13	5,13	5,13	5,13	5,13	5,13	5,13	5,13	5,13	5,13	5,13	5,13
	P	0.353	0.452	0.396	0.306	0.436	0.295	0.296	0.583	0.277	0.277	0.447	0.172
2-way ANOVA													
Sex	SS	0.563	0.063	0.420	0.046	4.23E-04	0.024	0.013	0.080	0.018	0.001	0.003	0.029
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	3.015	2.457	2.974	0.693	0.019	0.790	0.735	1.797	0.944	0.099	0.380	0.628
	P	0.106	0.141	0.108	0.420	0.892	0.390	0.407	0.203	0.349	0.757	0.548	0.442
TW	SS	0.588	0.616	0.828	0.578	0.074	0.005	0.209	0.257	0.016	0.010	0.044	0.342
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	1.576	12.058	2.934	4.312	1.684	0.076	6.004	2.891	0.421	0.336	2.630	3.730
	P	0.244	0.001 **	0.089	0.037 *	0.224	0.928	0.014 *	0.091	0.665	0.721	0.110	0.052
	%	-	6.76	-	4.50	-	-	8.11	-	-	-	-	-
Sex×TW	SS	0.116	0.011	0.246	0.033	0.046	0.020	0.056	0.206	0.005	0.011	0.058	0.600
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	0.312	0.210	0.871	0.250	1.041	0.335	1.595	2.319	0.128	0.400	3.461	6.541
	P	0.737	0.814	0.442	0.783	0.381	0.721	0.240	0.138	0.881	0.678	0.062	0.011 *

component axis. On the first principal component axis, width across the outer surfaces of the upper canines (WOUC), between the inner surfaces of the upper first molars (WIUM1) and condylo-incisor skull length (CIL) loaded highest, whereas width of the upper fourth premolar (WUPM4) loaded least. These measurements were not the same as those showing significant variation between the tooth wear classes in the two-way ANOVA analyses. On the second principal component axis which explained 16.88% of the variation, greatest width of the foramen magnum (WFM) loaded highest and length of the upper first molar (LUM1) loaded least.

Both a two-group DFA of the sexes and a three-group DFA of the tooth wear classes produced 100% *a posteriori* correct assignments of specimens to different sexes and tooth wear classes. In a plot of the first two discriminant function axes of the three-group DF analysis (Fig. 5.3) the first discriminant function axis explained 96.1% of the variation and separated tooth wear classes B, C and D. Greatest width of the articular surface (WAS) together with moment arm of the temporal (MAOT) loaded highest, and width across the outer surfaces of the upper canine teeth (WOUC) loaded the least. On the second discriminant function axis, which explained 3.9% of the variation and separated tooth wear class C from tooth wear classes B and D, braincase height (BH) and width across the outer surfaces of the upper canine teeth (WOUC) loaded highest, while condylo-incisor length (CIL) loaded the least. Two of the important measurements in the DFA of tooth wear classes were also significantly different among tooth wear classes in the two-way ANOVAs (WAS, BH), and two were important in the PCA (WOUC, CIL).

5.3.1.2.2 External measurements

These analyses were based on 15 specimens from six localities in Namibia (Fig. 5.4), occurring in three different biomes: Desert, Nama-Karoo and Savanna. The summary statistics and results of the normality tests for sexes and tooth wear classes are reported in Appendix 5.7 A. To accommodate missing data 11 specimens from four localities were used in the multivariate analyses. Two (18.2%) measurements, forearm length and length of the third metacarpal (FA, TMETA) were significantly sexually dimorphic in the one-way ANOVA tests with females being 5.21 and 6.78% respectively larger than males. The relative differences of the sexually dimorphic measurements ranged from 5.21 to 6.78% (Table 5.4). No measurements were significantly different between the tooth wear classes in one-way ANOVA tests. A one-way MANOVA of 11 specimens and six measurements (HF, TIB, FA, TMETA, TRL, TRB) showed no significant difference between the different sexes (Wilks = 0.195, $F_{(7,3)} = 1.764$, $P = 0.346$).

The phenogram (Fig. 5.5) formed two major clusters. The smaller cluster contained four females, three of which belonged to tooth wear class D. In addition, three were from Eronga Mountain (# 1), the most northerly occurring locality in the analysis and one of two localities from the Savanna biome. The fourth specimen was a single individual from Rheinvels Farm, the most southerly occurring locality in the analysis from the Nama-Karoo biome. The second cluster contained a mixture of both sexes and different tooth wear classes, although there was a clustering within this group of specimens from Klein Aus (# 3), which was the only locality occurring in the Desert biome.

The PCA (Fig. 5.5) showed a different separation to that in the UPGMA phenogram. The first principal component axis that explained 48.17% of the variation, separated specimens from Klein Aus (# 3), which occurred in the Desert biome, from specimens from the other localities occurring in the Savanna biome. Within each of these separate locality groups males were smaller than females, and specimens of tooth wear class B were smaller than those of tooth wear class D. Metacarpal (TMETA), forearm (FA) and tibia lengths (TIB) loaded highest and tragus breadth (TRB) loaded least on the first principal component axis. Two of these measurements, metacarpal (TMETA) and forearm (FA) lengths, also showed significant sexual dimorphism in the ANOVA analyses. The second principal component explained 29.10% of the variation, with hind foot (HF) and tragus lengths (TRL) loading highest and lowest respectively on the second principal component axis.

A two-group DFA of the sexes produced a 100% *a posteriori* correct assignment of specimens to the different sexes. There were too few specimens for a DFA of tooth wear classes and one-way ANOVA and MANOVA of external measurements.

5.3.1.3 *Hypsugo anchietae*

5.3.1.3.1 Cranial measurements

The analyses were based on ten specimens from eight localities in South Africa and Zimbabwe (Fig. 5.6), all occurring in the Savanna biome. Since the number of specimens was

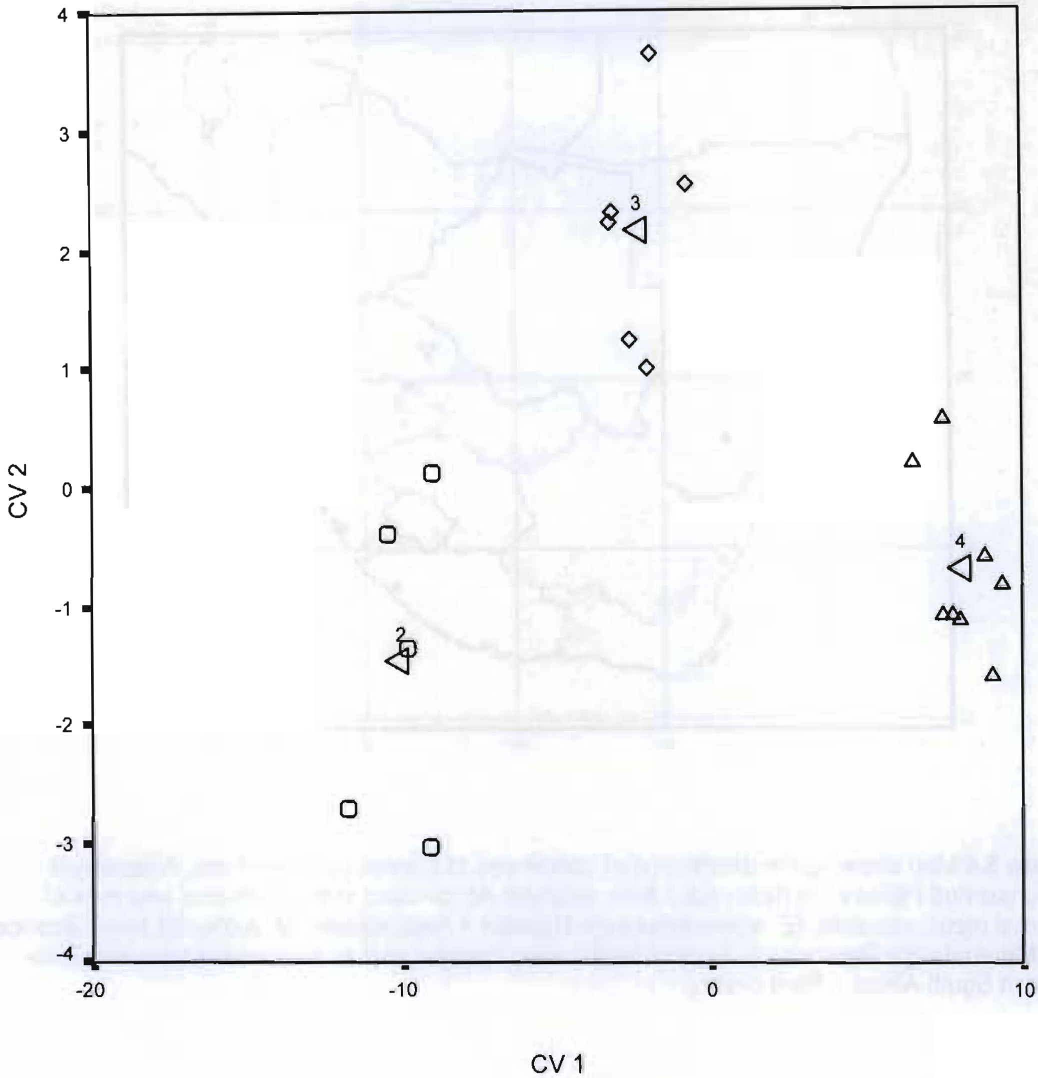


Figure 5.3 Plot of the first two discriminant functions of cranial measurements of three different tooth wear classes (2 and ○ = tooth wear class B; 3 and ◇ = tooth wear class C; 4 and △ = tooth wear class D) of *Eptesicus hottentotus* from Namibia.

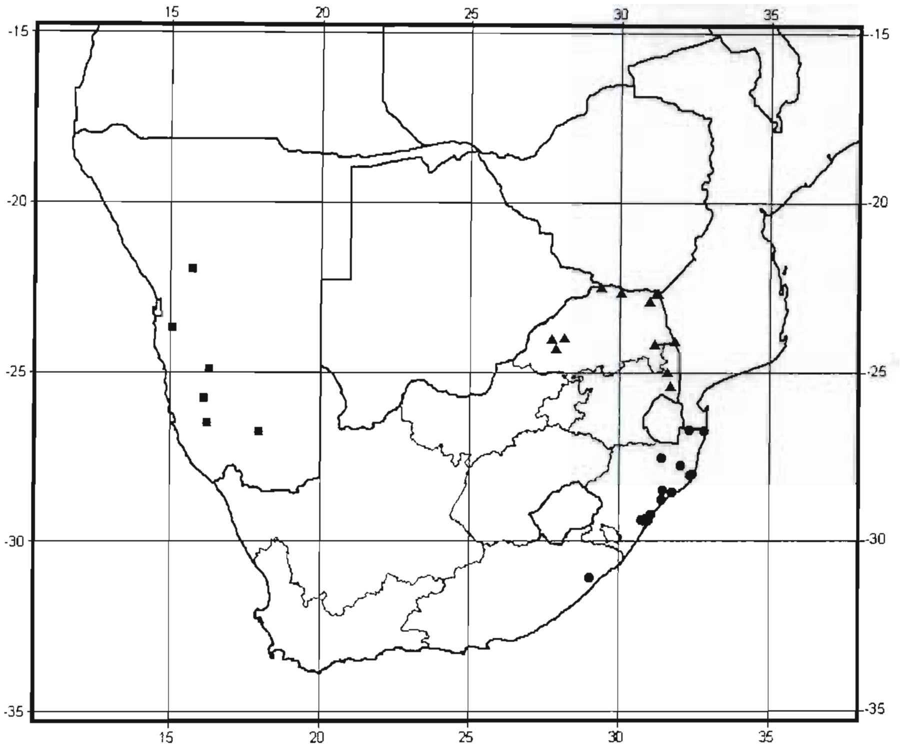
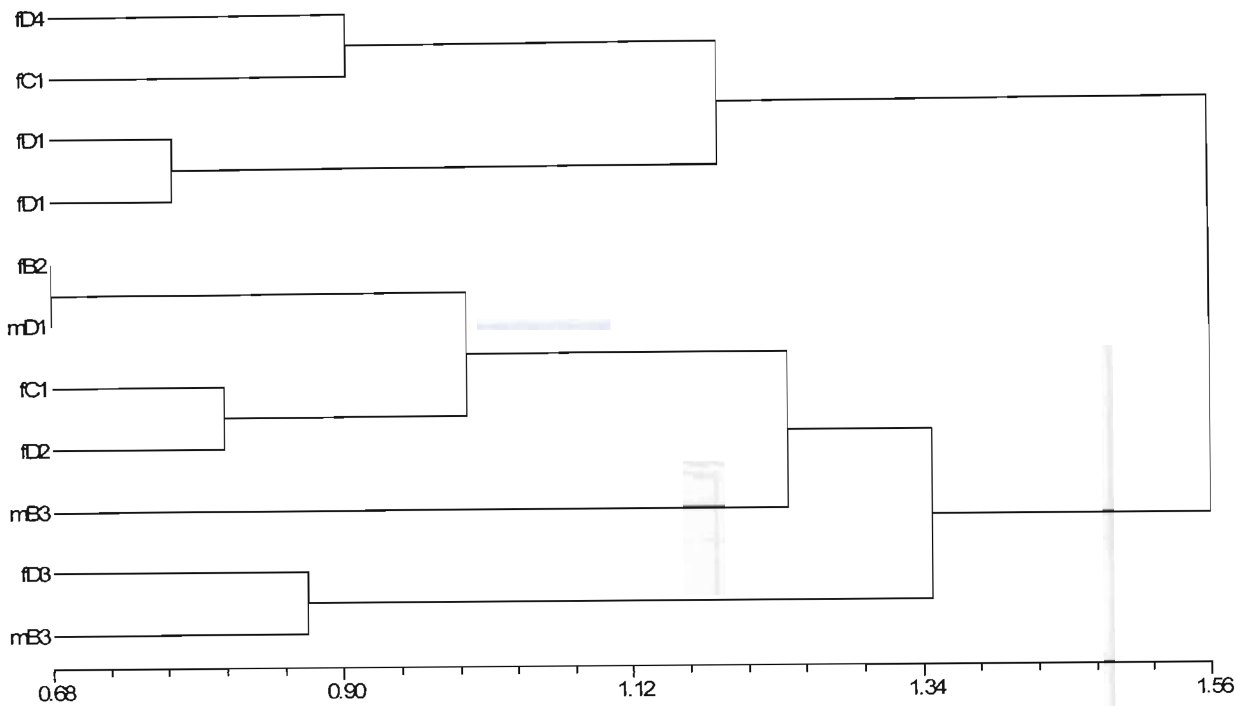


Figure 5.4 Map showing the distribution of specimens of *Eptesicus hottentotus*, *Neoromicia zuluensis* and *Pipistrellus hesperidus* from southern Africa used in the statistical analyses of external measurements. [*E. hottentotus* from Namibia = filled square; *N. zuluensis* from Limpopo and Mpumalanga Provinces in South Africa = filled triangle; and *P. hesperidus* from KwaZulu-Natal in South Africa = filled circle.]

A)



Cophenetic correlation coefficient = 0.641.

B)

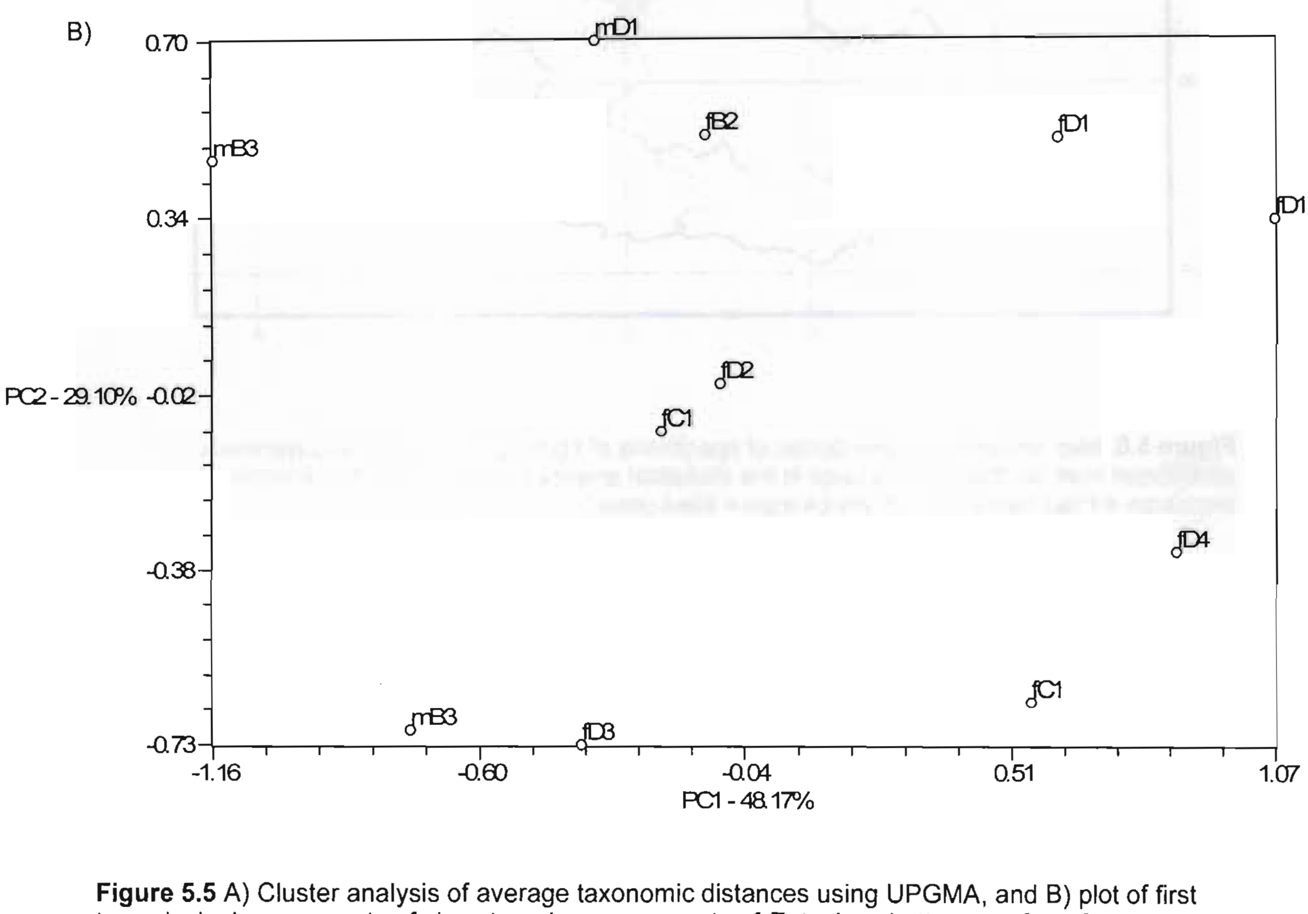


Figure 5.5 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of first two principal components of six external measurements of *Eptesicus hottentotus* from four localities in Namibia. The sex (male = m, female = f), tooth wear class (B, C, or D) and locality code (1-4, see Appendix 5.1 for locality data) of individuals are indicated.

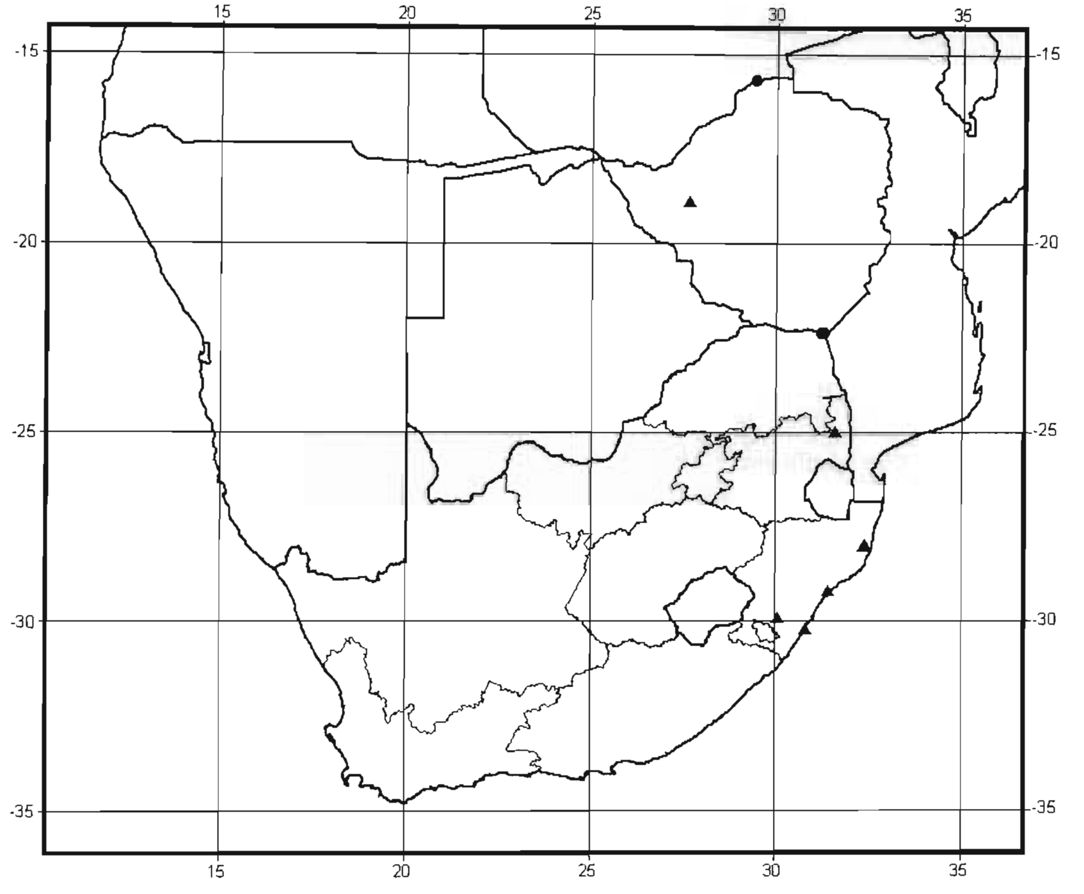


Figure 5.6 Map showing the distribution of specimens of *Hypsugo anchietae* and *Neoromicia* cf. *melckorum* from southern Africa used in the statistical analyses of cranial measurements. [*H. anchietae* = filled triangle; *N.* cf. *melckorum* = filled circle.]

Table 5.4 Results of Levene's homogeneity and one-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in external measurements of *Eptesicus hottentotus* from six localities in Namibia, with mean size differences for significantly different measurements expressed as a percentage (%). *n* = sample size, df = degrees of freedom, *P* = significance of *F* values, *** denotes significance at *P* < 0.001. SS = sum of squares.

Levene's		HB	T	TL	HFL	HF	FA	E	TIB	TMETA	TRL	TRB
Sex	*F*	1.003	0.271	5.272	0.001	3.639	2.427	0.538	0.067	0.516	0.919	0.474
	df	1,4	1,7	1,8	1,7	1,12	1,13	1,7	1,11	1,13	1,11	1,13
	P	0.373	0.619	0.051	0.976	0.081	0.143	0.487	0.800	0.485	0.358	0.503
TW	*F*	0.901	39.847	0.163	0.001	1.347	1.152	0.538	0.461	0.157	1.448	0.740
	df	1,4	1,7	2,7	1,7	2,11	2,12	1,7	2,10	2,12	2,10	2,12
	P	0.396	3.99E-04 ***	0.853	0.976	0.300	0.349	0.487	0.644	0.856	0.280	0.498
ANOVA												
Sex	SS	43.200	15.365	50.647	0.198	1.029E-02	20.118	0.00E-16	4.469	33.215	1.885E-02	1.670E-02
	df	1	1	1	1	1	1	1	1	1	1	1
	F	3.857	0.447	2.040	0.414	0.044	6.571	0.00E-16	3.809	6.499	0.029	0.114
	P	0.121	0.525	0.191	0.541	0.837	0.024 *	1.000	0.077	0.024 *	0.868	0.741
	%	-	-	-	-	-	5.21	-	-	6.78	-	-
TW	*n*	-:-:2:4	-:-:2:7	-:2:2:6	-:-:2:7	-:3:2:9	-:3:2:10	-:-:2:7	-:3:2:8	-:3:2:10	-:3:2:8	-:3:2:10
	SS	0.00E-16	10.865	87.663	0.198	0.187	10.954	0.00E-16	4.105	28.511	1.201	2.236E-02
	df	1	1	2	1	2	2	1	2	2	2	2
	F	0.00E-16	0.310	1.899	0.414	0.391	1.342	0.00E-16	1.546	2.404	1.005	0.071
	P	1.000	0.595	0.219	0.541	0.685	0.298	1.000	0.260	0.132	0.400	0.932

less than the number of variables, only univariate tests were performed. The summary statistics and results of the normality tests for sexes and tooth wear classes are shown in Appendix 5. 6 C1 and C2. Two (16.7%) measurements, length of the upper first molar (LUM1) and moment arm of the temporal (MAOT) were significantly sexually dimorphic in the one-way ANOVA tests, with females being 5.07 and 5.37%, respectively larger than males (Table 5.5). One (8.3%) measurement, least inter-orbital width (LIW), was significantly different between the different tooth wear classes. A single specimen of tooth wear class D from Zimbabwe had the smallest least inter-orbital width (LIW), and may have caused least inter-orbital width (LIW) to be significantly different between tooth wear classes, as the post-hoc test excluding the specimen from Zimbabwe found no sub-groups between the remaining tooth wear classes. The relative difference in least inter-orbital width between tooth wear classes D and A was 8.17% (Table 5.5).

5.3.1.3.2 External measurements

The analyses were of nine specimens from six localities in South Africa and Zimbabwe (Fig. 5.7), all occurring in the Savanna biome. The summary statistics and results of the normality tests for sexes are given in Appendix 5.7 B. Since the number of specimens was less than the number of variables, only univariate tests were performed. There were also too few specimens to run analyses of tooth wear classes variation in the external measurements, hence analyses were only made between sexes. One (8.3%) measurement, length of the third metacarpal (TMETA) showed significant sexual dimorphism in the ANOVAs, with females being 6.11% larger than males (Table 5.6).

5.3.1.4 *Neoromicia capensis* – Namibia and South Africa, Nama-Karoo biome

5.3.1.4.1 Cranial measurements

These analyses were based on 23 specimens from three localities, one in Namibia and two in South Africa (Fig. 5.8), all occurring in the Nama-Karoo biome. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendix 6 D1 and D2. In a two-way ANOVA test, one (8.3%) measurement, condylo-incisor skull length (CIL) was significantly sexually dimorphic with females being 2.55% larger than males, while two (16.7%) measurements, zygomatic breadth (ZB) and braincase breadth (BB) were significantly different between the tooth wear classes, and zygomatic breadth (ZB) and least inter-orbital width (LIW) that showed a significant interaction between sex and tooth wear class (Table 5.7). In braincase breadth (BB), the Tukey test identified three overlapping subsets of tooth wear classes B and A, tooth wear classes A and D, and tooth wear classes D and C, that separated tooth wear classes B and C. The post-hoc test did not show a normal progression of growth in braincase breadth (BB) since the mean, minimum and maximum values of tooth wear class A were larger than those of tooth wear class B, and the mean and minimum values of tooth wear class C were larger than those of tooth wear class D. The relative difference between tooth wear classes B and C was 4.06% (Table 5.7). The post-hoc Tukey test for zygomatic breadth (ZB) identified two overlapping subsets of tooth wear classes B and A, and tooth wear classes A, C and D, that separated tooth wear class B from tooth wear classes C and D. The post-hoc test thus showed a normal progression of growth in zygomatic breadth. Unlike the two-way ANOVA test, the Kruskall-Wallis test did not find a significant variation between tooth wear classes in zygomatic breadth (ZB), although the probability was just outside the significant range (Appendix 5.5). A two-way MANOVA showed no significant sexual dimorphism (Wilks = 0.206, $F_{(4,12)} = 1.282$, $P = 0.441$), significant variation between the tooth wear classes (Wilks = 0.034, $F_{(12.546,36)} = 0.749$, $P = 0.760$), or significant interaction between sex and tooth wear class (Wilks = 0.041, $F_{(12.546,36)} = 0.678$, $P = 0.824$).

The phenogram (Fig. 5.9) identified two male specimens (TM32547, TM35599) from different tooth wear classes and localities, as outliers. The remaining specimens clustered into three major clusters which appeared not to separate on the basis of sex or locality. There did however, appear to be some clustering along the lines of tooth wear class, given the preponderance of tooth wear class B in one cluster and tooth wear class D in another cluster. The PCA (Fig. 5.9) which explained 35.25% and 18.98% of the variation on the first and second principal component axes, respectively, identified the same outliers as the phenogram. However, there was no distinct separation of different sexes, tooth wear classes or localities amongst the remaining specimens. On the first principal component axis condylo-incisor skull length (CIL), zygomatic breadth (ZB) and width across the outer surfaces of the upper canines (WOUC) loaded highest, and width of the upper fourth premolar tooth (WUPM4) loaded least. On the second

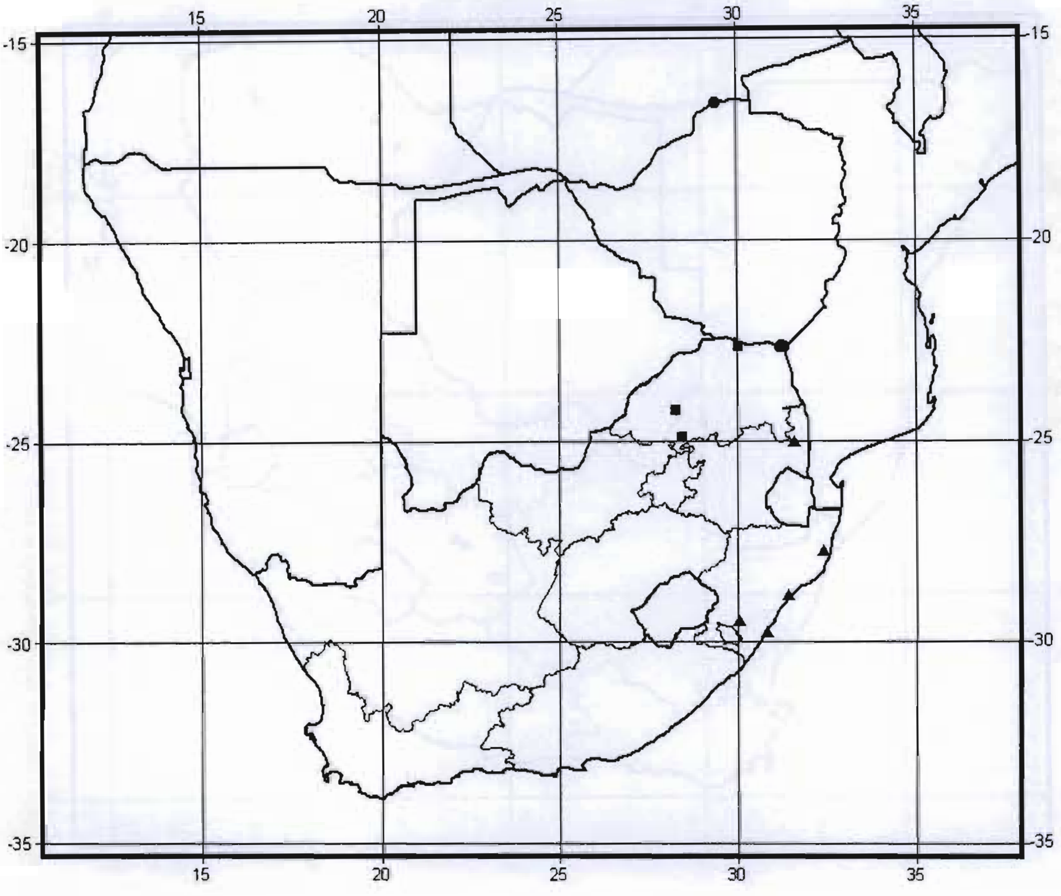


Figure 5.7 Map showing the distribution of specimens of *Hypsugo anchietae*; *Neoromicia* cf. *melckorum*; and *Pipistrellus rusticus* used in the statistical analyses of external measurements. [*H. anchietae* = filled triangle; *N.* cf. *melckorum* = filled circle; *P. rusticus* = filled square.]

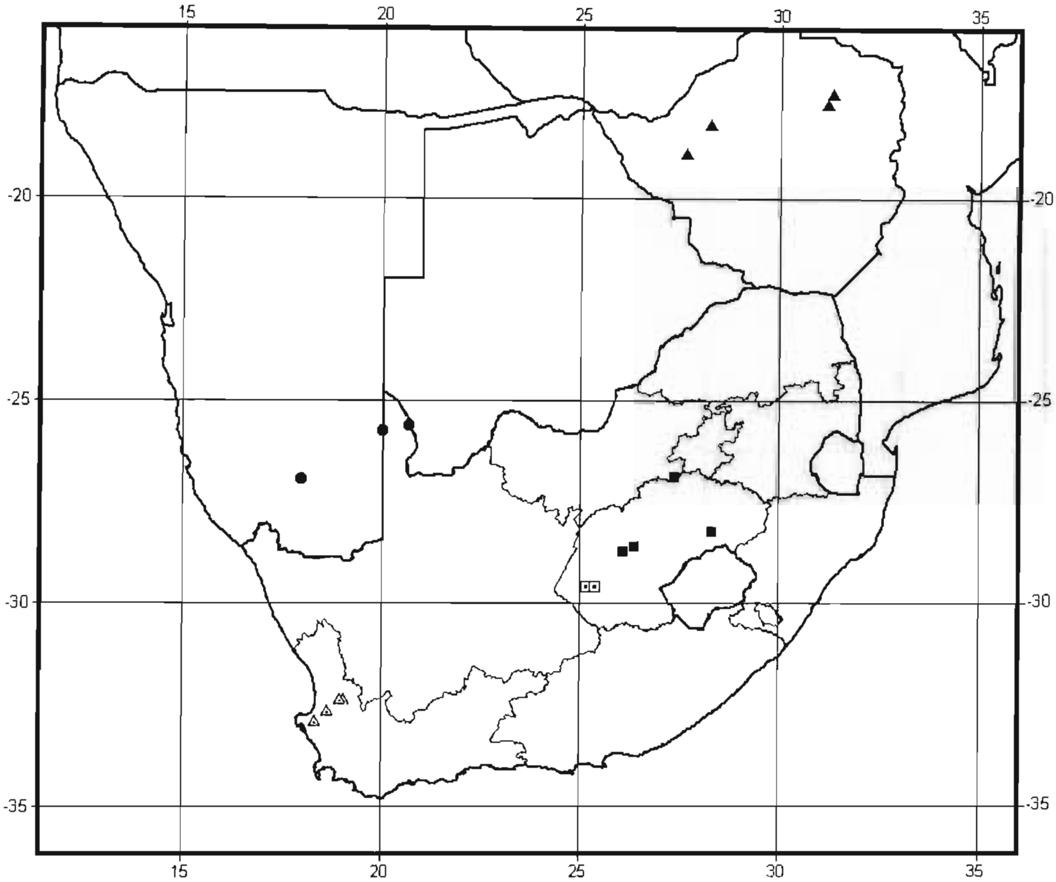
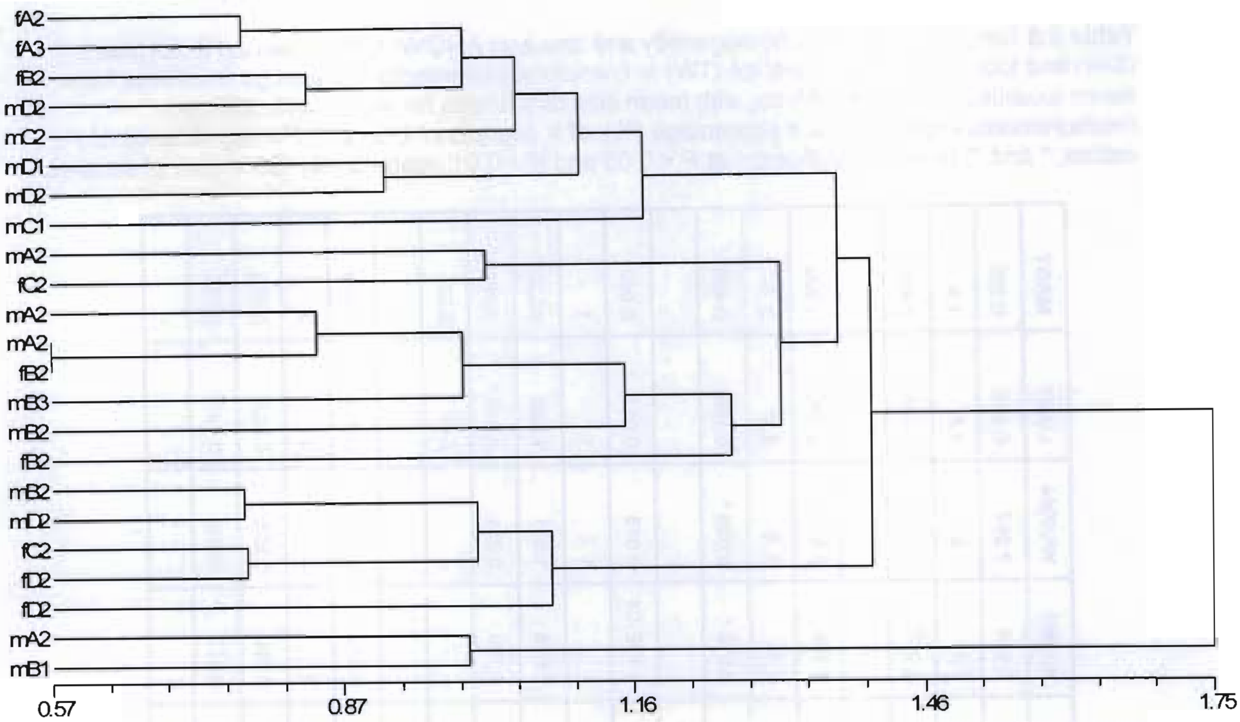


Figure 5.8 Map showing the distribution of specimens of *Neoromicia capensis* from the Nama-Karoo biome of Namibia and South Africa, the Western Cape Province of South Africa, the Grassland biome in the Free State Province of South Africa, the Nama-Karoo biome in the Free State Province of South Africa, and Zimbabwe used in the statistical analyses of cranial measurements. [*N. capensis* from Zimbabwe = filled triangle; Western Cape Province of South Africa = open dotted triangle; Nama-Karoo biome of Namibia and South Africa = filled circle; Nama-Karoo biome in the Free State Province of South Africa = open dotted square; Grassland biome in the Free State Province of South Africa = filled square.]

A)



Cophenetic correlation coefficient = 0.676.

B)

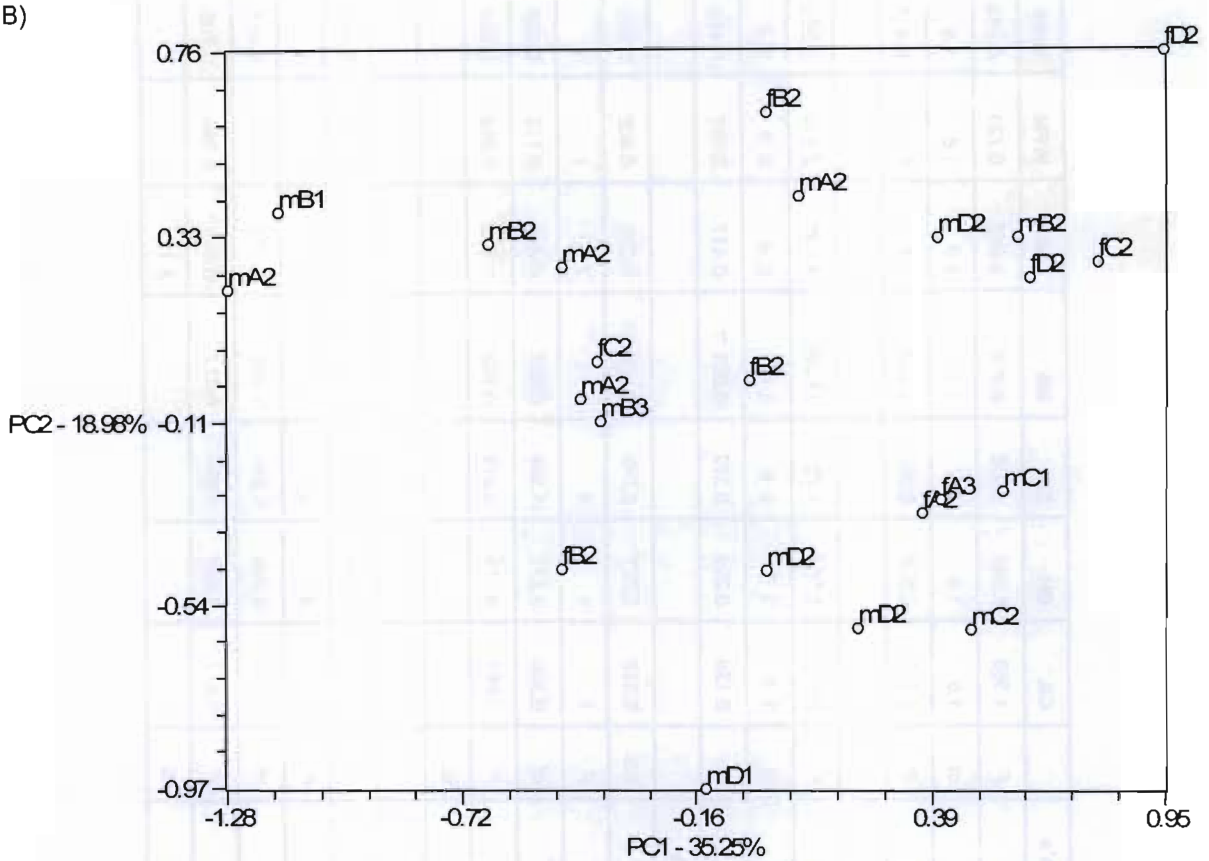


Figure 5.9 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of first two principal components of 12 cranial measurements of *Neoromicia capensis* from three localities in Namibia and the Northern Cape Province in South Africa. The sex (male = m, female = f), tooth wear class (A, B, C, or D) and locality code (1-3, see Appendix 5.1 for locality data) of individuals are indicated.

Table 5.5 Results of Levene's homogeneity and one-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in cranial measurements of *Hypsugo anchietae* from seven localities in southern Africa, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, *P* = significance of *F* values, * and ** denote significance at *P* < 0.05 and *P* < 0.01, respectively. SS = sum of squares.

Levene's		**CIL**	**BH**	**ZB**	**BB**	**LIW**	**WFM**	**WAS**	**WOUC**	**WIUM1**	**WUPM4**	**LUM1**	**MAOT**
Sex	*F*	1.393	1.087	0.306	0.016	0.045	0.731	0.743	1.271	3.524	7.562	0.636	0.535
	df	1,8	1,8	1,8	1,8	1,8	1,8	1,8	1,8	1,8	1,8	1,8	1,8
	P	0.272	0.328	0.595	0.903	0.837	0.417	0.414	0.292	0.097	0.025 *	0.448	0.485
TW	*F*	2.837	1.564	1.251	25.292	1.105	2.490	0.960	0.631	9.168	6.510	2.200	0.920
	df	3, 6	3, 6	3, 6	3, 6	3, 6	3, 6	3, 6	3, 6	3, 6	3, 6	3, 6	3, 6
	P	0.128	0.293	0.372	0.001 **	0.417	0.157	0.470	0.622	0.012 *	0.026 *	0.189	0.486
ANOVA													
Sex	SS	0.015	0.027	0.049	2.50E-04	0.005	0.002	0.022	4.16E-05	4.13E-04	0.013	0.011	0.062
	F	1	1	1	1	1	1	1	1	1	1	1	1
	df	0.200	2.212	1.354	0.037	0.446	0.172	0.923	0.002	0.076	1.531	9.530	12.381
	P	0.667	0.175	0.278	0.852	0.523	0.689	0.365	0.967	0.790	0.251	0.015 *	0.008 **
	%	-	-	-	-	-	-	-	-	-	-	5.07	5.37
TW	SS	0.153	0.006	0.038	0.023	0.073	0.017	0.041	0.085	0.013	0.020	0.003	0.019
	F	3	3	3	3	3	3	3	3	3	3	3	3
	df	0.649	0.098	0.249	1.457	5.273	0.384	0.484	1.656	0.856	0.655	0.402	0.453
	P	0.612	0.958	0.859	0.317	0.041 *	0.769	0.706	0.274	0.513	0.609	0.757	0.725
	%	-	-	-	-	8.17	-	-	-	-	-	-	-

Table 5.6 Results of Levene's homogeneity and one-way ANOVA tests for sexual dimorphism (Sex) in external measurements of *Hypsugo anchietae* from five localities in southern Africa, with mean size differences for significantly different measurements expressed as a percentage (%). *n* = sample size, df = degrees of freedom, *P* = significance of *F* values. * denotes significance at *P* < 0.05. SS = sum of squares.

Levene's		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Sex	*F*	0.063	7.138	0.029	4.679	0.198	0.814	0.680	0.042	5.290	4.982	0.136	3.763
	df	1,5	1,5	1,4	1,5	1,6	1,5	1,6	1,5	1,4	1,7	1,7	1,7
	P	0.812	0.044 *	0.872	0.083	0.672	0.408	0.441	0.846	0.083	0.061	0.723	0.094
ANOVA													
Sex	*n*	4:3	4:3	4:2	4:3	6:2	4:3	5:3	4:3	4:2	6:3	6:3	6:3
	SS	55.048	4.762	0.154	7.440E-02	7.482E-02	1.480	3.120	0.429	0.340	7.182	0.135	7.347E-02
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	3.895	0.776	0.031	0.436	0.416	1.163	1.506	0.429	0.668	7.072	1.094	0.324
	P	0.105	0.419	0.870	0.538	0.543	0.330	0.266	0.542	0.460	0.033 *	0.330	0.587
	%	-	-	-	-	-	-	-	-	-	6.11	-	-

Table 5.7 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in cranial measurements of *Neoromicia capensis* from three localities in Namibia and South Africa falling into the Nama-Karoo biome, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, P = significance of F values, * and ** denote significance at $P < 0.05$ and $P < 0.01$, respectively. SS = sum of squares.

Levene's		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
	F	1.569	2.120	0.934	0.690	2.048	1.533	1.270	0.575	1.600	2.860	3.463	3.862
	df	7,15	7,15	7,15	7,15	7,15	7,15	7,15	7,15	7,15	7,15	7,15	7,15
	P	0.219	0.105	0.509	0.680	0.116	0.230	0.328	0.766	0.210	0.042 *	0.021 *	0.013 *
2-way ANOVA													
Sex	SS	0.649	0.017	0.034	1.64E-04	8.11E-06	0.020	0.022	0.009	0.006	0.002	0.001	0.079
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	5.448	0.626	1.363	0.011	0.001	1.883	2.252	0.465	0.489	0.332	0.272	2.744
	P	0.034 *	0.441	0.261	0.919	0.978	0.190	0.154	0.506	0.495	0.573	0.610	0.118
	%	2.55	-	-	-	-	-	-	-	-	-	-	-
TW	SS	0.410	0.029	0.424	0.276	0.058	3.66E-04	0.033	0.132	0.039	0.006	0.004	0.088
	df	3	3	3	3	3	3	3	3	3	3	3	3
	F	1.147	0.363	5.590	5.927	1.861	0.012	1.102	2.186	1.135	0.283	0.285	1.023
	P	0.362	0.780	0.009 **	0.007 **	0.180	0.998	0.379	0.132	0.367	0.837	0.835	0.410
	%	-	-	4.37	4.06	-	-	-	-	-	-	-	-
Sex×TW	SS	0.321	0.012	0.370	0.072	0.207	0.040	0.019	0.076	0.031	0.019	0.025	0.087
	df	3	3	3	3	3	3	3	3	3	3	3	3
	F	0.899	0.149	4.885	1.553	6.621	1.256	0.625	1.270	0.901	0.845	1.967	1.016
	P	0.465	0.929	0.015 *	0.242	0.005 **	0.325	0.610	0.320	0.464	0.490	0.162	0.413

principal component axis length of the upper first molar (LUM1) loaded highest, and least inter-orbital width (LIW) loaded least.

A two-group DFA of the sexes produced a 95.65% overall *a posteriori* assignment of specimens to the correct sex [females (n = 9) - 88.89%, males (n = 14) - 100%]. A four-group DFA of tooth wear classes produced a 91.30% overall *a posteriori* assignment of specimens to the correct tooth wear class [tooth wear A (n = 6) - 83.33%, tooth wear B (n = 7) -100%, tooth wear C (n = 4) - 100%, tooth wear D (n = 6) - 83.33%]. A plot of the first two discriminant function axes of the four-group DF analysis (Fig. 5.10) separated tooth wear classes A and B from tooth wear classes C and D on the first discriminant function axis. Braincase breadth (BB) loaded highest and width of the foramen magnum (WFM) loaded least on the first discriminant function axis which explained 81.8% of the variation. Braincase breadth (BB) also showed a significant difference between the tooth wear classes in the two-way ANOVA analyses. The second discriminant function axis, which explained 12.6% of the variation, almost separated tooth wear class A from tooth wear class B, but a male of tooth wear class A (TM35597) overlapped with specimens of tooth wear class B. Length of the upper first molar (LUM1) loaded highest and moment arm of the temporal (MAOT) and width between the inner surfaces of the upper first molar teeth (WIUM1) loaded least on the second discriminant function axis. There were too few specimens with external measurements to run any analyses of external measurements.

5.3.1.5 *Neoromicia capensis* – South Africa, Western Cape Province

5.3.1.5.1 Cranial measurements

These analyses were based on 24 specimens from four localities in the Western Cape Province of South Africa (Fig. 5.8). The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendix 6 E1 and E2. Three of the localities occurred in the Fynbos biome, while the Olifants River locality occurred within an isolated area of Succulent Karoo, surrounded by Fynbos. In the two-way ANOVA, no measurements showed significant sexual dimorphism, while two (16.7%) measurements were significant between the tooth wear classes: width of the articular surface (WAS) and moment arm of the temporal (MAOT) (Table 5.8). Post-hoc Tukey tests found no subsets for width of the articular surface (WAS), in which the relative difference between tooth wear class A and C was 8.87% (Table 5.8). In moment arm of the temporal (MAOT), the Tukey test identified two different subsets, one of tooth wear classes A and B, and another of tooth wear classes D and C, and the relative difference between tooth wear class A and C was 9.88% (Table 5.8). In both measurements showing significant variation between the tooth wear class, tooth wear class D was smaller than tooth wear class C. No measurements were significant in the two-way ANOVA interaction between sex and tooth wear class. A two-way MANOVA showed no significant sexual dimorphism (Wilks = 0.298, $F_{(6,12)}$ = 1.179, P = 0.443), significant variation between the tooth wear classes (Wilks = 0.067, $F_{(18.455,36)}$ = 0.769, P = 0.756), or significant interaction between sex and tooth wear class (Wilks = 0.077, $F_{(12,24)}$ = 1.299, P = 0.326).

Besides a clustering of females of tooth wear class C from Kersefontein Farm (# 4), the phenogram (Fig. 5.11) did not show any other distinct clustering due to sex, tooth wear class or locality. The PCA (Fig. 5.11) showed a distinct separation on the first principal component axis between a male of tooth wear class A from Piketburg (KM29004) and the other specimens. This outlier was not as apparent in the phenogram. With the exception of two male specimens, the majority of male specimens clustered with smaller individuals on the first principal component axis, and specimens of tooth wear class C and D predominantly clustered with larger individuals on the first principal component axis. On the first principal component axis, which explained 45.68% of the variation, zygomatic breadth (ZB) and width across the outer surfaces of the upper canine teeth (WOUC) loaded highest and width of the upper fourth premolar (WUPM4) loaded least. None of these measurements were measurements that showed significant variation between sexes and tooth wear classes in the two-way ANOVA tests. On the second principal component axis which explained 13.67% of the variation, although the tooth wear classes overlapped, some specimens of tooth wear class B were larger than those of tooth wear classes A, C or D. On the second principal component, axis width of the upper fourth premolar (WUPM4) loaded highest and width of the foramen magnum (WFM) loaded least.

A two-group DFA of the sexes produced a 95.83% overall *a posteriori* assignment of specimens to the correct sex [females (n = 17) 94.12%, males (n = 7) 100%]. A four-group DFA of tooth wear classes produced an 87.5% overall *a posteriori* assignment of specimens to the correct tooth wear class [tooth wear A (n = 3) 100%, tooth wear B (n = 6) 100%, tooth wear C (n =

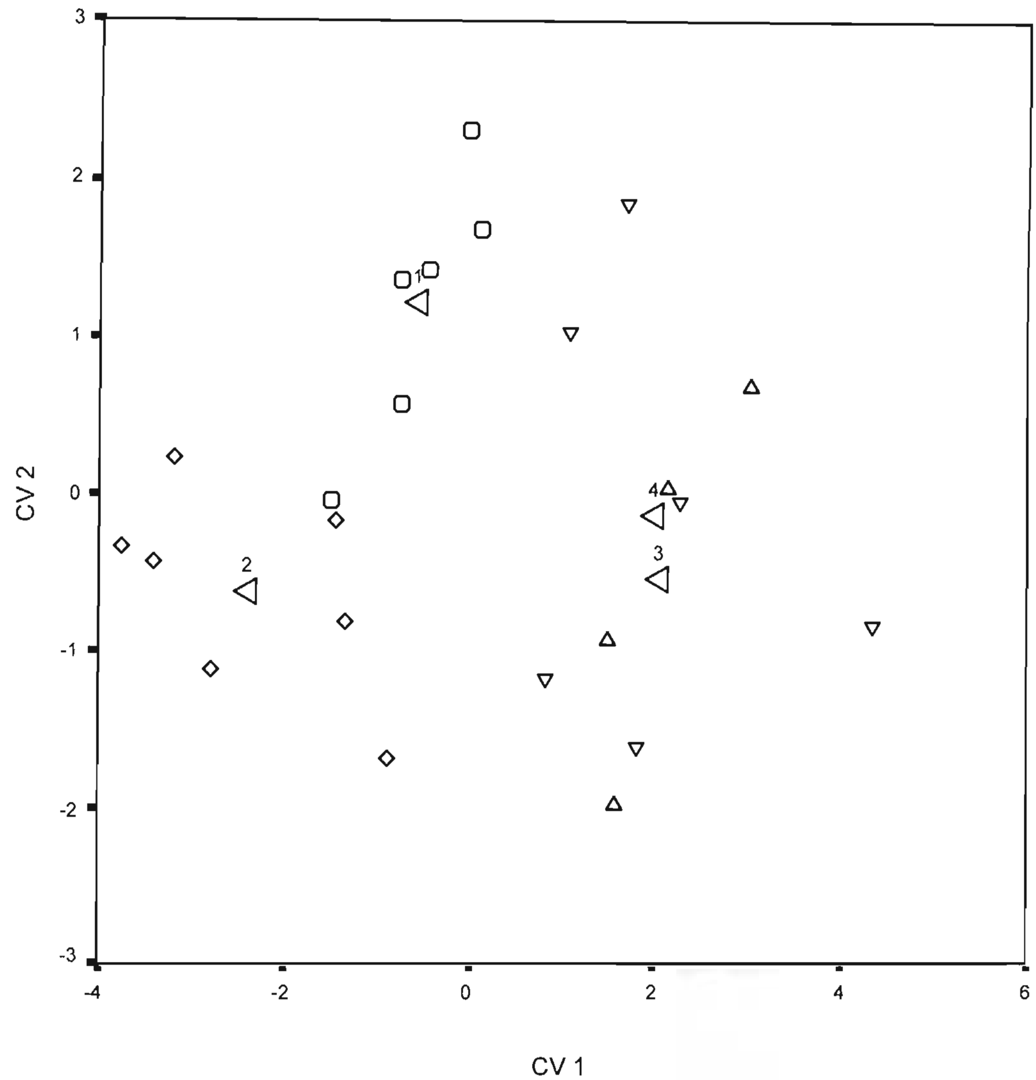
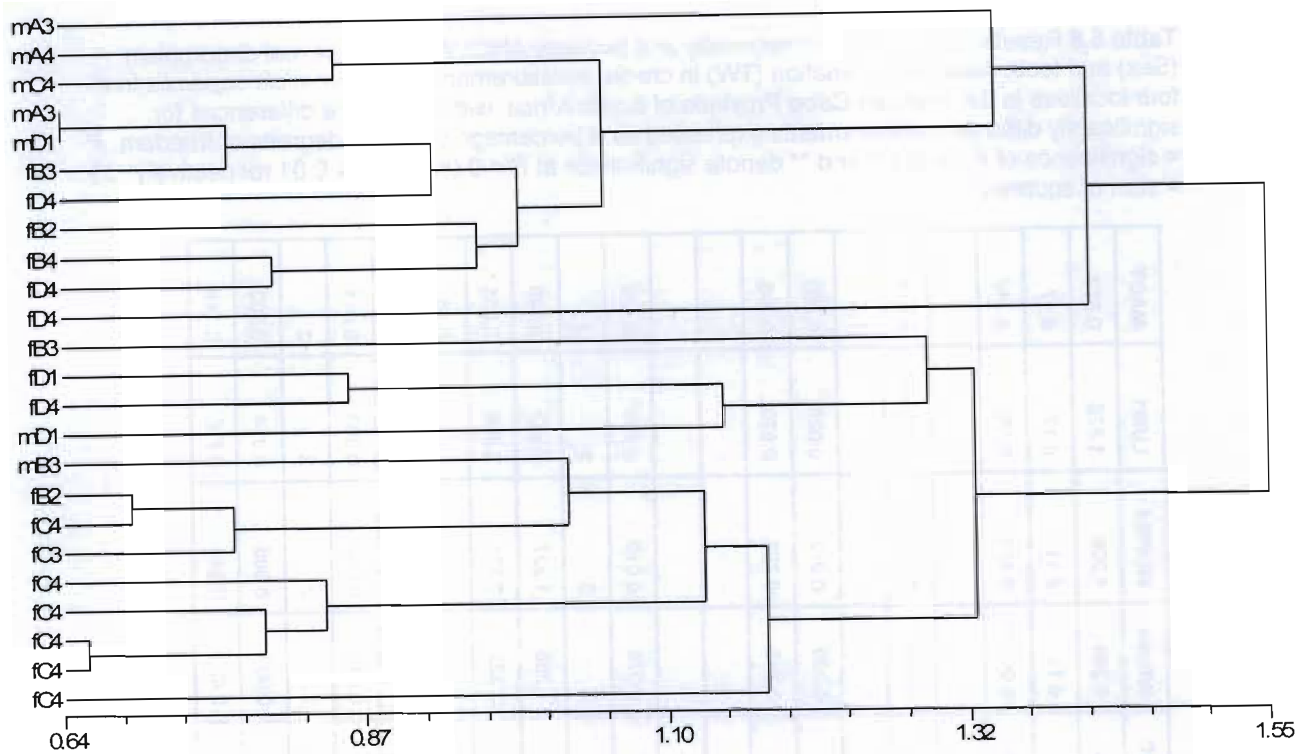


Figure 5.10 Plot of the first two discriminant functions of cranial measurements of four different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C; 4 and ▽ = tooth wear class D) of *Neoromicia capensis* from the Nama-Karoo biome of Namibia and South Africa.

A)



Cophenetic correlation coefficient = 0.629.

B)

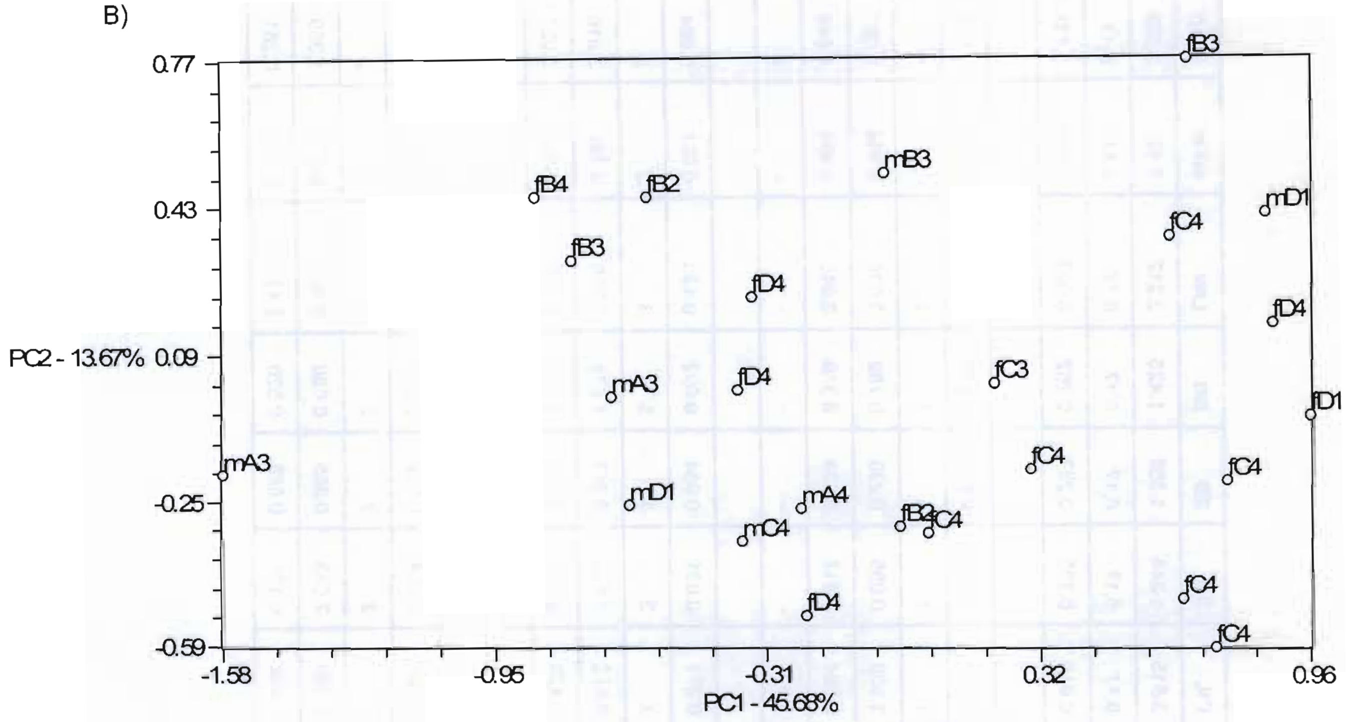


Figure 5.11 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of first two principal components of 12 cranial measurements of *Neoromicia capensis* from four localities in the Western Cape Province in South Africa. The sex (male = m, female = f), tooth wear class (A, B, C, or D) and locality code (1-4, see Appendix 5.1 for locality data) of individuals are indicated.

Table 5.8 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in cranial measurements of *Neoromicia capensis* from four localities in the Western Cape Province of South Africa, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, *P* = significance of *F* values, * and ** denote significance at *P* < 0.05 and *P* < 0.01 respectively. SS = sum of squares.

Levene's		**CIL**	**BH**	**ZB**	**BB**	**LIW**	**WFM**	**WAS**	**WOUC**	**WIUM1**	**WUPM4**	**LUM1**	**MAOT**
2-way	*F*	3.513	1.244	1.356	1.425	2.212	2.197	3.022	1.673	6.296	1.200	1.826	0.572
	df	6,17	6,17	6,17	6,17	6,17	6,17	6,17	6,17	6,17	6,17	6,17	6,17
	P	0.019 *	0.333	0.287	0.262	0.093	0.094	0.034 *	0.188	0.001 **	0.353	0.154	0.747
2-way ANOVA													
Sex	SS	0.313	0.001	0.020	0.022	8.87E-05	0.009	2.69E-04	0.016	0.001	1.98E-04	1.31E-04	0.014
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	3.358	0.055	0.230	0.782	0.005	0.494	0.037	0.425	0.039	0.072	0.028	0.760
	P	0.084	0.817	0.638	0.389	0.945	0.492	0.849	0.523	0.845	0.792	0.870	0.395
	%	3.03	-	-	-	-	-	-	-	-	-	-	-
TW	SS	0.271	0.031	0.064	0.092	0.125	0.021	0.084	0.085	0.079	0.010	0.003	0.209
	df	3	3	3	3	3	3	3	3	3	3	3	3
	F	0.972	1.020	0.247	1.075	2.269	0.397	3.910	0.770	1.250	1.227	0.242	3.746
	P	0.429	0.409	0.862	0.386	0.117	0.757	0.027 *	0.527	0.323	0.331	0.866	0.031 *
	%	-	-	-	-	-	-	8.87	-	-	-	-	9.88
TW×Sex	SS	0.624	0.054	0.067	0.039	0.033	0.129	0.020	0.025	0.038	0.002	0.003	0.011
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	3.350	2.635	0.385	0.680	0.906	3.572	1.369	0.342	0.907	0.386	0.314	0.302
	P	0.059	0.101	0.686	0.520	0.423	0.051	0.281	0.715	0.422	0.686	0.735	0.743

8) 62.5%, tooth wear D (n = 7) 100%]. A plot of the first two discriminant function axes of the four-group DFA (Fig. 5.12) shows tooth wear classes A and B separated from tooth wear classes C and D on the first discriminant function axis, although a male of tooth wear class D (ZM41457) and a female of tooth wear class C (KM29010) plotted closer to tooth wear classes A and B, respectively. On the first discriminant function axis, which described 64% of the variation, moment arm of the temporal (MAOT) loaded highest, and least inter-orbital width (LIW) and width across the outer surfaces of the upper canine teeth (WOUC) loaded least. Of the important measurements on the first axis, moment arm of the temporal was also significantly different between the tooth wear classes in the two-way ANOVA analyses, and width across the outer surfaces of the upper canine teeth was also important on the first axis of the PCA which showed some separation of the tooth wear classes. On the second discriminant function axis which separated tooth wear class D from tooth wear C, and which explained 24.7% of the variation, condylo-incisor length (CIL) loaded highest and least inter-orbital width (LIW) loaded least. There were too few specimens with external measurements to run any analyses of external measurements.

5.3.1.6 *Neoromicia capensis* – South Africa, Free State Province, Grassland

5.3.1.6.1 Cranial measurements

These analyses were based on 25 specimens from four localities in the Free State Province of South Africa (Fig. 5.8), all occurring in the Grassland biome. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendix 5.6 F1 and F2. Two (16.7%) measurements were sexually dimorphic in the two-way ANOVA, condylo-incisor length (CIL) and braincase height (BH), with females being 2.48 and 2.52% larger than males, but no measurements were significantly difference between the tooth wear classes, or in the interaction between sex and tooth wear class (Table 5.9). Kruskall-Wallis tests identified one difference to the results of the ANOVA, since the Kruskall-Wallis test found significant variation between the tooth wear classes in moment arm of the temporal (MAOT) which the ANOVA test had not detected (Appendix 5). In the two-way MANOVA test, there were no significant differences between sexes (Wilks = 0.236, $F_{(7,12)}$ = 1.886, P = 0.204), tooth wear classes (Wilks = 0.020, $F_{(21.41,36)}$ = 1.655, P = 0.110), or the interaction of sex and tooth wear classes (Wilks = 0.180, $F_{(14,24)}$ = 0.790, P = 0.703).

The phenogram (Fig. 5.12) showed little clustering due to sex, tooth wear class or locality, besides a single cluster of females of two different tooth wear classes from two different localities. The PCA (Fig. 5.13) which showed 26.05% and 16.09% variation on the first and second principal component axes, respectively, also showed no distinct separation in relation to sex, tooth wear class or locality. On the first principal component axis width between the inner surfaces of the upper first molar teeth (WIUM1) and width of the upper fourth premolar (WUPM4) loaded highest and lowest, respectively. On the second principal component axis, braincase height (BH) loaded highest, and zygomatic breadth (ZB), and width across the outer surfaces of the upper canine teeth (WOUC) loaded least.

A two-group DFA of the sexes produced a 92% overall *a posteriori* assignment of specimens to the correct sex [females (n = 14) - 92.86%, males (n =11) - 90.91%]. A three-group DFA of tooth wear classes A, B and C produced an 86.96% overall *a posteriori* assignment of specimens to the correct tooth wear class [tooth wear A (n = 4) - 100%, tooth wear B (n = 11) - 90.91%, tooth wear C (n = 8) - 75%]. A plot of the first two discriminant function axes of the three-group DFA (Fig. 5.14) separated tooth wear classes B and C from tooth wear class A on the first discriminant function axis. On the first DF axis which described 84% of the variation, moment arm of the temporal (MAOT) loaded highest and braincase breadth (BB) loaded least. However, neither of these measurements were among the important measurements on the first principal component axis of the PCA, or the measurement that were significantly different between tooth wear classes in the one-way two-way ANOVA tests. Tooth wear classes B and C almost separated on the second discriminant function axis, which described 16% of the variation, with width between the inner surfaces of the upper first molar teeth (WIUM1) loading highest and width of the foramen magnum (WFM) loading least.

5.3.1.6.2 External measurements

Nineteen specimens from two localities in the Free State Province of South Africa (Fig. 5.15), all occurring in the Grassland biome, were used in the univariate analyses. In order to compensate for missing data, multivariate analyses were based on 18 specimens using nine

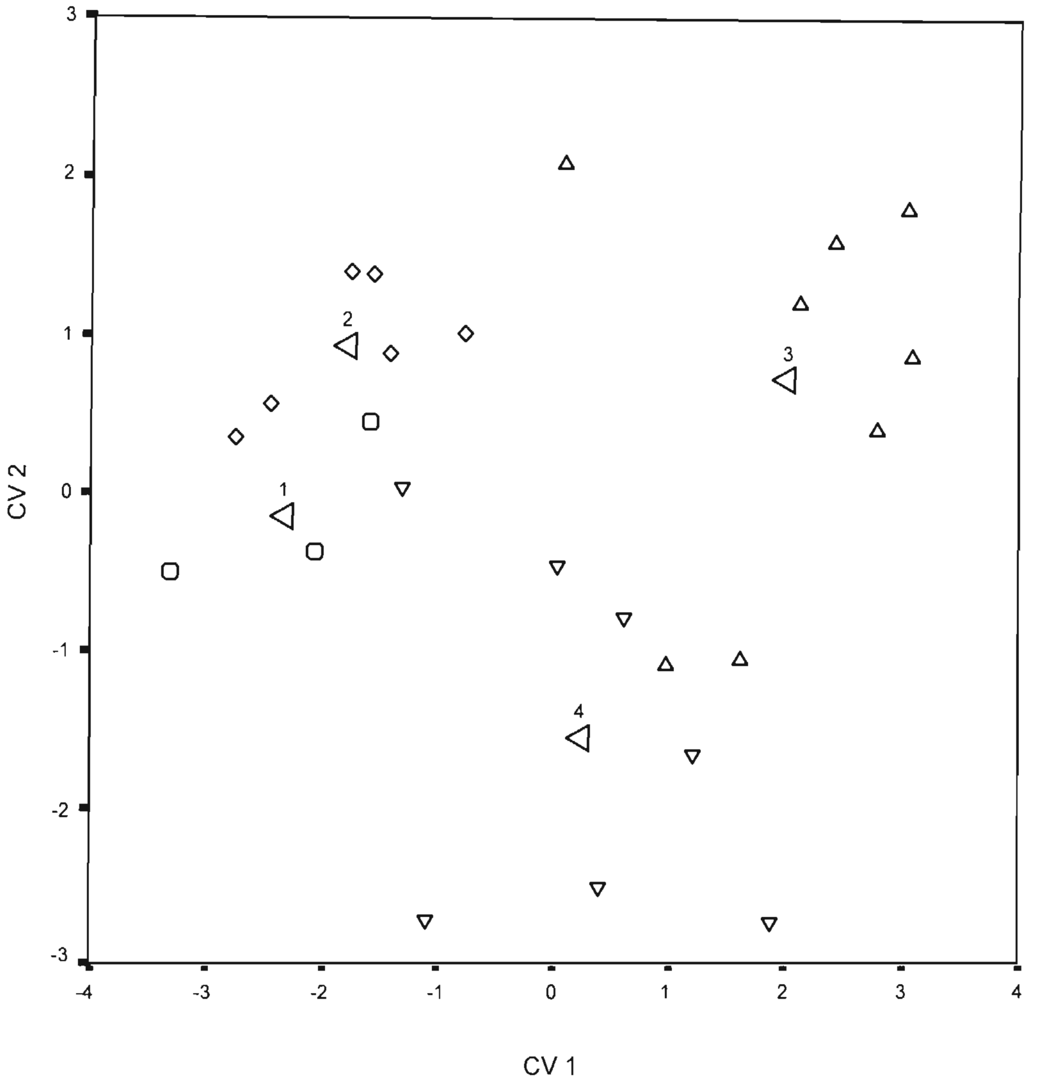
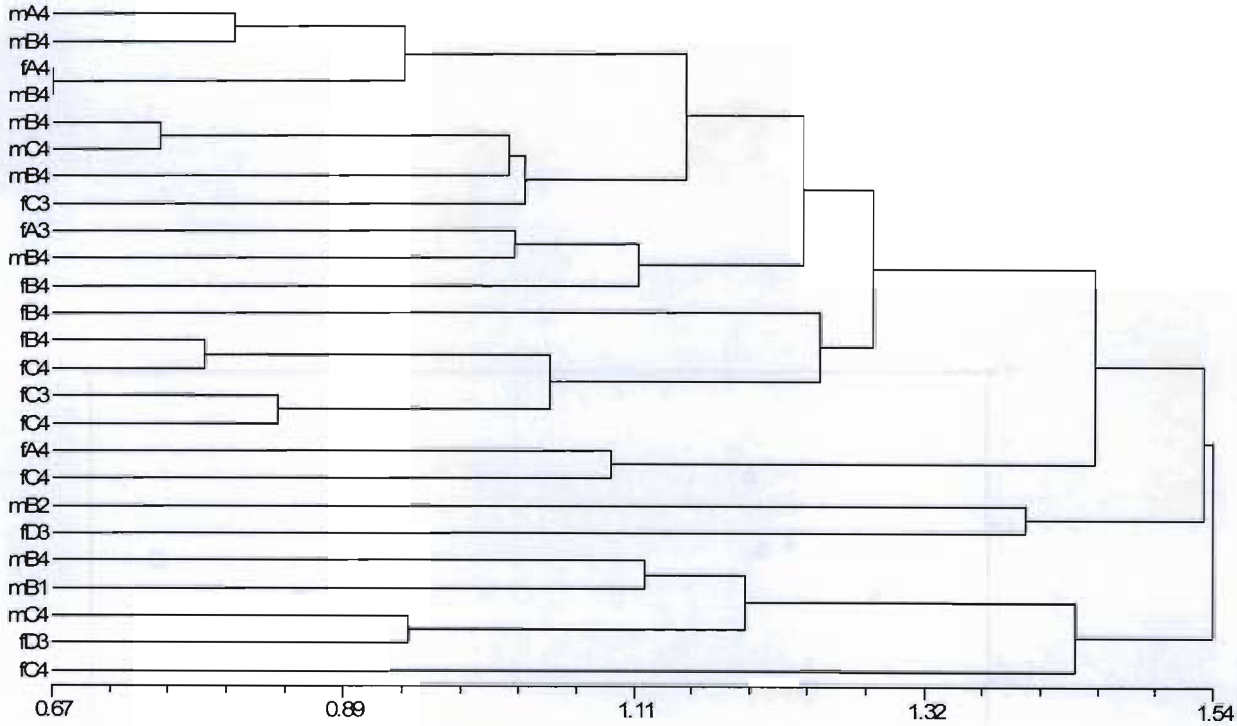


Figure 5.12 Plot of the first two discriminant functions of cranial measurements of four different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C; 4 and ▽ = tooth wear class D) of *Neoromicia capensis* from the Western Cape Province of South Africa.

A)



Cophenetic correlation coefficient = 0.627.

B)

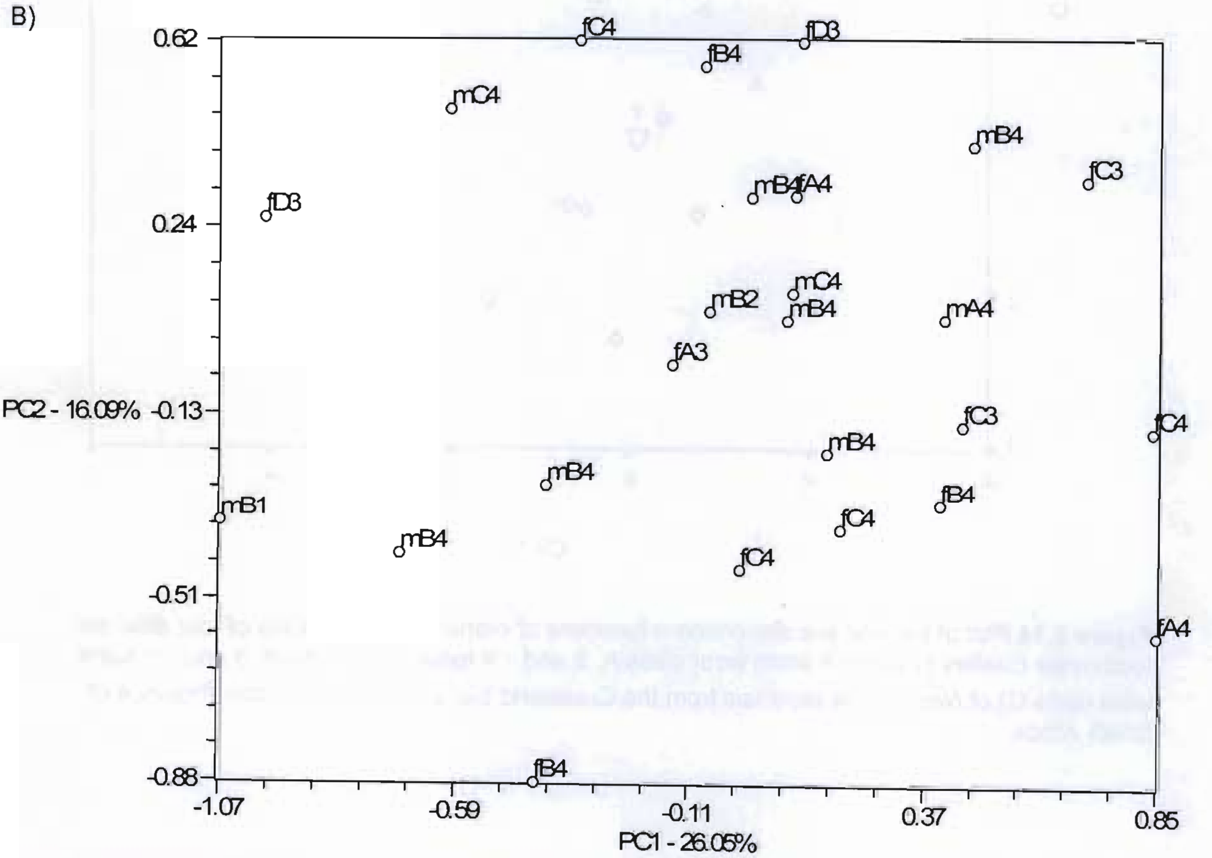


Figure 5.13 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of first two principal components of 12 cranial measurements of *Neoromicia capensis* from four localities in the Free State Province in South Africa, occurring in the Grassland biome. The sex (male = m, female = f), tooth wear class (A, B, C, or D) and locality code (1-4, see Appendix 5.1 for locality data) of individuals are indicated.

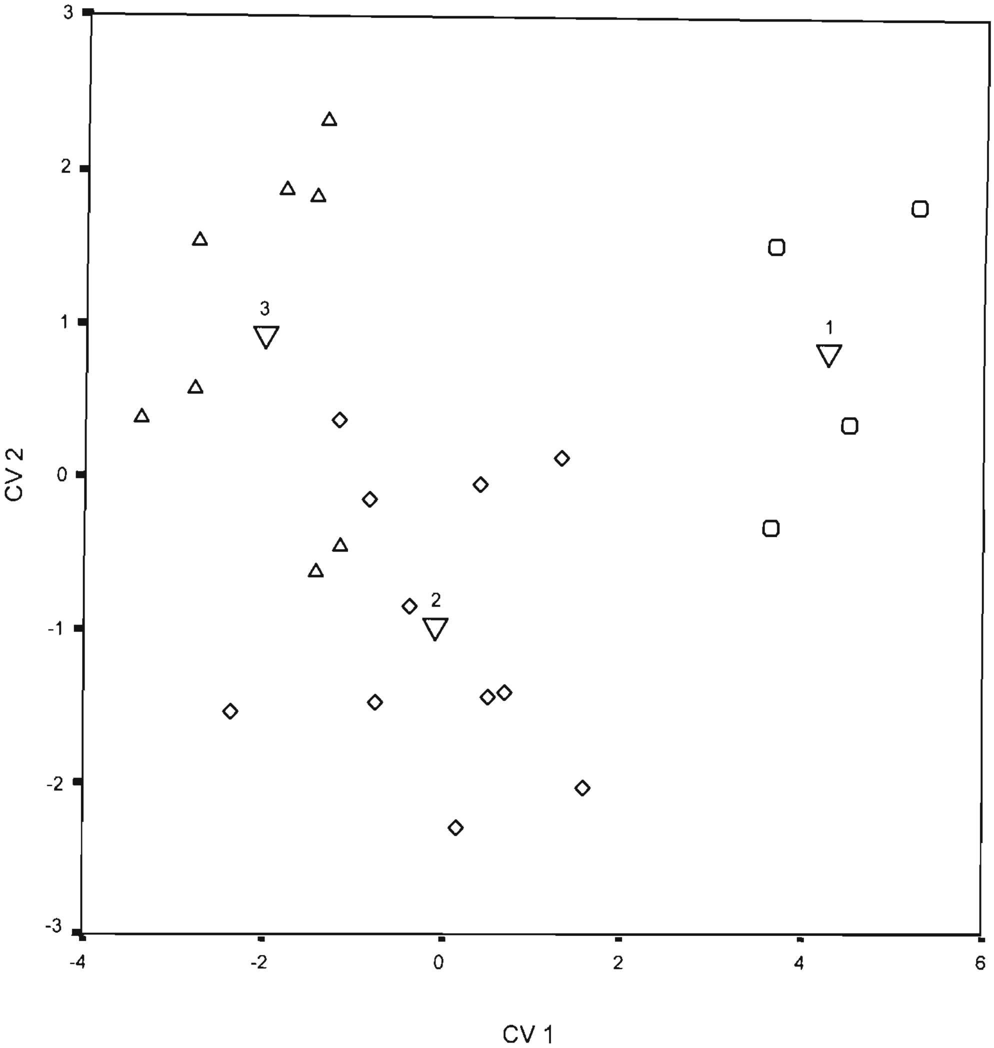


Figure 5.14 Plot of the first two discriminant functions of cranial measurements of four different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C) of *Neoromicia capensis* from the Grassland biome in the Free State Province of South Africa.

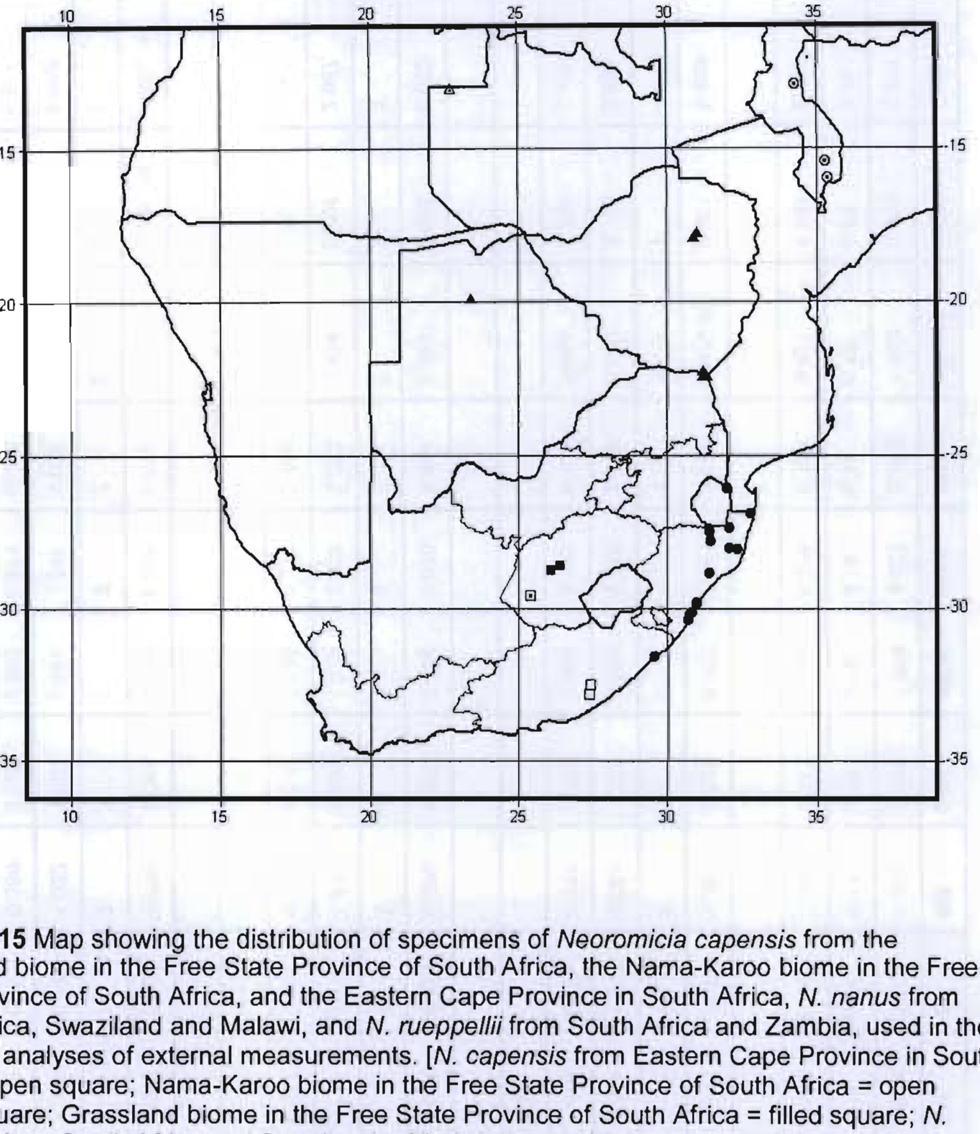


Figure 5.15 Map showing the distribution of specimens of *Neoromicia capensis* from the Grassland biome in the Free State Province of South Africa, the Nama-Karoo biome in the Free State Province of South Africa, and the Eastern Cape Province in South Africa, *N. nanus* from South Africa, Swaziland and Malawi, and *N. rueppellii* from South Africa and Zambia, used in the statistical analyses of external measurements. [*N. capensis* from Eastern Cape Province in South Africa = open square; Nama-Karoo biome in the Free State Province of South Africa = open dotted square; Grassland biome in the Free State Province of South Africa = filled square; *N. africanus* from South Africa and Swaziland = filled circle; and Malawi = open dotted circle; *N. rueppellii* from Southern Africa = filled triangle; and Zambia = open dotted triangle.]

Table 5.9 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in cranial measurements of *Neoromicia capensis* from three localities in the Free State Province of South Africa falling into the Grassland biome, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, *P* = significance of *F* values, * and ** denote significance at *P* < 0.05 and *P* < 0.01respectively. SS = sum of squares.

Levene's		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
2-way	*F*	1.498	1.692	0.863	1.031	2.038	1.978	1.427	2.032	1.060	0.802	0.837	0.495
	df	6,18	6,18	6,18	6,18	6,18	6,18	6,18	6,18	6,18	6,18	6,18	6,18
	P	0.235	0.180	0.540	0.438	0.113	0.122	0.258	0.114	0.421	0.581	0.558	0.804
2-way ANOVA													
Sex	SS	0.428	0.152	0.071	0.001	0.037	0.000	0.003	0.030	3.97E-05	0.001	0.002	0.004
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	5.970	7.344	1.009	0.087	1.962	0.000	0.310	2.348	0.003	0.148	0.638	0.183
	P	0.025 *	0.014 *	0.328	0.771	0.178	0.995	0.585	0.143	0.954	0.705	0.435	0.674
	%	2.48	2.52	-	-	-	-	-	-	-	-	-	-
TW	SS	0.017	0.044	0.428	0.070	0.070	0.120	0.070	0.034	0.085	0.005	0.032	0.140
	df	3	3	3	3	3	3	3	3	3	3	3	3
	F	0.078	0.705	2.032	1.810	1.239	1.239	2.308	0.882	2.404	0.204	2.967	2.276
	P	0.971	0.562	0.145	0.181	0.325	0.325	0.111	0.469	0.101	0.893	0.060	0.115
	%	-	-	-	-	-	-	-	-	-	-	10.14	-
Sex×TW	SS	0.003	0.045	0.038	0.026	0.049	0.038	0.025	0.027	3.24E-04	4.26E-04	6.59E-05	0.020
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	0.024	1.090	0.269	1.022	1.302	0.595	1.246	1.039	0.014	0.025	0.009	0.498
	P	0.976	0.358	0.767	0.380	0.296	0.562	0.311	0.374	0.986	0.975	0.991	0.616

measurements. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendix 5.7 C1 and C2. Six (50%) measurements: total (TOT), tail (T), both forearm (FAL, FA), ear (E), and third metacarpal (TMETA) lengths, showed significant sexual dimorphism with females being 4.54 to 10.65% larger than males (Table 5.10). Two (16.7%) measurements, ear (E) and third metacarpal length (TMETA) showed significant variation between the different tooth wear classes. Since tooth wear class A was represented by a single specimen, this specimen was removed from the post-hoc Tukey tests, which identified the same subsets separating tooth wear classes B and C from tooth wear class D. The relative difference of ear length between tooth wear classes B and D was 25.40%, while the relative difference between tooth wear classes A and D of the third metacarpal length was 11.63% (Table 5.10). The Kruskall-Wallis tests identified one inconsistency between this test and the ANOVA tests, since the Kruskall-Wallis test found ear length (E) not to be sexually dimorphic, whereas the ANOVA test showed sexual dimorphism (Appendix 5.5). A one-way MANOVA of 18 specimens of nine measurements (TOT, T, HFL, E, TIB, FA, TMETA, TRL, TRB) showed no significant sexual dimorphism (Wilks = 0.394, $F_{(8,9)}$ = 1.366, P = 0.335), or significant difference between the tooth wear classes (Wilks = 0.020, $F_{(18.165,27)}$ = 1.878, P = 0.083).

The phenogram (Fig. 5.16) showed some clustering due to sex and locality, given the cluster of males from Florisbad (# 2), and the cluster of females from Brandfort (# 1). However, there were also two other clusters which contained both males and females from Florisbad (# 2). The PCA (Fig. 5.16) which explained 43.94% and 21.18% of the variation on the first two principal component axes, respectively, identified more males clustered with smaller individuals on the first principal component axis, as well as some separation of the Brandfort (# 1) specimens from the Florisbad (# 2) specimens, but no obvious separation of the different tooth wear classes. On the first principal component axis, tail length (T), length of the third metacarpal (TMETA) and forearm length (FA) loaded highest, and tragus length (TRL) loaded least. Three of these measurements, tail length, length of the third metacarpal and forearm length, also showed significant variation between the sexes in the two-way ANOVAs. On the second principal component, tragus (TRL), hind foot (HFL) and ear (E) lengths loading highest, and tragus breadth (TRB) loading least.

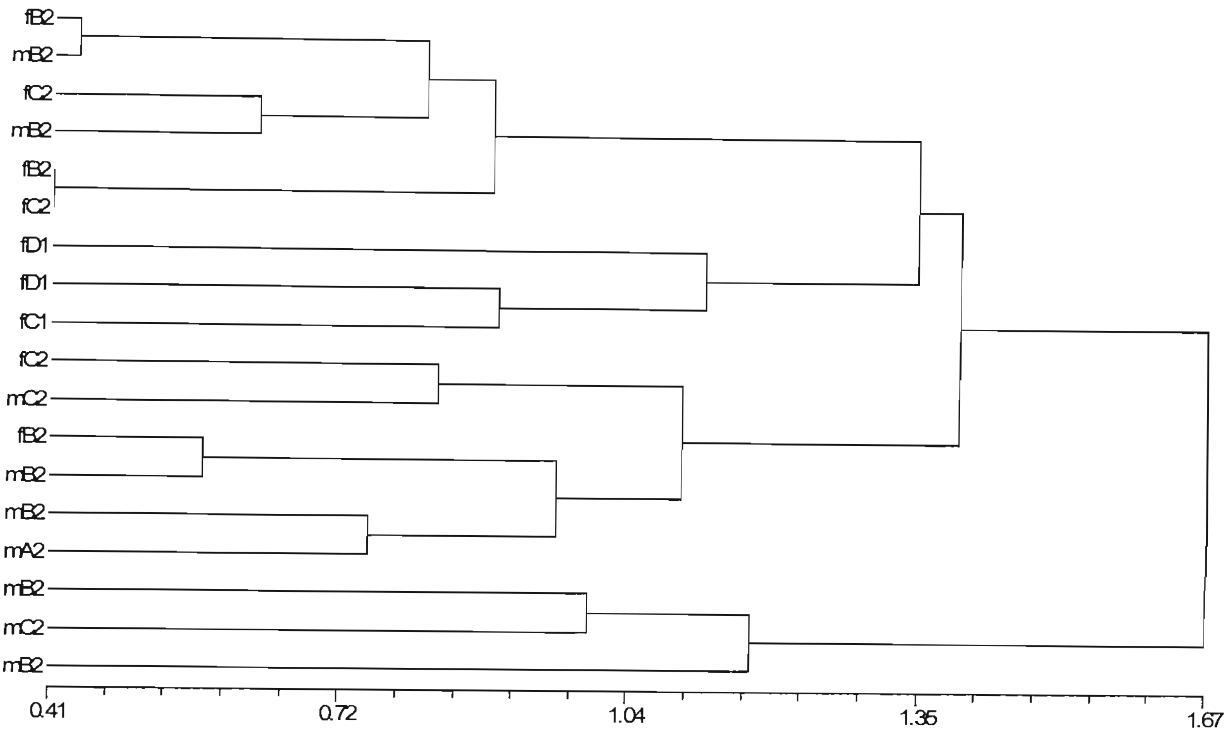
A two-group DFA of the sexes produced an 83.33% overall *a posteriori* assignment of specimens to the correct sex [females (n = 9) - 88.89%, males (n = 9) - 77.78%]. A two-group DFA of tooth wear classes produced a 93.33% overall a posteriori assignment of specimens to the correct tooth wear class [tooth wear B (n = 9) - 88.89%, tooth wear C (n = 6) - 100%].

5.3.1.7 *Neoromicia capensis* – South Africa, Free State Province, Nama-Karoo
5.3.1.7.1 Cranial measurements

These analyses were run on 45 specimens from two localities in the Free State Province of South Africa (Fig. 5.8), both occurring in the Nama-Karoo biome. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendix 5.6 G1 andG2. In two-way ANOVA tests, six (50%) measurements showed sexual dimorphism, condylo-incisor length of the skull (CIL), zygomatic breadth (ZB), width across the outer surfaces of the upper canine teeth (WOUC), moment arm of the temporal (MAOT), braincase height (BH) and width of the articular surface (WAS), with females being 2.07 to 4.85% larger than males (Table 5.11). Zygomatic breadth (ZB) was significantly different between the tooth wear classes, the post-hoc Tukey test identified two subsets separating tooth wear class A from tooth wear classes B, C and D, and the relative difference between tooth wear classes A and D was 6.53% (Table 5.11). No measurements showed a significant interaction between sex and tooth wear class (Table 5.11). A two-way MANOVA test showed significant sexual dimorphism (Wilks = 0.428, $F_{(12,27)}$ = 3.010, P = 0.008), but no significant variation between the tooth wear classes (Wilks = 0.223, $F_{(36:80,502)}$ = 1.482, P = 0.074), and no significant interaction between sex and tooth wear class (Wilks = 0.541, $F_{(24,54)}$ = 0.808, P = 0.711).

The phenogram (Fig. 5.17) identified an outlier cluster of females of tooth wear class D from both localities. The other specimens form three major clusters, the smallest of which contains males only, of two different tooth wear classes from Jagersfontein Commonage (# 2), whereas the other two clusters show little sign of clustering due to sex, tooth wear class or locality, although the specimens with one exception were from a single locality, and there were far more males than females in the analysis. Although males and females overlapped on the first principal component axis of the PCA (Fig. 5.17), which explained 38.27% of the variation, females were larger and males were smaller. Within each sex, specimens of tooth wear class A were clustered with smaller individuals on the first principal component axis, whereas there was no distinct

A)



Cophenetic correlation coefficient = 0.722.

B)

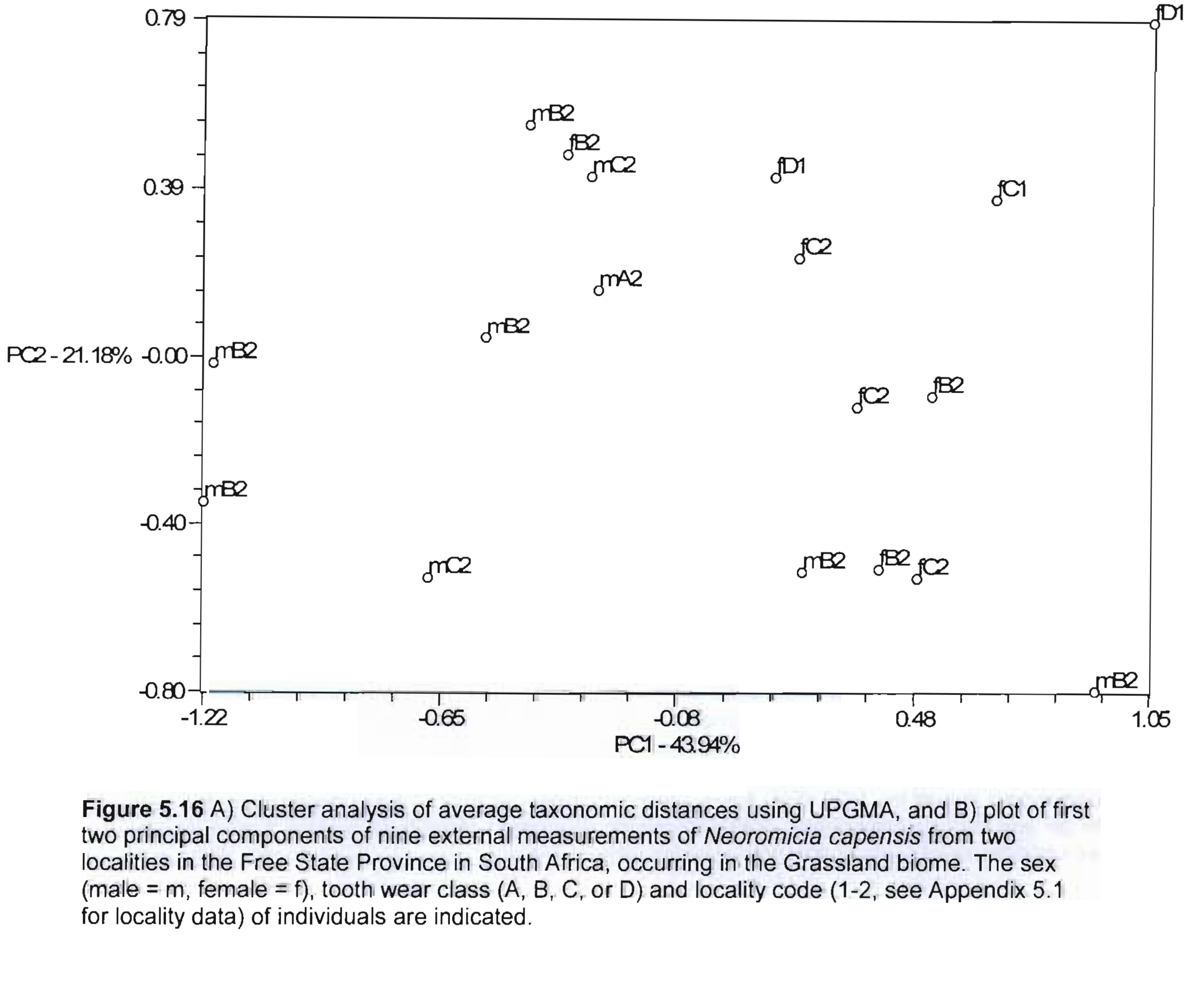


Figure 5.16 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of first two principal components of nine external measurements of *Neoromicia capensis* from two localities in the Free State Province in South Africa, occurring in the Grassland biome. The sex (male = m, female = f), tooth wear class (A, B, C, or D) and locality code (1-2, see Appendix 5.1 for locality data) of individuals are indicated.

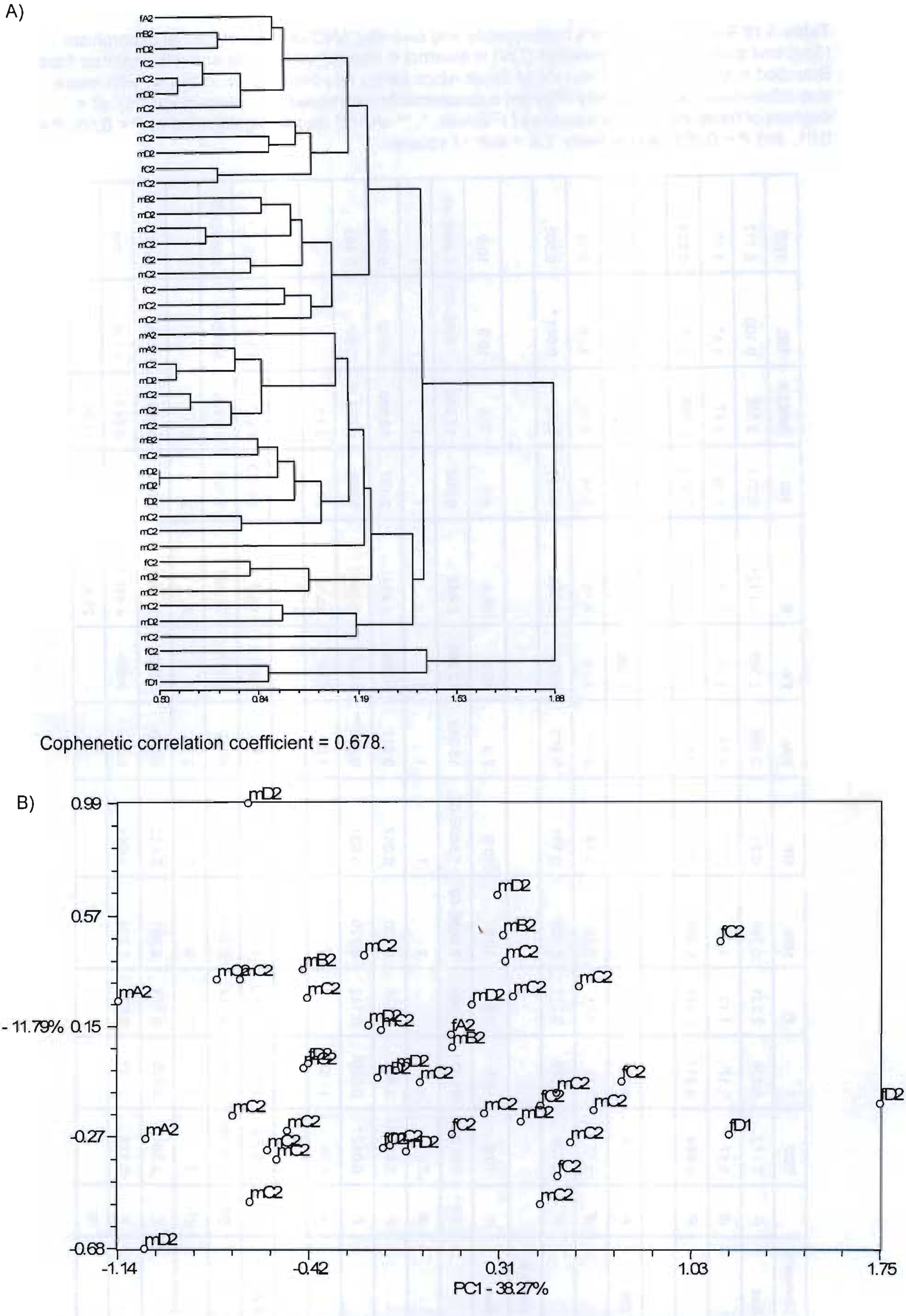


Figure 5.17 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of first two principal components of 12 cranial measurements of *Neoromicia capensis* from two localities in the Free State Province in South Africa, occurring in the Nama-Karoo biome. The sex (male = m, female = f), tooth wear class (A, B, C, or D) and locality code (1-2, see Appendix 5.1 for locality data) of individuals are indicated.

Table 5.10 Results of Levene's homogeneity and one-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in external measurements of *Neoromicia capensis* from Brandfort in the Free State Province of South Africa falling into the Grassland biome, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, *P* = significance of *F* values, *, ** and *** denote significance at *P* < 0.05, *P* < 0.01, and *P* < 0.001, respectively. SS = sum of squares.

Levene's		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Sex	*F*	0.172	0.136	2.231	0.545	0.891	0.686	2.368	10.124	0.012	3.105	0.100	6.112
	df	1,17	1,17	1,12	1,17	1,17	1,14	1,17	1,17	1,16	1,17	1,17	1,17
	P	0.684	0.717	0.161	0.470	0.358	0.421	0.142	0.005 **	0.913	0.096	0.755	0.024 *
TW	*F*	0.601	0.661	1.457	1.253	0.764	0.703	0.586	2.558	2.097	1.251	3.527	0.815
	df	3,15	3,15	2,11	3,15	3,15	2,13	3,15	3,15	3,14	3,15	3,15	3,15
	P	0.624	0.589	0.275	0.326	0.531	0.513	0.633	0.094	0.147	0.327	0.041 *	0.505
ANOVA													
Sex	*n*	10:9	10:9	9:5	10:9	10:9	7:9	10:9	10:9	9:9	10:9	10:9	10:9
	SS	137.558	61.011	9.060	2.865E-02	1.880E-02	13.349	12.268	6.447	0.902	17.086	1.405E-03	7.495E-03
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	7.917	6.607	2.476	0.133	0.047	9.511	9.364	4.474	2.197	10.685	0.002	0.564
	P	0.012 *	0.020*	0.142	0.720	0.831	0.008 **	0.007 **	0.049 *	0.158	0.005 **	0.961	0.463
	%	5.95	10.65	-	-	-	5.23	4.54	10.15	-	5.79	-	-
TW	*n*	1:9:7:2	1:9:7:2	-:6:6:2	1:9:7:2	1:9:7:2	1:9:6:-	1:9:7:2	1:9:7:2	1:9:6:2	1:9:7:2	1:9:7:2	1:9:7:2
	SS	134.797	24.254	3.354	0.200	2.386	4.167	3.362	21.297	1.101	18.120	0.745	1.967E-02
	df	3	3	2	3	3	2	3	3	3	3	3	3
	F	2.261	0.626	0.372	0.287	2.683	0.939	0.539	11.034	0.807	3.464	0.405	0.460
	P	0.123	0.609	0.698	0.834	0.084	0.416	0.663	4.42E-04 ***	0.511	0.043 *	0.752	0.714
	%	-	-	-	-	-	-	-	25.40	-	11.63	-	-

Table 5.11 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in cranial measurements of *Neoromicia capensis* from two localities in the Free State Province of South Africa falling into the Nama-Karoo biome, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, *P* = significance of *F* values, * and ** denote significance at *P* < 0.05 and *P* < 0.01, respectively. SS = sum of squares.

Levene's		**CIL**	**BH**	**ZB**	**BB**	**LIW**	**WFM**	**WAS**	**WOUC**	**WIUM1**	**WUPM4**	**LUM1**	**MAOT**
2-way	*F*	0.784	1.696	1.037	1.317	0.507	0.472	1.858	2.090	1.202	1.643	0.432	1.072
	df	6,38	6,38	6,38	6,38	6,38	6,38	6,38	6,38	6,38	6,38	6,38	6,38
	P	0.588	0.149	0.417	0.273	0.799	0.824	0.114	0.077	0.326	0.162	0.853	0.396
2-way ANOVA													
Sex	SS	0.651	0.158	0.441	0.001	0.003	0.001	0.055	0.231	0.045	0.021	0.001	0.214
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	11.442	7.166	11.948	0.021	0.129	0.031	5.464	10.867	3.022	2.960	0.231	13.109
	P	0.002 **	0.011 *	0.001 **	0.887	0.721	0.861	0.025 *	0.002 **	0.090	0.093	0.634	0.001 **
	%	2.07	2.19	3.04	-	-	-	3.77	3.28	-	-	-	4.85
TW	SS	0.322	0.088	0.709	0.043	0.001	0.039	0.017	0.149	0.123	0.009	0.015	0.039
	df	3	3	3	3	3	3	3	3	3	3	3	3
	F	1.887	1.334	6.410	0.401	0.021	0.789	0.561	2.326	2.756	0.438	1.189	0.792
	P	0.148	0.278	0.001**	0.753	0.996	0.508	0.644	0.090	0.056	0.727	0.327	0.506
	%	-	-	6.53	-	-	-	-	-	-	-	-	-
Sex×TW	SS	0.055	0.061	0.101	0.012	0.010	0.014	0.035	0.044	0.051	0.001	0.001	0.033
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	0.484	1.390	1.368	0.170	0.257	0.434	1.745	1.023	1.725	0.046	0.092	1.009
	P	0.620	0.261	0.267	0.844	0.775	0.651	0.188	0.369	0.192	0.955	0.913	0.374

separation among the other tooth wear classes. Zygomatic breadth (ZB) and width across the outer surfaces of the upper canine teeth (WOUC) loaded highest and width of the foraman magnum (WFM) loaded least on the first principal component axis. Both zygomatic breadth (ZB) and width across the outer surfaces of the upper canine teeth (WOUC) were also sexually dimorphic in the two-way ANOVAs. A single male of tooth wear class D from Jagersfontein Commonage (NMBZ7693) was separated from the rest of the specimens on the second principal component axis which explained 11.79% of the variation, this difference was not as distinct in the phenogram. Braincase breadth (BB) and width of the foramen magnum (WFM) loaded highest and width of the upper fourth premolar (WUPM4) loaded least on the second principal component axis.

A two-group DFA of the sexes produced a 91.11% overall *a posteriori* assignment of specimens to the correct sex [females (n = 10) - 100%, males (n = 35) - 88.57%]. A four-group DFA of tooth wear classes produced a 75.56% overall a posteriori assignment of specimens to the correct tooth wear class [tooth wear A (n = 3) - 100%, tooth wear B (n = 3) - 100%, tooth wear C (n = 27) - 70.37%; tooth wear D (n = 12) - 75%]. A plot of the first two discriminant function axes of the four-group DFA (Fig. 5.18) largely separated tooth wear class A from the other tooth wear classes on the first discriminant function axis, with the exception of the overlap of two specimens, a female of tooth wear class C (NMB7634) and a male of tooth wear class D (NMB7685). Moment arm of the temporal (MAOT) loaded highest and zygomatic breadth (ZB) and width across the outer surfaces of the upper canine teeth (WOUC) loaded least on the first discriminant function axis which explained 59.1% of the variation. Zygomatic breadth (ZB) was also the only measurement that showed significant variation between the tooth wear classes in the two-way ANOVAs. There was no separation between the tooth wear classes on the second discriminant function axis which explained 33.7% of the variation.

5.3.1.7.2 External measurements

The univariate analyses were run on 56 specimens from one locality in the Free State Province of South Africa (Fig. 5.15), occurring in the Nama-Karoo biome. To accommodate missing data, multivariate analyses were based on nine measurements of 49 specimens with information on sex and tooth wear class. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendix 5.7 D1 and D2. In a two-way ANOVA five (55.56%) measurements, total (TOT), tail (T), forearm (FAL), tibia (TIB), and third metacarpal (TMETA) lengths, showed significant sexual dimorphism with females being 3.32 to 6.12% larger than males, two (22.22%) measurements, third metacarpal (TMETA) and tragus (TRL) lengths showed significant variation between the tooth wear classes, and no measurements showed any significant interaction between sex and tooth wear class. A post-hoc Tukey test identified in third metacarpal length (TMETA), two overlapping subgroups separating tooth wear classes A and B, and the relative difference between tooth wear classes A and B was 6.24% (Table 5.12). In tragus length (TRL) a post-hoc Tukey test identified two separate subgroups separating tooth wear classes A and C from tooth wear classes B and D, and the relative difference between tooth wear classes A and D was 8.68%. Tragus length (TRL) of tooth wear class C, being smaller than tooth wear class B, was due to16 of 28 specimens of tooth wear class C having tragus lengths (TRL) smaller than the smallest tragus length (TRL) of the four specimens of tooth wear class B. A two-way MANOVA showed significant sexual dimorphism (Wilks = 0.504, $F_{(9,33)}$ = 3.606, P = 0.003), but no significant variation between the tooth wear classes (Wilks = 0.428, $F_{(27,97.019)}$ = 1.213, P = 0.244), and no significant interaction between sex and tooth wear class (Wilks = 0.610, $F_{(27,97.019)}$ = 0.663, P = 0.888).

The phenogram (Fig. 5.19) identified no distinct clustering due to sex or tooth wear class. Although males and females overlapped on the first principal component axis of the PCA (Fig. 5.19), males were smaller and females larger on the first principal component axis which explained 33.13% of the variation. Within each sex, there was little evidence of separation of the different tooth wear classes. Forearm (FAL) and tibia (TIB) lengths loaded highest and tragus length (TRL) loaded least on the first principal component axis. Forearm (FAL) and tibia (TIB) lengths also showed significant difference between the sexes in the two-way ANOVAs, and tragus length (TRL) showed a significant difference between tooth wear classes in two-way ANOVAs. The second principal component axis explained 15.50% of the variation, with tragus breadth (TRB) and tail length (T) loading highest and ear length (E) loading least.

A two-group DFA of the sexes produced a 89.80% overall a posteriori assignment of specimens to the correct sex [females (n = 13) - 92.31%, males (n = 36) - 88.89%]. A four-group

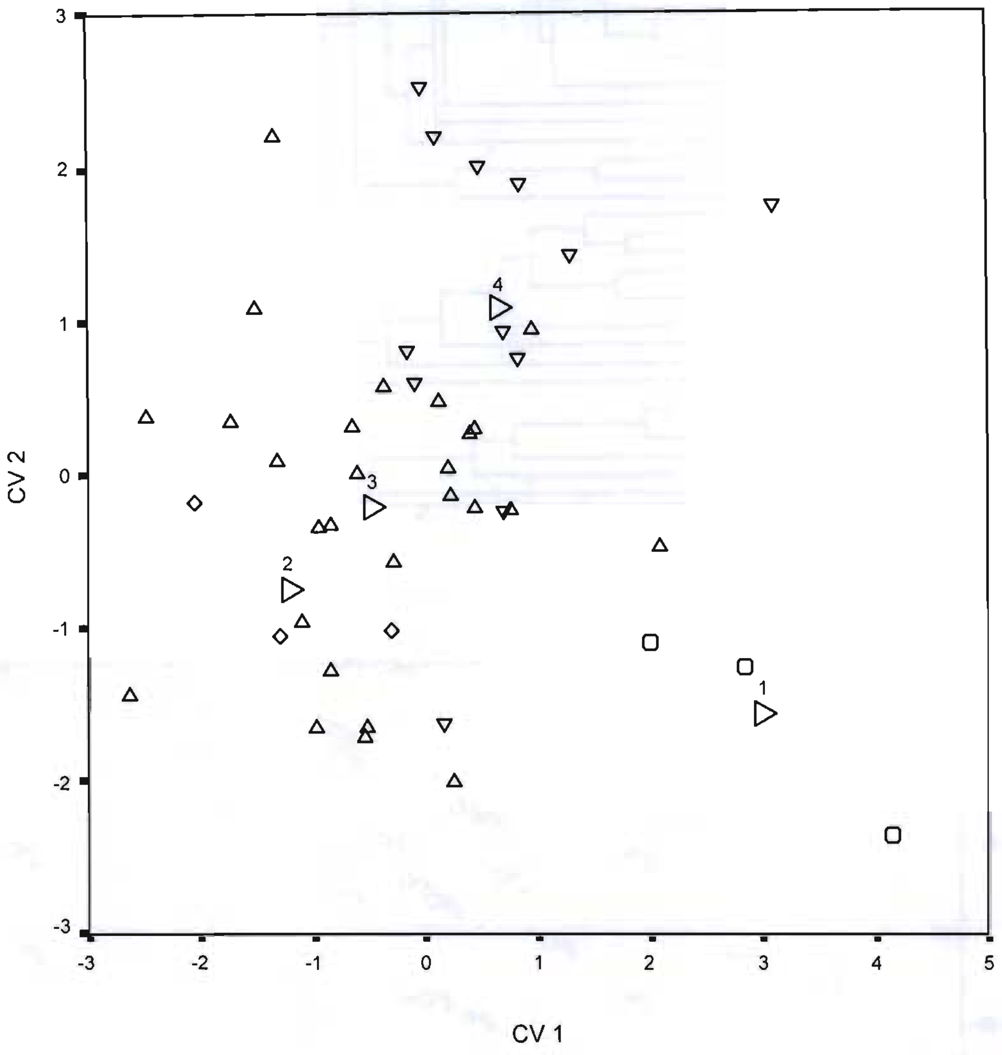
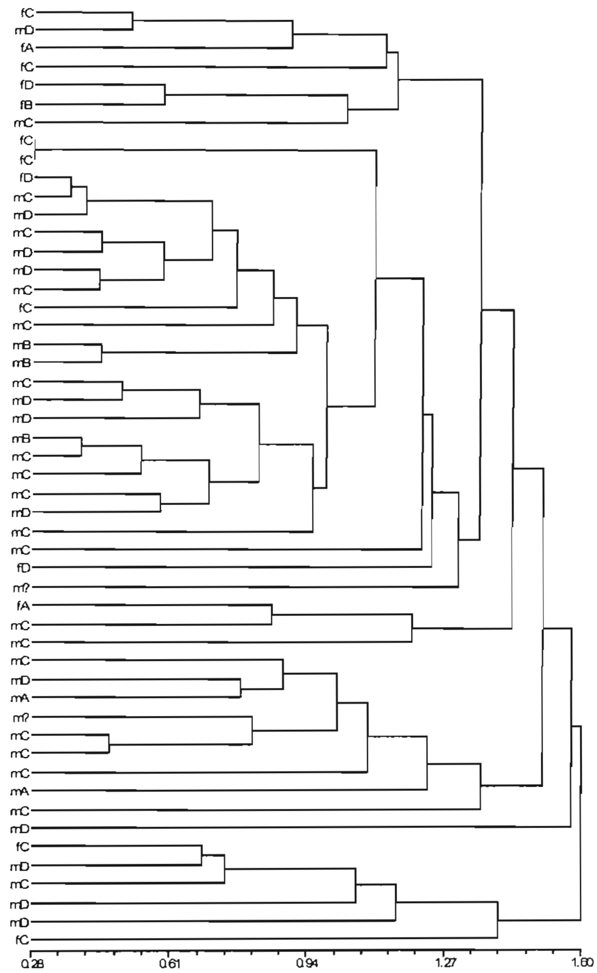


Figure 5.18 Plot of the first two discriminant functions of cranial measurements of four different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C; 4 and ▽ = tooth wear class D) of *Neoromicia capensis* from the Nama-Karoo biome in the Free State Province of South Africa.

A)



Cophenetic correlation coefficient = 0.669.

B)

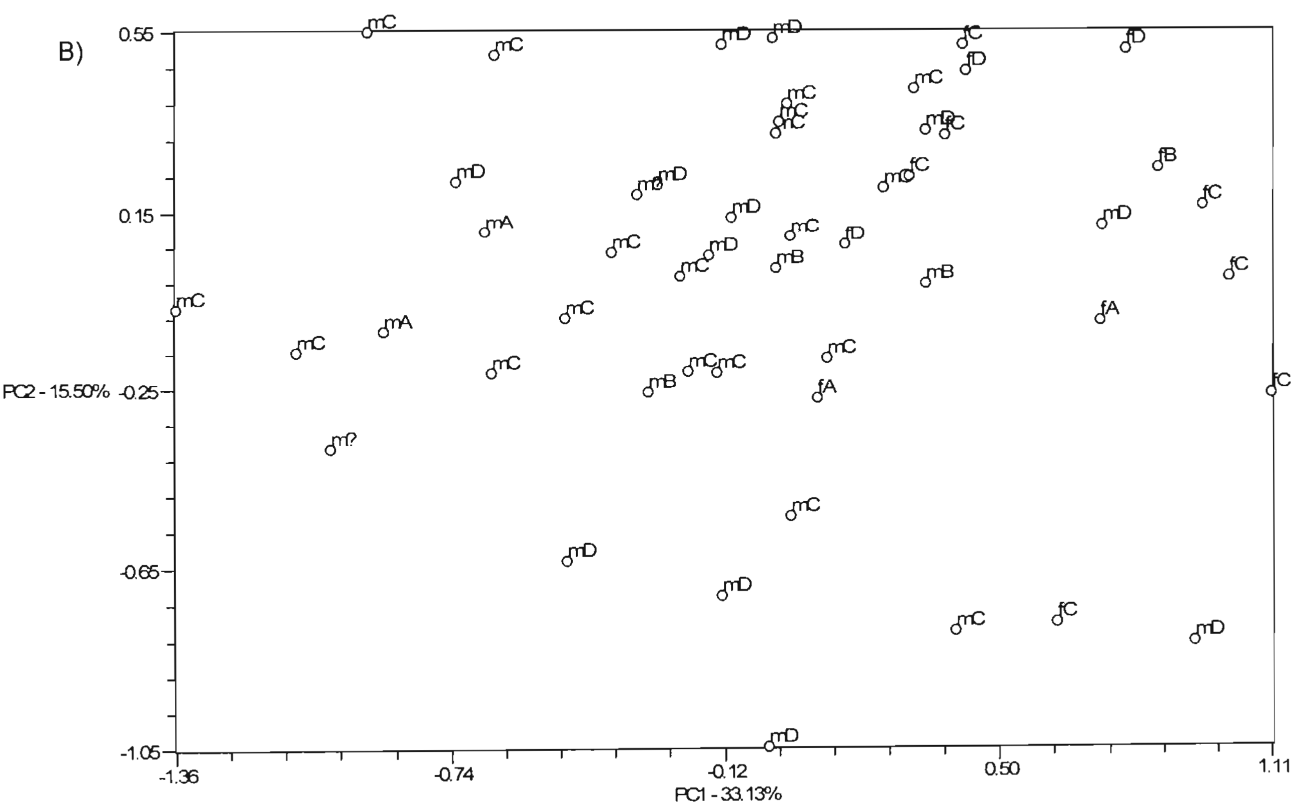


Figure 5.19 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of first two principal components of nine external measurements of *Neoromicia capensis* from Jagersfontein Commonage in the Free State Province in South Africa, occurring in the Nama-Karoo biome. The sex (male = m, female = f), and tooth wear class (A, B, C, D, or unknown = ?) of individuals are indicated.

Table 5.12 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in external measurements of *Neoromicia capensis* from Jagersfontein in the Free State Province of South Africa falling into the Nama-Karoo biome, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, *P* = significance of *F* values. *, ** and *** denote significance at *P* < 0.05, *P* < 0.01, and *P* < 0.001, respectively. SS = sum of squares.

Levene's		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
2-way	*F*	0.844	2.263	-	1.603	-	0.874	-	1.021	2.105	3.249	2.134	1.323
	df	7,41	7,41	-	7,41	-	7,41	-	7,41	7,41	7,41	7,41	7,41
	P	0.558	0.048 *	-	0.162	-	0.535	-	0.431	0.065	0.008 **	0.061	0.264
2-way ANOVA													
Sex	SS	88.698	55.315	-	0.089	-	11.436	-	0.700	1.865	23.856	0.243	0.011
	df	1	1	-	1	-	1	-	1	1	1	1	1
	F	6.399	14.298	-	0.379	-	5.713	-	0.265	6.022	18.555	0.939	0.367
	P	0.015 *	4.99E-04 ***	-	0.542	-	0.022 *	-	0.610	0.018 *	1.01E-04 ***	0.338	0.548
	%	3.32	6.12		-	-	3.97		-	4.25	5.50	-	-
TW	SS	25.206	10.435	-	0.253	-	2.439	-	3.874	0.671	17.112	2.371	0.092
	df	3	3	-	3	-	3	-	3	3	3	3	3
	F	0.606	0.899	-	0.359	-	0.406	-	0.488	0.722	4.437	3.05	1.016
	P	0.615	0.450	-	0.783	-	0.749	-	0.693	0.545	0.009 **	0.039 *	0.395
	%	-	-	-	-	-	-	-	-	-	6.24	8.68	-
Sex×TW	SS	30.131	7.586	-	1.950	-	4.771	-	7.458	0.052	1.282	0.368	0.003
	df	3	3	-	3	-	3	-	3	3	3	3	3
	F	0.725	0.654	-	2.768	-	0.795	-	0.94	0.055	0.332	0.474	0.031
	P	0.543	0.585	-	0.054	-	0.504	-	0.430	0.983	0.802	0.702	0.993

DFA of tooth wear classes produced a 48.98% overall a posteriori assignment of specimens to the correct tooth wear class [tooth wear A (*n* = 4) - 100%, tooth wear B (*n* = 4) - 50%, tooth wear C (*n* = 26) - 34.62%; tooth wear D (*n* = 15) - 60%]. A plot of the first two discriminant function axes of the four-group DFA (Fig. 5.20) showed no separation between the different tooth wear classes.

5.3.1.8 *Neoromicia capensis* – Zimbabwe

5.3.1.8.1 Cranial measurements

These analyses were based on 21 specimens from four localities in Zimbabwe (Fig. 5.8), all of which occurred in the Tropical and Subtropical Grasslands, Savannas, and Shrublands biomes (Olsen *et al.* 2001). The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendix 5.6 H1 and H2. A two-way ANOVA test found one (8.3%) measurement, width of the upper fourth premolar (WUPM4) was significantly sexually dimorphic, with females being 9.58% larger than males, whereas no measurements were significantly different between the different tooth wear classes (Table 5.13), and no measurements showed a significant interaction between sex and tooth wear class. A two-way MANOVA showed no significant difference between the different sexes (Wilks = 0.150, $F_{(2,12)} = 0.942$, $P = 0.624$), different tooth wear classes (Wilks = 0.011, $F_{(6.637,36)} = 0.659$, $P = 0.805$), or significant interaction between sex and tooth wear classes (Wilks = 0.016, $F_{(6.637,36)} = 0.564$, $P = 0.874$).

There was little clustering in the five major clusters identified in the phenogram (Fig. 5.21) in relation to sex, tooth wear class and locality. Although, 40% of specimens from Sengwa (# 3) made up 80% of a cluster, while the remainder of the Sengwa specimens made up 55% of another cluster, together with specimens from three other localities. There were also two small clusters of two specimens each of the same sex, which in one cluster, were of the same tooth wear class (TW A), and in the other cluster were from the same locality (Volunteer Farms, # 4). The PCA (Fig. 5.21) which explained 28.30% and 19.82 % of the variation on the first and second principal components, identified no clear separation of the specimens in relation to sex, tooth wear class or locality. On the first principal component axis condylo-incisor length (CIL) and width of the articular surface (WAS) loaded highest, and least inter-orbital width (LIW) loaded least, while on the second principal component axis braincase breadth (BB) and width across the outer surfaces of the upper canines (WOUC) loaded highest and lowest, respectively. None of these measurements had shown significant differences between sexes or tooth wear classes in the ANOVA tests.

A two-group DFA of the sexes and a three-group DF analysis of tooth wear classes A, B and C produced a 100% *a posteriori* correct assignment of specimens to the different sexes and tooth wear classes. A plot of the first two discriminant function axes of the three-group DFA (Fig. 5.22) shows tooth wear classes A and B separated from tooth wear class C on the first discriminant function axis. Least inter-orbital width (LIW) loaded highest and braincase breadth (BB) loaded least on the first discriminant function axis, which explained 87.2% of the variation. Both of these measurements were also important in the separation on first and second principal component axes respectively. Tooth wear classes A and B were almost separated on the second discriminant function axis which explained 12.8% of the variation, apart from the overlap of a female of tooth wear class A (NMBZ31973) and a female of tooth wear class B (NMBZ31989). Width across the outer surfaces of the upper canine teeth (WOUC) loaded highest and width between the inner surfaces of the upper first molar teeth (WIUM1) loaded least on the second discriminant function axis. Width across the outer surfaces of the upper canine teeth (WOUC) was also important in the second principal component axis. Neither of these measurements had shown a significant difference between the tooth wear classes in the two-way ANOVA tests. There were too few specimens with external measurements to run any analyses of external measurements.

5.3.1.9 *Neoromicia capensis* – South Africa, Eastern Cape Province

5.3.1.9.1 External measurements

The univariate analyses were based on 21 specimens from two localities in the Eastern Cape Province of South Africa (Fig. 5.15) occurring in the Savanna and Grassland biomes. Accounting for missing data, multivariate analyses were based on seven measurements from 15 specimens. The multivariate analyses were also based on specimens from a single locality (King Williamstown) occurring in the Savanna biome. The summary statistics and results of the normality tests for sexes are given in Appendix 5.7 E. Four (33.3%) measurements, head and body (HB), tail (T), forearm (FA), and third metacarpal (TMETA) lengths, were significantly

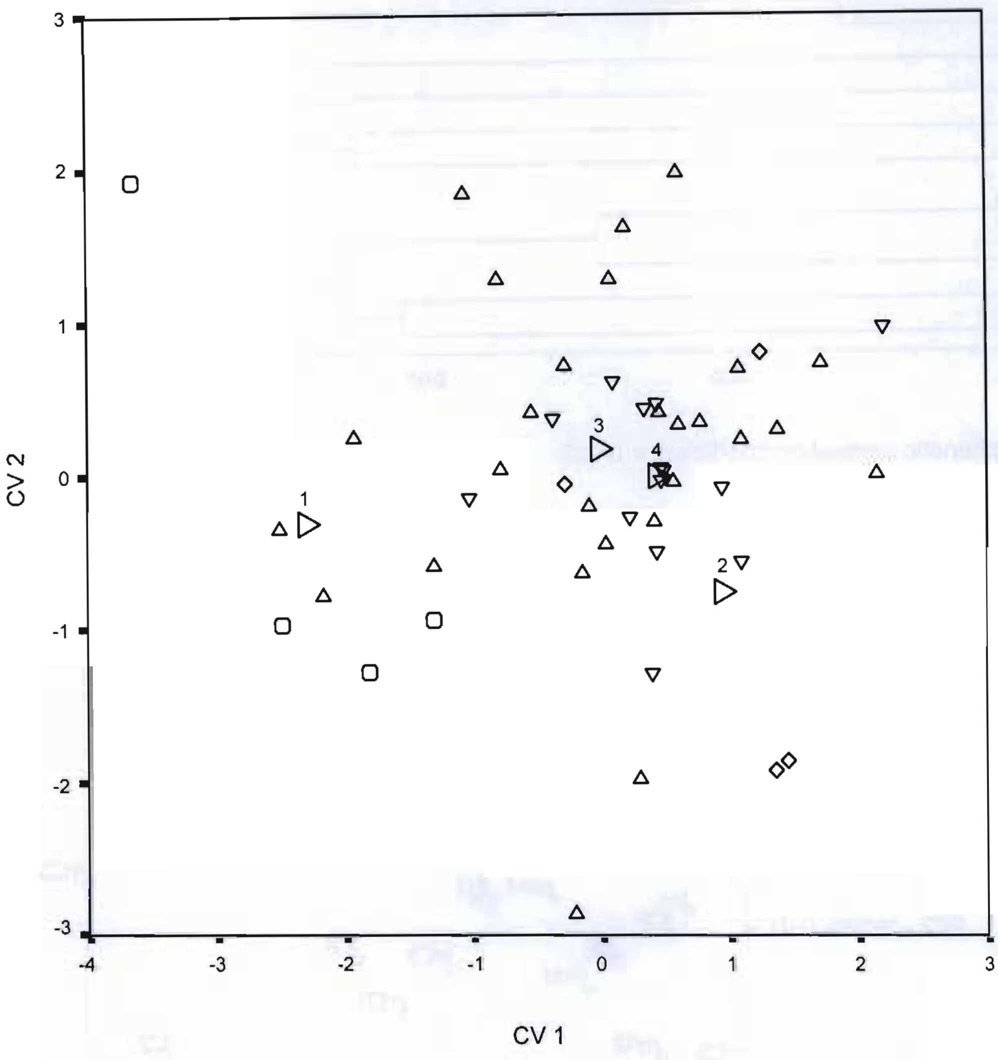


Figure 5.20 Plot of the first two discriminant functions of external measurements of four different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C; 4 and ▽ = tooth wear class D) of *Neoromicia capensis* from the Nama-Karoo biome in the Free State Province of South Africa.

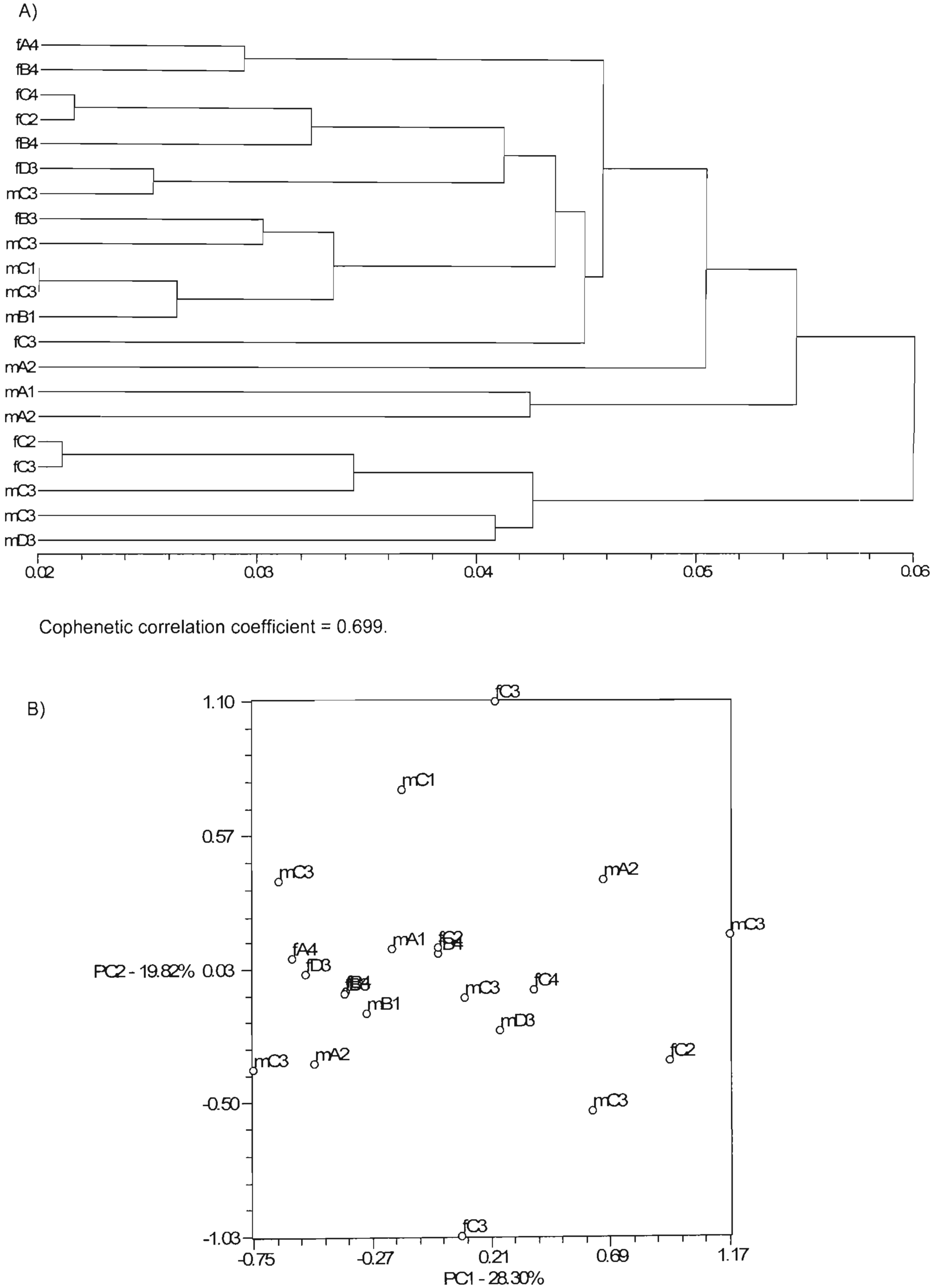


Figure 5.21 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of first two principal components of 12 cranial measurements of *Neoromicia capensis* from four localities in Zimbabwe. The sex (male = m, female = f), tooth wear class (A, B, C, or D) and locality code (1-4, see Appendix 5.1 for locality data) of individuals are indicated.

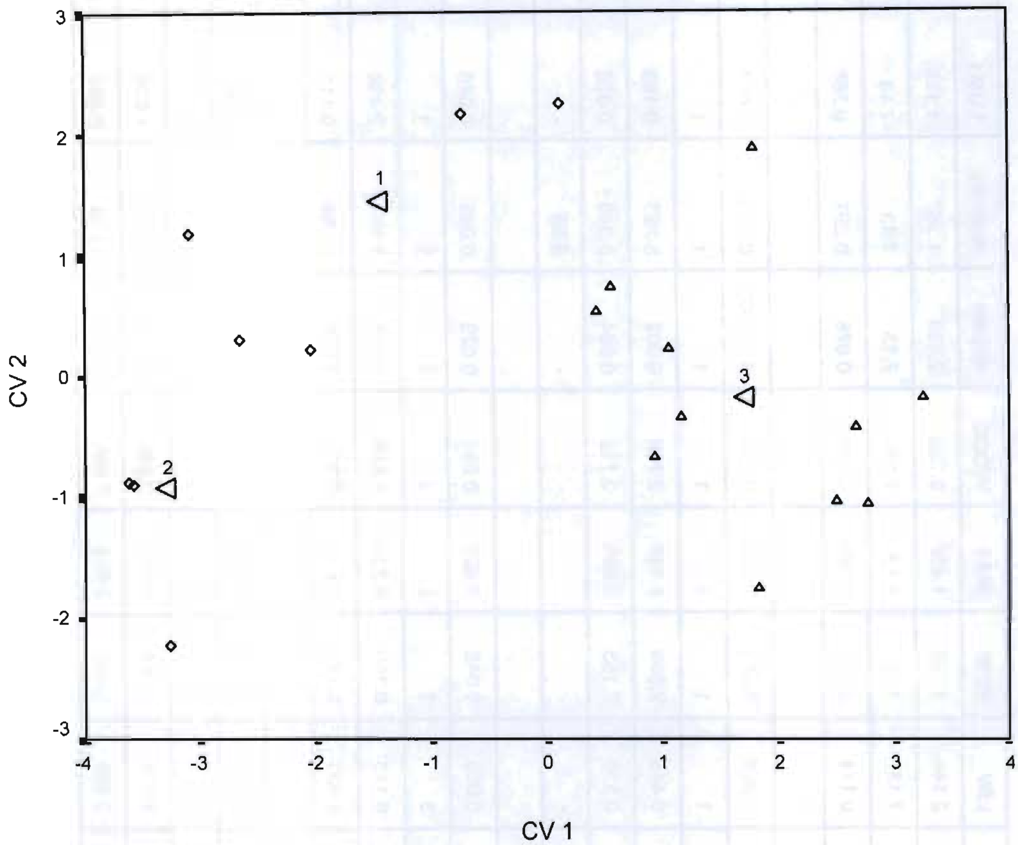


Figure 5.22 Plot of the first two discriminant functions of cranial measurements of four different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C) of *Neoromicia capensis* from the Zimbabwe.

Table 5.13 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in cranial measurements of *Neoromicia capensis* from four localities in Zimbabwe, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, P = significance of F values. * and ** denote significance at $P < 0.05$ and $P < 0.01$, respectively. SS = sum of squares.

Levene's		**CIL**	**BH**	**ZB**	**BB**	**LIW**	**WFM**	**WAS**	**WOUC**	**WIUM1**	**WUPM4**	**LUM1**	**MAOT**
2-way	*F*	1.564	1.536	2.004	0.791	2.144	2.148	1.455	2.795	2.439	1.367	1.158	1.236
	df	7,13	7,13	7,13	7,13	7,13	7,13	7,13	7,13	7,13	7,13	7,13	7,13
	P	0.231	0.239	0.132	0.608	0.111	0.111	0.265	0.052	0.078	0.297	0.388	0.352
2-way ANOVA													
Sex	SS	0.009	0.020	0.032	0.008	0.008	0.084	0.002	0.062	3.00E-05	0.043	0.001	0.009
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	0.117	0.970	0.969	0.296	0.445	2.309	0.195	2.778	0.002	5.223	0.183	0.377
	P	0.738	0.343	0.343	0.595	0.516	0.153	0.666	0.119	0.964	0.040 *	0.676	0.550
	%	-	-	-	-	-	-	-	-	-	9.58	-	-
TW	SS	0.346	0.079	0.079	0.028	0.006	0.040	0.007	0.084	0.029	0.045	0.045	0.041
	df	3	3	3	3	3	3	3	3	3	3	3	3
	F	1.422	1.251	0.805	0.339	0.113	0.366	0.230	1.248	0.697	1.847	2.434	0.601
	P	0.281	0.331	0.513	0.798	0.951	0.779	0.874	0.333	0.570	0.188	0.111	0.625
Sex ×TW	SS	0.212	0.008	0.036	0.070	0.065	0.114	0.020	0.036	0.026	0.004	0.020	0.023
	df	3	3	3	3	3	3	3	3	3	3	3	3
	F	0.872	0.119	0.365	0.848	1.170	1.044	0.630	0.536	0.630	0.177	1.088	0.338
	P	0.480	0.947	0.780	0.492	0.359	0.406	0.608	0.666	0.608	0.910	0.389	0.798

sexually dimorphic in the one-way ANOVAs, with females being 7.82 to 11.58% larger than males (Table 5.14). No measurements showed a significant difference between tooth wear classes in one-way ANOVAs of males and females together and females only. However, in an analysis of males only, one (8.3%) measurement, third metacarpal length (TMETA), was significantly different between the tooth wear classes. A post-hoc Tukey test identified overlapping subsets of tooth wear classes D and B and tooth wear classes B and C that separated tooth wear classes D and C, with third metacarpal length being shortest in tooth wear class D, and longest in tooth wear class C, which is contrary to the assumption that measurements would increase in size with increasing tooth wear as a measure of increasing age. One-way MANOVA tests between sexes and tooth wear classes of 15 specimens of seven measurements (T, HFL, E, FA, TMETA, TRL, TRB) showed significant sexual dimorphism (Wilks = 0.151, $F_{(7,7)}$ = 5.607, P = 0.018) but no significant difference between the tooth wear classes (Wilks = 0.253, $F_{(14.907,21)}$ = 0.435, P = 0.960).

Of the five major clusters in the phenogram (Fig. 5.23), two consisted of specimens of one sex only, whereas the other three were of mixed sex. There was also little indication of clustering in relation to tooth wear class in the phenogram. The PCA (Fig. 5.23) identified that, although males and females largely overlapped on the first principal component axis, which explained 46.15% of the variation, males were smaller and females were larger, and there was no obvious separation between the tooth wear classes. On the first principal component axis, third metacarpal (TMETA) and forearm (FA) lengths loaded highest, and hind foot length (HFL) loaded least. The second principal component axis explained 22.31% of the variation, and tail (T) and tragus (TRL) lengths loaded highest and lowest, respectively. Forearm (FA), third metacarpal (TMETA), and tail (T) lengths were also significantly different between the sexes in the one-way ANOVA tests. Tail (T), forearm (FA), and third metacarpal (TMETA) lengths were also significantly sexually dimorphic in the one-way ANOVA tests.

A two-group DFA of the sexes produced a 100% *a posteriori* correct assignment of specimens to the different sexes, and a two-group DF analysis of tooth wear classes B and D produced a 90.91% *a posteriori* correct assignment of specimens to the different tooth wear classes [tooth wear B (n = 7) - 85.71%; tooth wear D (n = 4) - 100%].

5.3.1.10 *Neoromicia* cf. *melckorum*

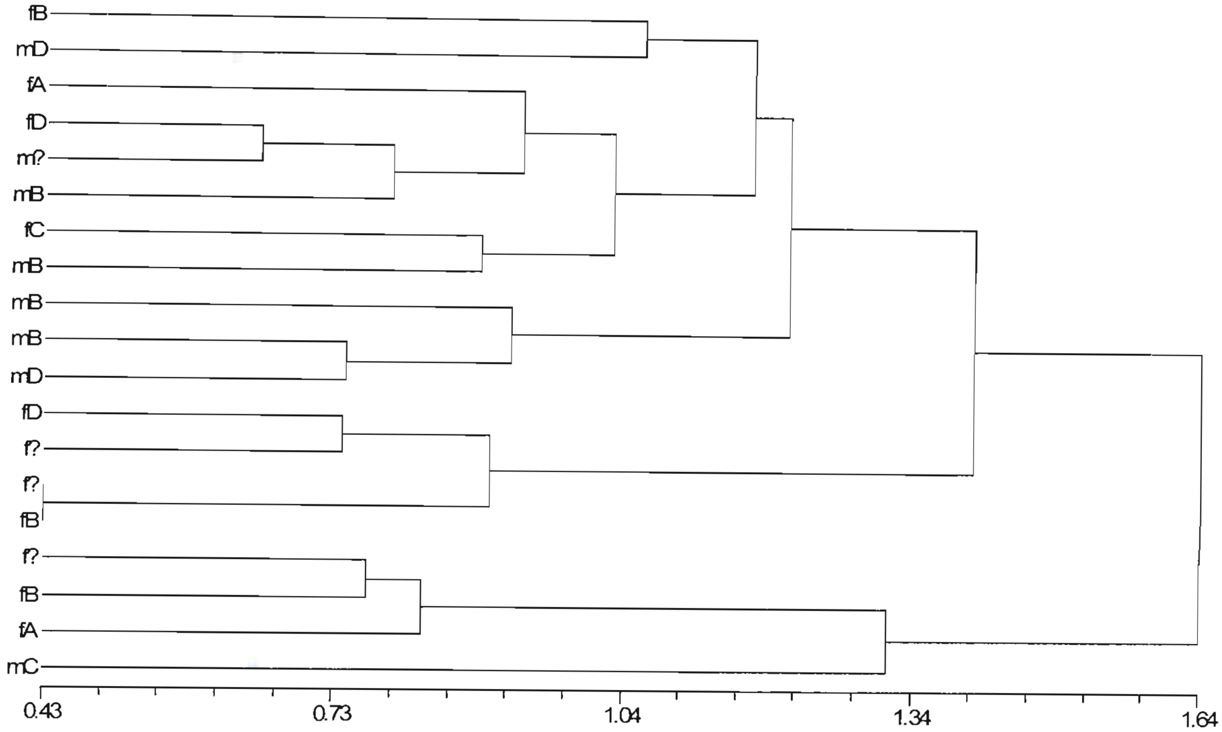
5.3.1.10.1 Cranial measurements

These analyses were based on 17 specimens from nine different localities, eight in South Africa and one in Zimbabwe (Fig. 5.6), all occurring in the Savanna biome. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendix 5.6 I1 and I2. Two-way ANOVA tests found no measurements were significantly sexually dimorphic, significantly different between the tooth wear classes, or significant in the interaction between sex and tooth wear class (Table 5.15). A two-way MANOVA test showed no significant differences between sexes (Wilks = 0.132, $F_{(1,10)}$ = 0.659, P = 0.754) and tooth wear classes (Wilks = 0.027, $F_{(3.611,30)}$ = 0.289, P = 0.977), or in the interaction between the sexes and tooth wear classes (Wilks = 0.049, $F_{(2,20)}$ = 0.354, P = 0.917).

The smallest of the three major clusters in the phenogram (Fig. 5.24) contained 67% (two of the three) of the specimens from Mana Pools (# 9) in Zimbabwe. Both of these specimens were females of tooth wear class D. Mana Pools National Park is the most northerly occurring locality of the localities pooled for this analysis, and is separated by some 765 km from the other localities in the Pafuri region of the Limpopo Province of South Africa. The other specimen from Mana Pools (also a female but of tooth wear class C) clustered with specimens from Pafuri in the Kruger National Park in the Limpopo Province of South Africa. Besides this clustering in relation to sex, tooth wear class and locality there was little indication of such clustering among the other specimens which formed fairly mixed clusters in relation to sex, tooth wear class and locality. The PCA (Fig. 5.24) which explained 32.31% and 22.36% on the first and second principal component axes, respectively, showed no separation between the specimens in relation to sex, tooth wear class or locality. On the first principal component axis, zygomatic breadth (ZB) and length of the first upper molar (LUM1) loaded highest and lowest, respectively. On the second principal component axis, length of the first upper molar (LUM1) and width between the inner surfaces of the upper first molar teeth (WIUM1) loaded highest, and braincase breadth (BB), least inter-orbital width (LIW) and brain case height (BH) loaded least. None of these measurements showed significant differences between sexes or tooth wear classes in the two-way ANOVA tests.

A two-group DFA of the sexes produced a 94.12% *a posteriori* correct assignment of

A)



Cophenetic correlation coefficient = 0.684.

B)

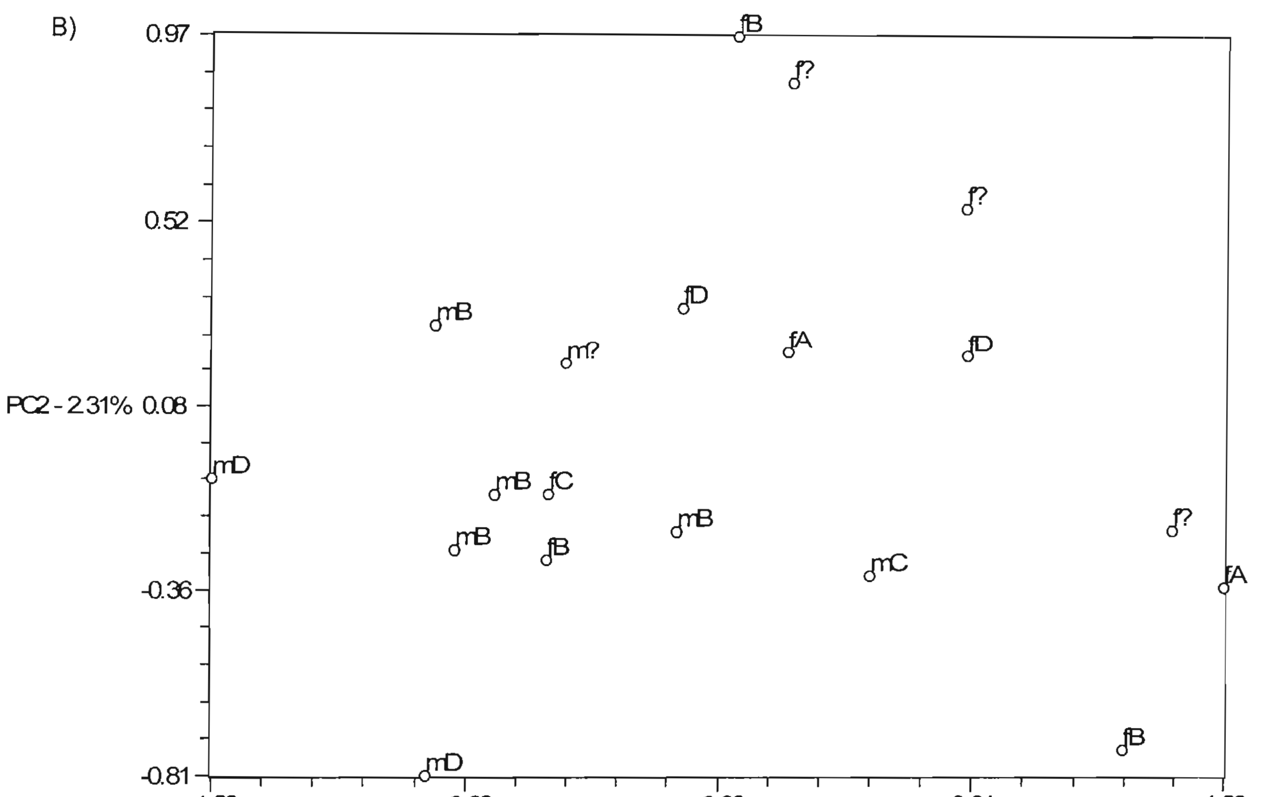


Figure 5.23 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of the first two principal components of seven external measurements of *Neoromicia capensis* from King William's Town in the Eastern Cape Province in South Africa. The sex (male = m, female = f) and tooth wear class (A, B, C, D, or unknown = ?) of individuals are indicated.

A)

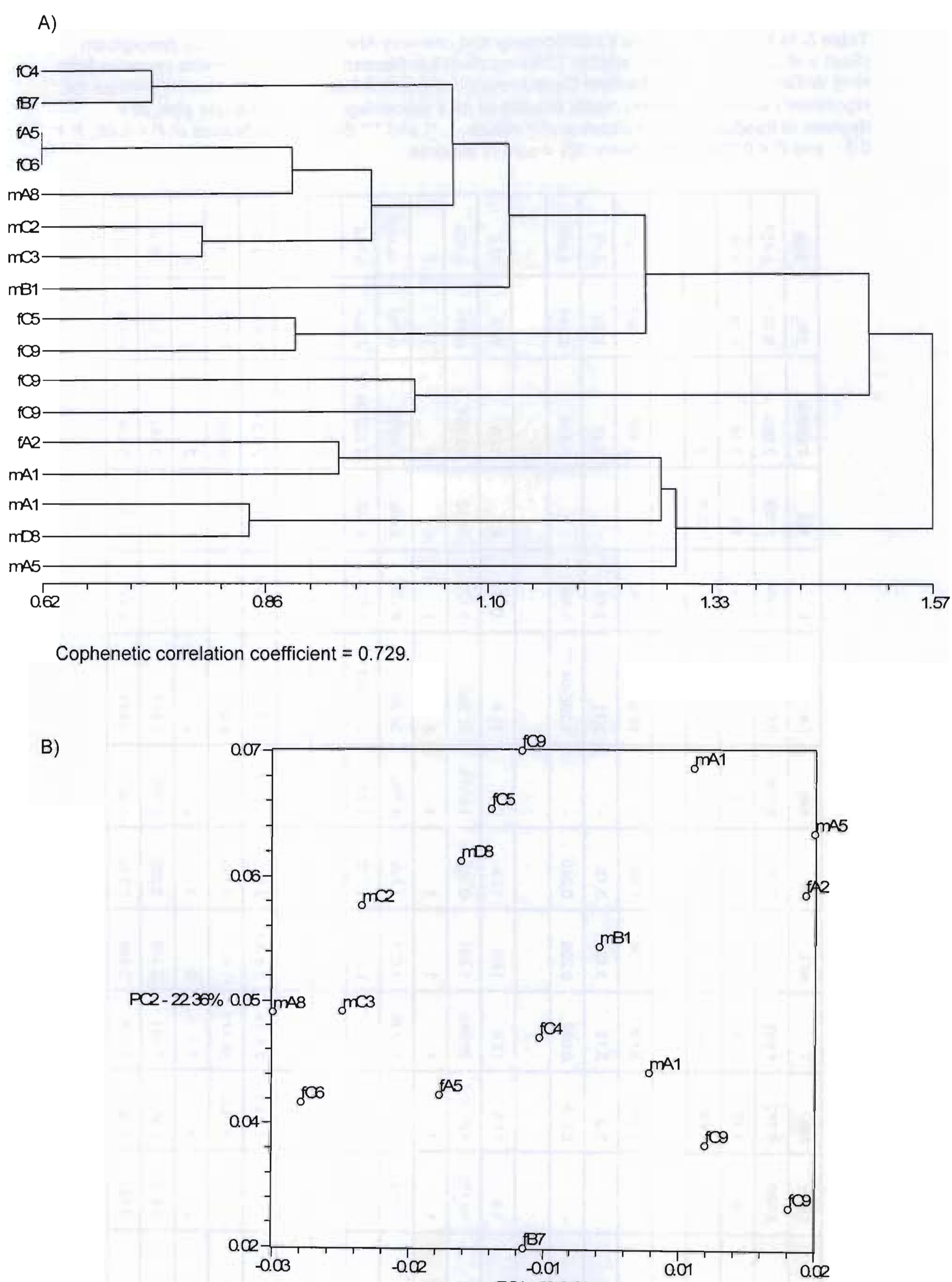


Figure 5.24 A) Cluster analysis of average taxonomic distances using UPGMA, B) plot of the first two principal components of 12 cranial measurements of *Neoromicia* cf. *melckorum* from nine localities in South Africa and Zimbabwe. The sex (male = m, female = f), tooth wear class (A, B, C, or D), and locality code (1-9, see Appendix 5.1 for locality data) of individuals are indicated.

Table 5.14 Results of Levene's homogeneity and one-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in external measurements of *Neoromicia capensis* from King Williams Town in the Eastern Cape Province of South Africa, with mean size differences for significantly different measurements expressed as a percentage (%). *n* = sample size, df = degrees of freedom, *P* = significance of *F* values. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. SS = sum of squares.

Levene's		TOT	HB	T	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Sex	*F*	3.000	0.172	4.865	0.001	0.563	6.338	0.004	1.084	1.359	2.069	5.207	0.658
	df	1,2	1,15	1,19	1,19	1,19	1,3	1,17	1,19	1,3	1,19	1,19	1,19
	P	0.225	0.685	0.040 *	0.977	0.462	0.086	0.952	0.311	0.328	0.167	0.034	0.427
TW	*F*	-	3.588	0.590	1.738	1.586	-	18.622	0.142	-	1.447	1.563	1.510
	df	-	3,9	3,13	3,13	3,13	-	3,11	3,13	-	3,13	3,13	3,13
	P	-	0.059	0.632	0.209	0.240	-	1.28E-04 ***	0.933	-	0.274	0.246	0.259
ANOVA													
Sex	*n*	1:3	11:6	12:9	12:9	12:9	2:3	11:8	12:9	4:1	12:9	12:9	12:9
	SS	18.750	125.000	90.840	1.433	0.302	12.675	32.990	0.173	0.612	35.964	0.479	0.123
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	2.679	10.020	15.438	1.071	1.226	4.680	20.267	0.135	0.460	20.507	0.760	12.095
	P	0.243	0.006 **	0.001 **	0.314	0.282	0.119	3.14E-04 ***	0.718	0.546	2.30E-04 ***	0.394	0.164
	%	-	10.89	11.58	-	-	-	7.82	-	-	8.38	-	-
TW	*n*	-:1:2:1	2:7:1:3	2:8:3:4	2:8:3:4	2:8:3:4	-:1:2:1	2:7:2:4	2:8:3:4	-:2:1:2	2:8:3:4	2:8:3:4	2:8:3:4
	SS	14.750	37.427	39.473	1.615	0.193	0.563	8.417	0.727	1.277	8.432	0.722	0.157
	df	2	3	3	3	3	2	3	3	2	3	3	3
	F	0.410	0.551	1.181	0.355	0.235	0.090	0.971	0.146	0.383	0.887	0.370	0.676
	P	0.741	0.660	0.355	0.786	0.870	0.921	0.441	0.931	0.723	0.474	0.776	0.582

Table 5.15 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism and tooth wear class variation in cranial measurements *Neoromicia* cf. *melckorum* from two localities in Zimbabwe and South Africa, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, P = significance of F values. * and ** denote significance at $P < 0.05$ and $P < 0.01$, respectively. SS = sum of squares.

Levene's		**CIL**	**BH**	**ZB**	**BB**	**LIW**	**WFM**	**WAS**	**WOUC**	**WIUM1**	**WUPM4**	**LUM1**	**MAOT**
2-way	*F*	4.639	1.496	2.384	0.817	5.915	2.629	1.012	1.805	1.257	1.945	3.813	2.334
	df	6,10	6,10	6,10	6,10	6,10	6,10	6,10	6,10	6,10	6,10	6,10	6,10
	P	0.017 *	0.273	0.108	0.581	0.007 **	0.085	0.469	0.195	0.357	0.168	0.031 *	0.113
2-way ANOVA													
Sex	SS	0.035	1.36E-06	0.032	0.052	0.009	0.056	1.78E-04	0.039	0.037	0.002	0.008	0.001
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	0.718	0	0.458	1.504	0.461	2.446	0.036	1.875	2.935	0.412	2.011	0.054
	P	0.417	0.994	0.514	0.248	0.512	0.149	0.853	0.201	0.117	0.535	0.187	0.821
TW	SS	0.458	0.089	0.406	0.294	0.127	0.037	0.053	0.071	0.039	0.011	0.009	0.044
	df	3	3	3	3	3	3	3	3	3	3	3	3
	F	3.157	1.209	1.963	2.848	2.204	0.533	3.594	1.135	1.041	0.933	0.725	0.744
	P	0.073	0.356	0.184	0.091	0.151	0.670	0.054	0.381	0.416	0.460	0.560	0.550
Sex×TW	SS	0.002	0.006	0.059	0.016	0.028	0.042	0.040	0.008	0.026	0.008	0.006	0.004
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	0.023	0.132	0.424	0.238	0.731	0.909	4.032	0.204	1.039	0.995	0.774	0.091
	P	0.977	0.878	0.665	0.793	0.505	0.434	0.052	0.819	0.389	0.404	0.487	0.914

specimens to the different sexes [females (n = 9) - 88.89%, males (n = 8) - 100%]. The three-group DFA of tooth wear classes A, B and C produced a 100% *a posteriori* correct assignment of specimens to the different tooth wear classes. A plot of the first two discriminant function axes of the three-group DFA (Fig. 5.25) shows the separation between the three tooth wear classes on the first discriminant function axis, with tooth wear classes A and B on either end of the first discriminant function axis with tooth wear class C between them. On the first discriminant function axis which explained 85.7% of the variation, length of the first upper molar (LUM1) loaded highest and width across the outer surfaces of the upper canines (WOUC) loaded least. Width across the outer surfaces of the upper canine teeth (WOUC) was also significantly sexually dimorphic in the two-way ANOVA tests, and yet the measurement that showed significant variation between the tooth wear classes in the two-way ANOVA tests, condylo-incisor length (CIL), is not one of the important measurements separating the tooth wear classes. The second discriminant function axis which explained 14.3% of the variation, separated tooth wear classes C and D, and almost separated tooth wear classes A and C, but for the overlap of a male of tooth wear class A (TM37924) with specimens of tooth wear class C. On the second discriminant function axis, least inter-orbital width (LIW) loaded highest and width between the inner surfaces of the upper first molar teeth (WIUM1) and zygomatic breadth (ZB) loaded least.

5.3.1.10.2 External measurements

The univariate analyses were based on 15 specimens from eight localities, seven from South Africa and one in Zimbabwe (Fig. 5.7), all occurring in the Savanna biome. To account for missing data, the multivariate analyses were run on 12 specimens from the seven localities in South Africa and seven measurements. The summary statistics and results of the normality tests for sexes are given in Appendix 5.7 F. Two (28.6%) measurements, forearm (FA) and third metacarpal (TMETA) lengths, were significantly sexually dimorphic in the one-way ANOVAs, with females being 5.61 and 2.46% respectively larger than males, but no measurements were significantly different between different tooth wear classes (Table 5.16). One-way MANOVAs of a reduced set of 12 specimens and seven measurements (HF, TIB, FA, TMETA, TRL, TRB, TL) showed no significant differences between the different sexes (Wilks = 0.186, $F_{(3,8)}$ = 1.639, P = 0.373) and tooth wear classes (Wilks = 0.042, $F_{(6.293,21)}$ = 0.601, P = 0.823).

The phenogram (Fig. 5.26) identified three major clusters of which one is a female of tooth wear class B from the Mockford's Garden at Pafuri in the Kruger National Park (TM37852). The second cluster consisted of three male specimens (42.86%) of different tooth wear classes and from different localities, while the largest cluster was a mixture of sexes, tooth wear classes and localities. The PCA (Fig. 5.26) separated the same of specimens as in the phenogram. The cluster of males separates from the other specimens on the first principal component axis which explains 32.80% of the variation. On the first principal component axis forearm (FA) and third metacarpal (TMETA) lengths loaded highest, while tragus length (TRL) loaded least. Both forearm (FA) and third metacarpal (TMETA) lengths were also significantly sexually dimorphic in the one-way ANOVA tests. The outlier female of tooth wear class B (TM37852) separated on the second principal component axis, which explains 25.65% of the variation. On the second principal component axis tragus (TRL) and tibia (TIB) lengths loaded highest and lowest, respectively.

Two-group DFAs produced 100% *a posteriori* correct assignments of specimens to the different sexes, and to tooth wear classes A and C.

5.3.1.11 *Neoromicia africanus* – South Africa, Limpopo Province, Pafuri area

5.3.1.11.1 Cranial measurements

These analyses were based on 29 specimens from eight different localities in the Pafuri region of the Kruger National Park (Fig. 5.27), all occurring in the Savanna biome. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendices 6 J1 and J2. In two-way ANOVA tests, two (16.7%) measurements showed sexual dimorphism, length of the upper first molar (LUM1) and moment arm of the temporal (MAOT) with females being 6.17 and 3.05% larger than males, while no measurements showed a significant difference between the tooth wear classes, and no measurements showed a significant interaction between sex and tooth wear class (Table 5.17). In a two-way MANOVA test, there was no significant difference between either sex (Wilks = 0.321, $F_{(12,21)}$ = 2.117, P = 0.104) or tooth wear classes (Wilks = 0.462, $F_{(24,24)}$ = 2.117, P = 0.104), nor in the interaction between sex or tooth wear class (Wilks = 0.396, $F_{(24,24)}$ = 0.589, P = 0.899).

The phenogram (Fig. 5.28) and PCA (Fig. 5.28) showed no distinct clustering in relation to

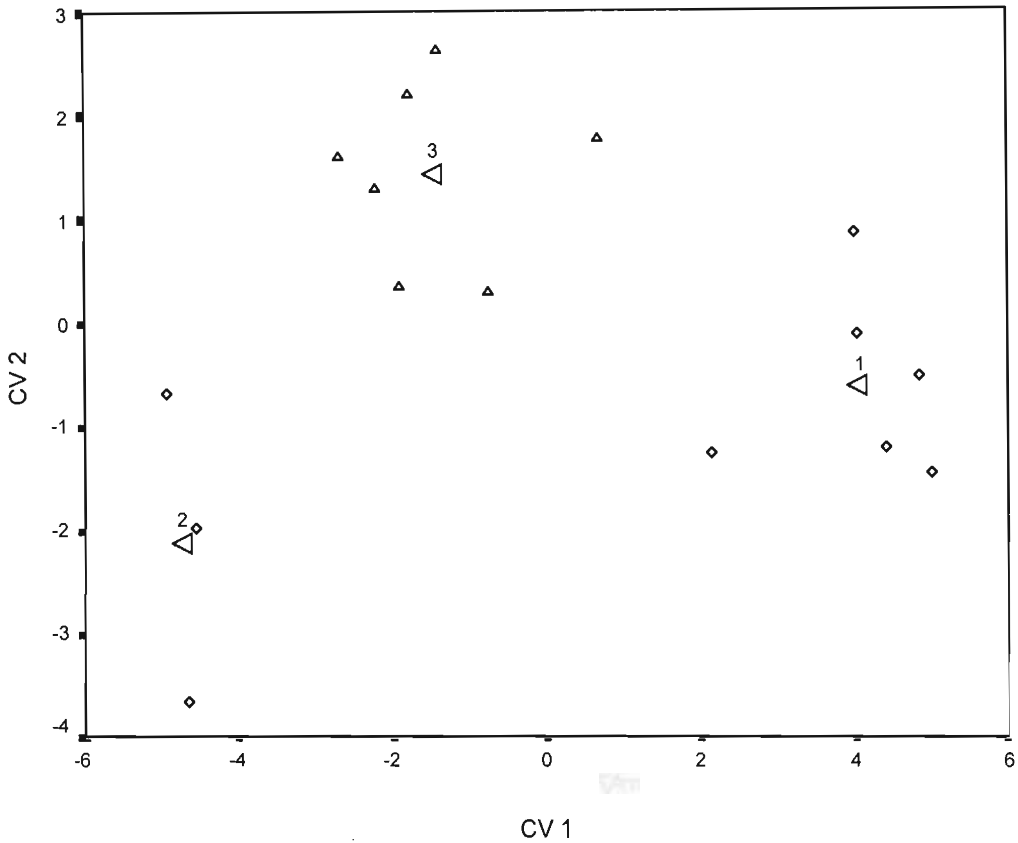
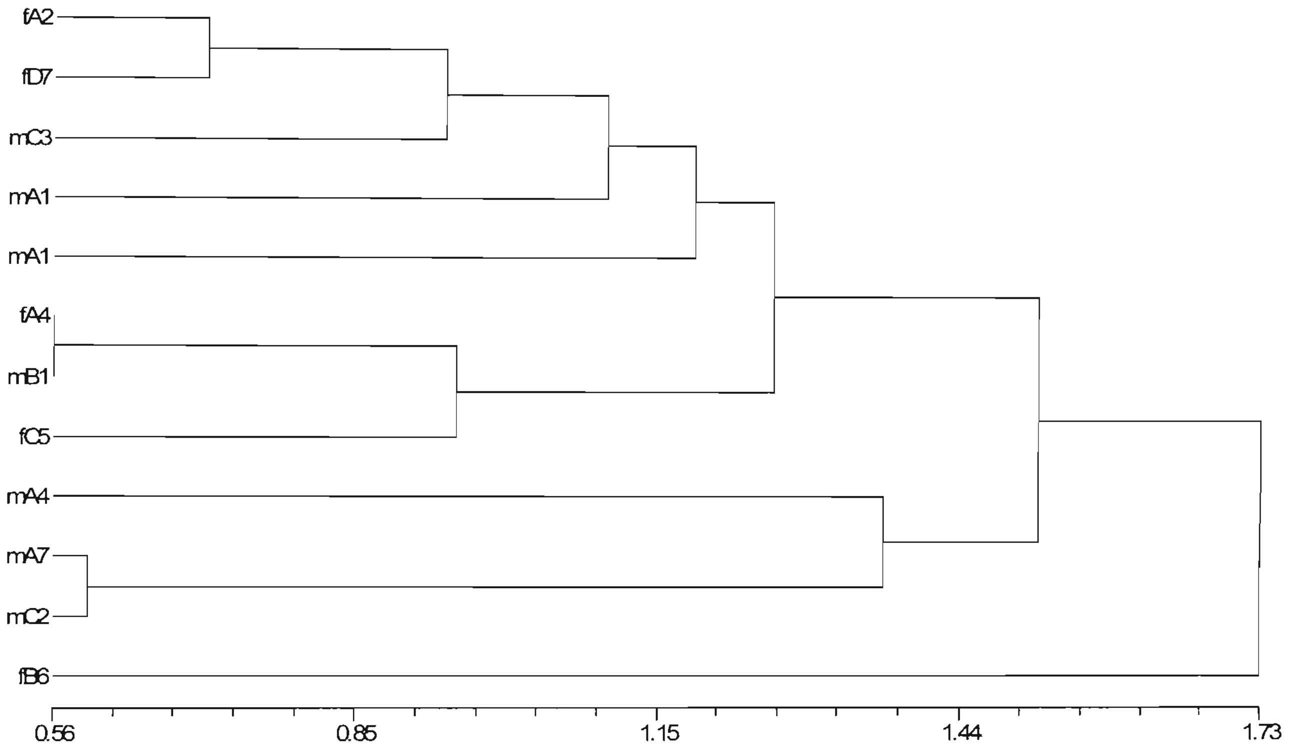


Figure 5.25 Plot of the first two discriminant functions of cranial measurements of three different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C) of *Neoromicia* cf. *melckorum* from South Africa and Zimbabwe.

A)



Cophenetic correlation coefficient = 0.792.

B)

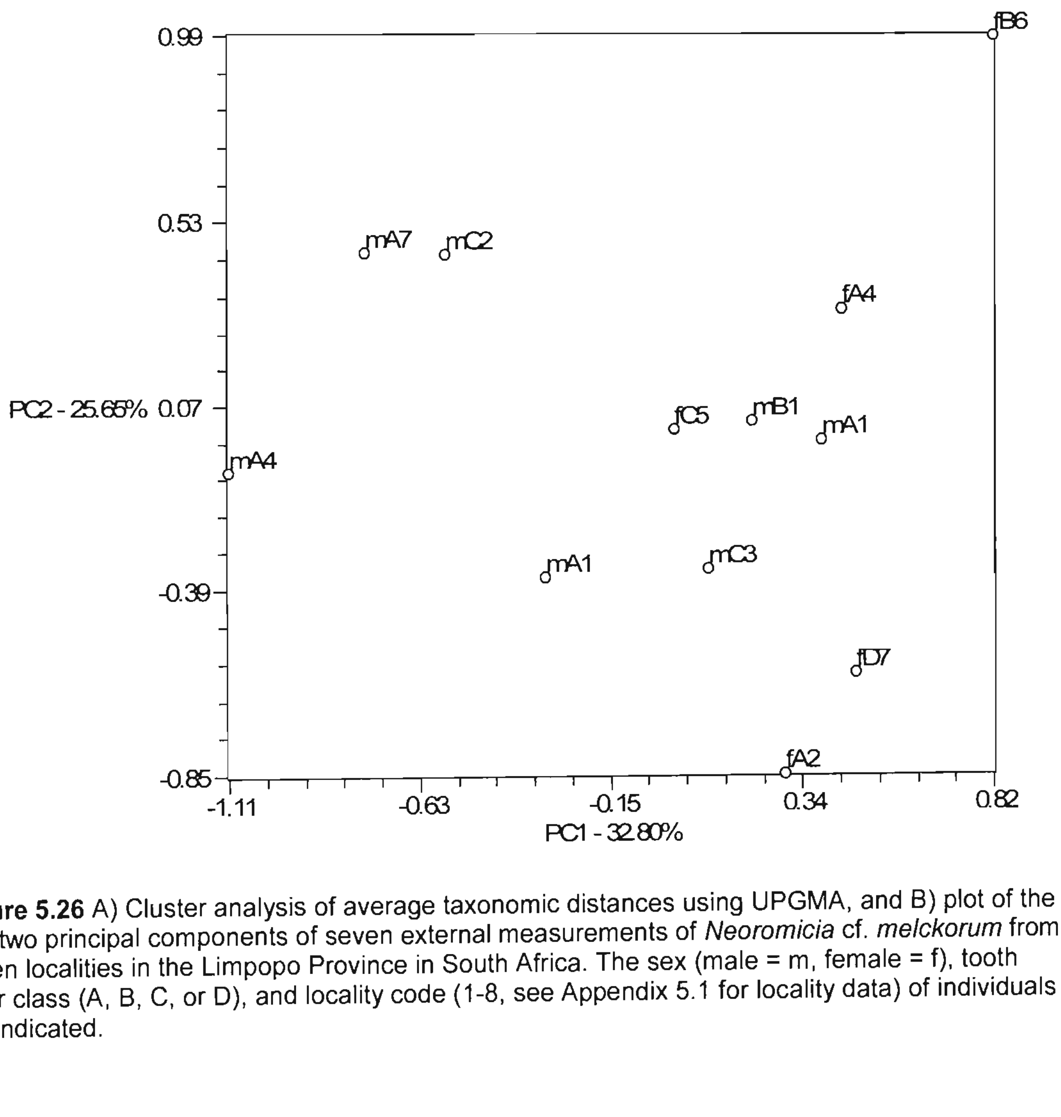


Figure 5.26 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of the first two principal components of seven external measurements of *Neoromicia* cf. *melckorum* from seven localities in the Limpopo Province in South Africa. The sex (male = m, female = f), tooth wear class (A, B, C, or D), and locality code (1-8, see Appendix 5.1 for locality data) of individuals are indicated.

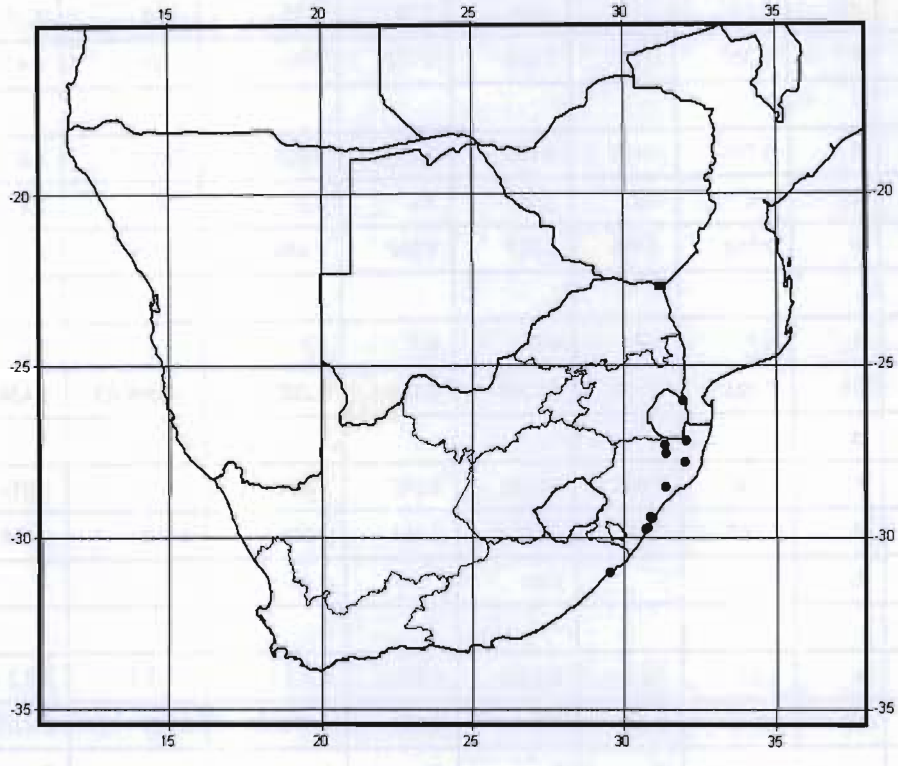


Figure 5.27 Map showing the distribution of specimens of *Neoromicia africanus* from Pafuri area in the Limpopo Province of South Africa, and South Africa and Swaziland used in the statistical analyses of cranial measurements. [*N. africanus* from South Africa and Swaziland = filled circle; Pafuri area in the Limpopo Province of South Africa = filled square.]

Table 5.16 Results of Levene's homogeneity and one-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in external measurements *Neoromicia* cf. *melckorum* from two localities in Zimbabwe and South Africa, with mean size differences for significantly different measurements expressed as a percentage (%). *n* = sample size, df = degrees of freedom, *P* = significance of *F* values. * and ** denote significance at $P < 0.05$ and $P < 0.01$, respectively. SS = sum of squares.

Levene's		**TL**	**HF**	**FA**	**TIB**	**TMETA**	**TRL**	**TRB**
Sex	*F*	0/843	0.355	0.386	0.124	0.663	7.445	0.772
	df	1,10	1,10	1,13	1,10	1,10	1,10	1,10
	P	0.380	0.565	0.545	0.732	0.434	0.021 *	0.400
TW	*F*	3.785	1.150	0.560	1.258	0.955	1.627	2.667
	df	3,8	3,8	3,11	3,8	3,8	3,8	3,8
	P	0.059	0.386	0.652	0.352	0.459	0.259	0.119
ANOVA								
Sex	*n*	5:7	5:7	8:7	5:7	5:7	5:7	5:7
	SS	0.223	0.123	16.291	0.157	2.200	1.269E-03	3.438E-04
	df	1	1	1	1	1	1	1
	F	0.030	0.854	20.362	0.946	6.154	0.016	0.019
	P	0.867	0.377	0.001 **	0.354	0.033 *	0.903	0.893
	%	-	-	5.61	-	2.46	-	-
TW	*n*	6:2:3:1	6:2:3:1	6:3:5:1	6:2:3:1	6:2:3:1	6:2:3:1	6:2:3:1
	SS	17.404	0.134	7.874	0.308	1.473	0.338	2.497E-02
	df	3	3	3	3	3	3	3
	F	0.801	0.250	1.534	0.547	0.913	1.876	0.423
	P	0.527	0.859	0.261	0.664	0.477	0.212	0.742

Table 5.17 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in cranial measurements of *Neoromicia africanus* from the Pafuri area in the Limpopo Province of South Africa, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, P = significance of F values. * and ** denote significance at $P < 0.05$ and $P < 0.01$, respectively. SS = sum of squares.

Levene's		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
2-way	*F*	0.877	1.175	2.112	0.468	2.457	1.256	1.147	0.671	2.781	1.189	0.647	0.845
	df	5,23	5,23	5,23	5,23	5,23	5,23	5,23	5,23	5,23	5,23	5,23	5,23
	P	0.512	0.352	0.100	0.796	0.064	0.316	0.364	0.650	0.042 *	0.345	0.666	0.532
2-way ANOVA													
Sex	SS	0.222	0.012	3.40E-04	0.014	0.008	0.007	0.003	0.012	0.004	0.005	0.024	0.041
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	3.484	0.423	0.006	0.504	0.482	0.361	0.283	0.466	0.530	0.554	10.086	5.001
	P	0.075	0.522	0.939	0.485	0.495	0.554	0.600	0.502	0.474	0.464	0.004 **	0.035 *
	%	-	-	-	-	-	-	-	-	-	-	6.17	3.05
TW	SS	0.091	0.031	0.040	0.014	0.004	0.061	0.014	2.95E-04	0.005	0.004	0.003	0.014
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	0.711	0.535	0.355	0.248	0.128	1.477	0.591	0.006	0.383	0.236	0.551	0.840
	P	0.501	0.593	0.705	0.782	0.880	0.249	0.562	0.994	0.686	0.791	0.584	0.444
Sex×TW	SS	0.176	0.054	0.067	4.41E-05	0.002	0.012	0.009	0.072	0.021	0.036	2.55E-04	0.011
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	1.379	0.934	0.595	0.001	0.058	0.291	0.392	1.397	1.575	2.144	0.055	0.644
	P	0.272	0.407	0.560	0.999	0.944	0.750	0.680	0.268	0.228	0.140	0.947	0.535

similar sexes, tooth wear class or locality. However, the PCA (Fig. 5.28) identified a single male of tooth wear class B from the Mockford's Garden in Pafuri (TM39467) as separate from the other specimens on the first principal component axis. On the first principal component axis which explained 31.03% of the variation braincase breadth (BB) and condylo-incisor length (CIL) loaded highest, and width of the upper fourth premolar (WUPM4) loaded least. Condylo-incisor skull length (CIL) also showed significant sexual dimorphism in the two-way ANOVA tests. On the second principal component axis which explained 13.62% of the variation, width of the articular surface (WAS) and least inter-orbital width (LIW) loaded highest and lowest respectively.

A two-group DFA of the sexes produced an 89.66% *a posteriori* correct assignment of specimens to the different sexes [females (n = 21) - 85.71%, males (n = 8) - 100%]. A three-group DFA of the tooth wear classes produced a 75.86% *a posteriori* correct assignment of specimens to the different tooth wear classes [tooth wear A (n = 12) - 66.67%, tooth wear B (n = 8) - 75%, tooth wear C (n = 9) - 88.89%]. A plot of the first two discriminant function axes of the three-group DFA (Fig. 5.29) showed the tooth wear classes do not separate. There were too few specimens with external measurements to run any analyses of external measurements.

5.3.1.12 *Neoromicia africanus* – South Africa and Swaziland

5.3.1.12.1 Cranial measurements

These analyses were based on 35 specimens from 12 different localities in the Eastern Cape and KwaZulu-Natal Provinces of South Africa and Swaziland (Fig. 5.27). With the exception of one locality (Ngome Forest) which occurs in the grassland biome, the rest of the localities occur in the Savanna biome. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendices 5.6 K1 – K3. In two-way ANOVA tests, two measurements (16.7%) showed sexual dimorphism, length of the first upper molar (LUM1), and condylo-incisor skull length (CIL), with females 2.61 and 1.03%, respectively, larger than males (Table 5.18). A single (8.3%) measurement, least inter-orbital width (LIW), was significant between the tooth wear classes, and no measurements were significant in the interaction between sex and tooth wear. A post-hoc Tukey test identified two overlapping subsets between the significantly different tooth wear classes, of tooth wear classes B, C and D, and tooth wear classes D, C and A, which separated tooth wear classes B and A. The relative difference between tooth wear classes A and B was 3.82% (Table 5.18). The mean of least inter-orbital width (LIW) in each tooth wear class indicates a progression in size from tooth wear class B, through tooth wear classes C and D, to tooth wear class A, which does not conform to the assumed growth pattern with increasing age. A male of tooth wear class A from Ngome Forest (TM39818) had a large least inter-orbital width (LIW) which caused tooth wear class A to be larger than the other tooth wear classes. A two-way MANOVA test showed no significant sexual dimorphism (Wilks = 0.500, $F_{(12,16)}$ = 1.335, P = 0.290), significant variation between the tooth wear classes (Wilks = 0.254, $F_{(36,48.001)}$ = 0.786, P = 0.773), or significant interaction between sex and tooth wear class (Wilks = 0.230, $F_{(36,48.001)}$ = 0.860, P = 0.679).

Of the first five clusters in the phenogram (Fig. 5.30), one identified a male (DM5870) of tooth wear class B from Stainbank Nature Reserve (# 7) as an outlier, another clustered together three specimens from Umkomaas (# 8) of different tooth wear classes and sexes, and a third cluster with the exception of one specimen from Renishaw (#10) was made entirely of specimens from Ngome Forest (# 2), which represent 66.67% of the total specimens from Ngome Forest, the only Grassland biome locality included in the analysis. The remaining two clusters, one of which contained the majority of the specimens used in the analysis, did not show distinct clustering in relation to sex, tooth wear class or locality. Although there was no obvious explanation why specimens from three of the 12 pooled localities (Umkomaas, Stainbank Nature Reserve and Ngome Forest Nature Reserve) clustered together with others from the same locality, yet specimens from the other nine localities did not. Ngome Forest Nature Reserve was the only locality falling into the grassland biome (the other localities plotted in the savanna biome), and relative to the other specimens in the analysis, the Umkomaas specimens were much older, having been collected roughly 70 years earlier than the most recently collected specimens.

The PCA (Fig. 5.30) which showed 31.17% and 13.94% of the variation on the first and second principal components, identified the same male outlier (DM5870) as in the phenogram, as well as a female (DM4555) of tooth wear class D from Vuma Farm (# 5), which both separate from the other specimens on the second principal component axis. The remaining specimens, however, showed no clear separation in relation to different sexes, tooth wear classes or localities. However, within the cluster of specimens from Ngome Forest (# 2) which included

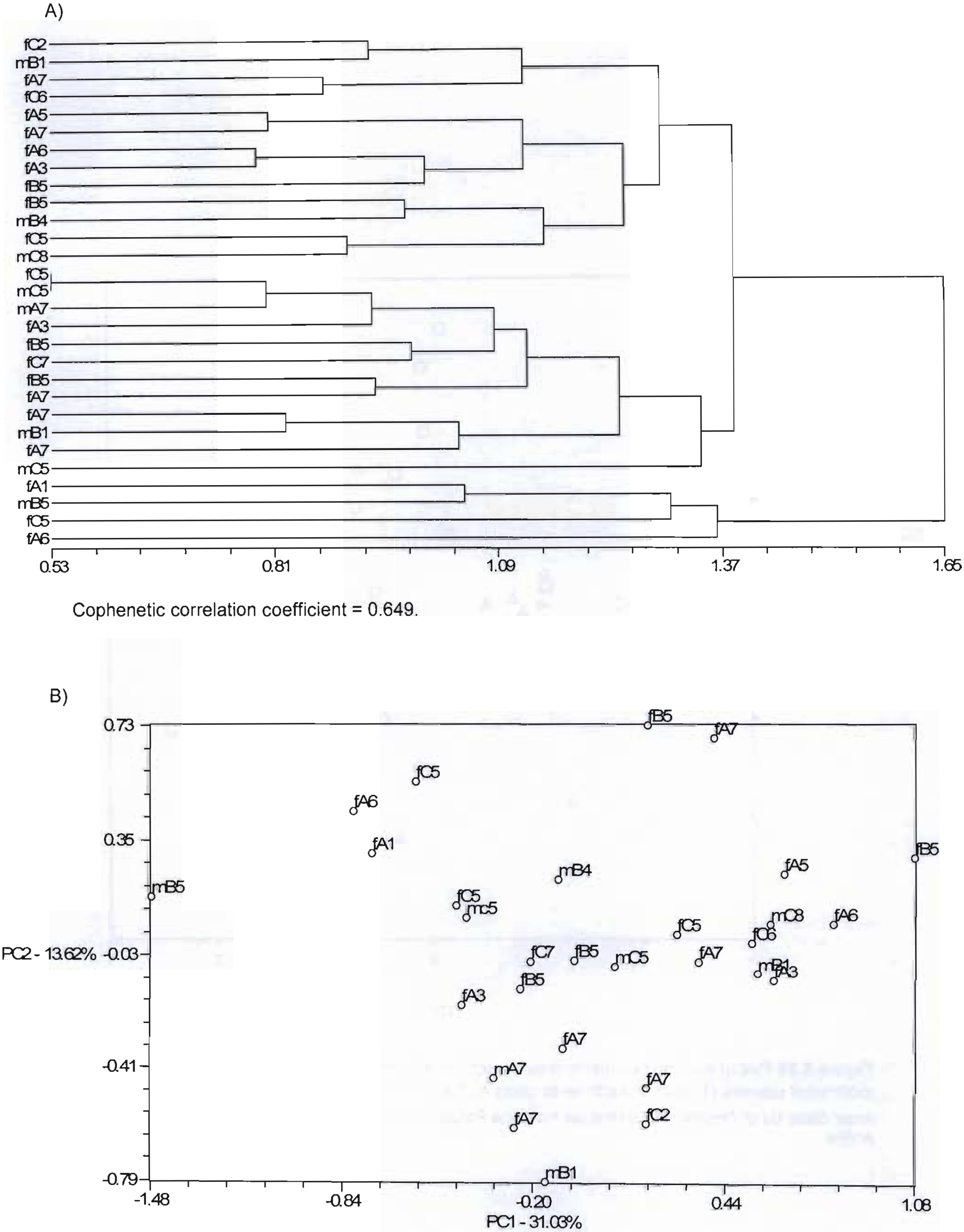


Figure 5.28 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of the first two principal components of 12 cranial measurements of *Neoromicia africanus* from eight localities in the Pafuri region of the Limpopo Province in South Africa. The sex (male = m, female = f), tooth wear class (A, B, or C), and locality code (1-8, see Appendix 5.1 for locality data) of individuals are indicated.

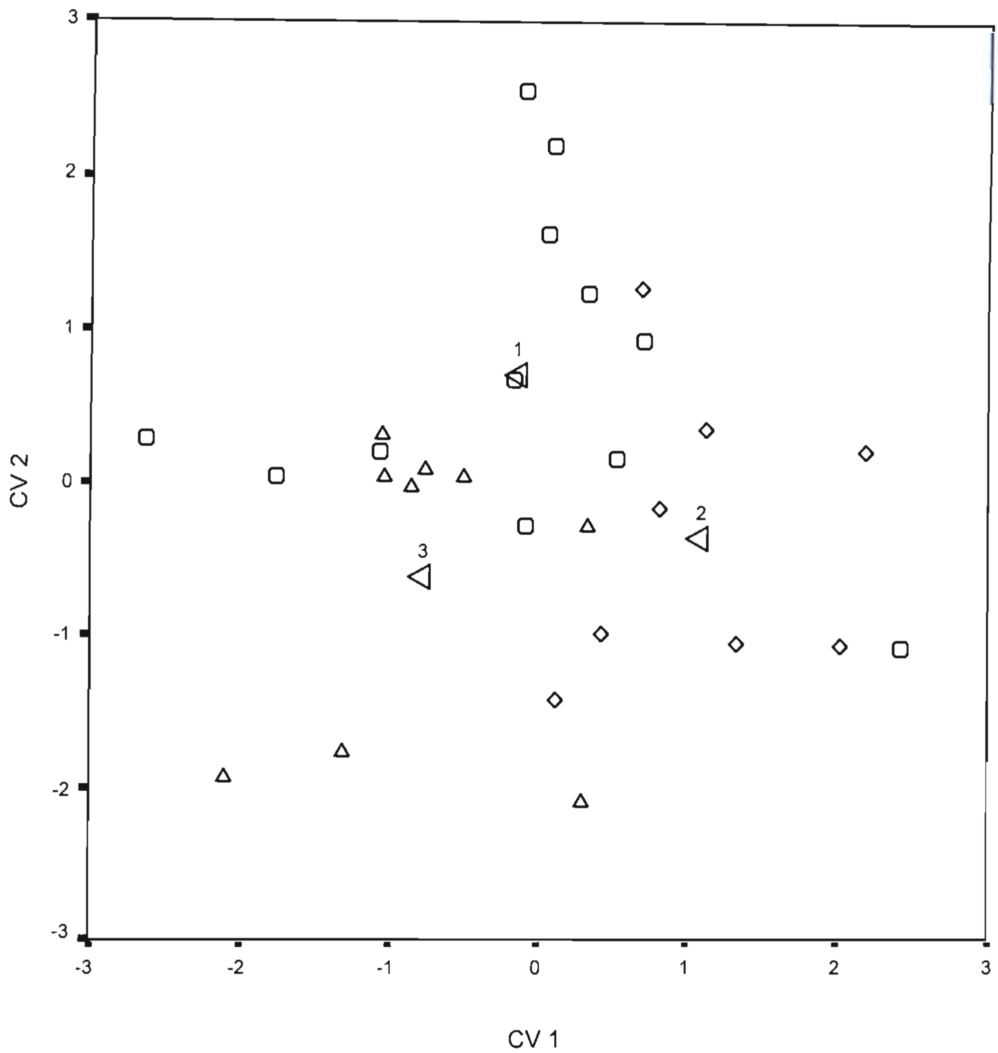


Figure 5.29 Plot of the first two discriminant functions of cranial measurements of three different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C) of *Neoromicia africanus* from the Pafuri area in the Limpopo Province of South Africa.

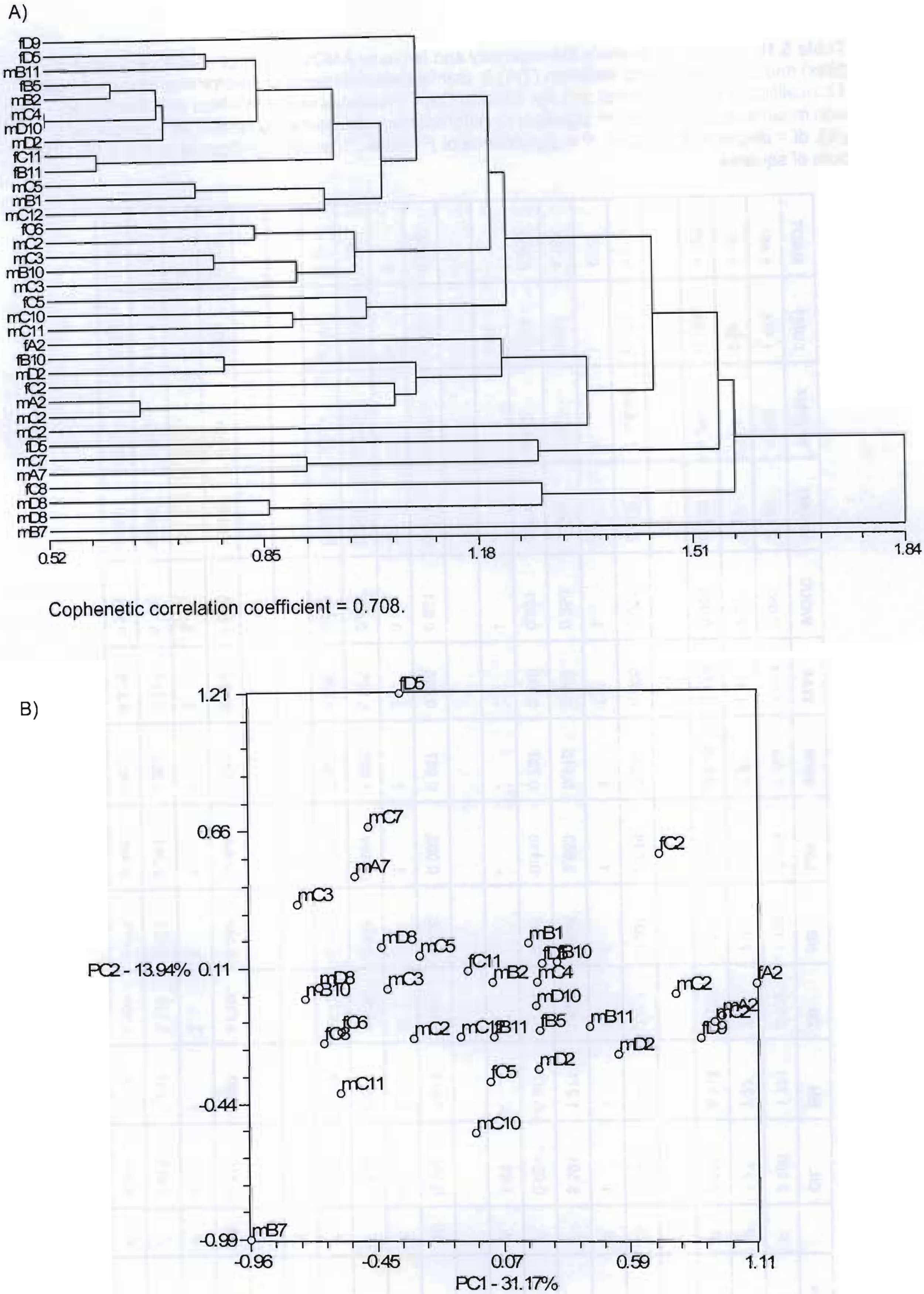


Figure 5.30 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of the first two principal components of 12 cranial measurements of *Neoromicia africanus* from 12 localities in the KwaZulu-Natal and Eastern Cape Provinces in South Africa, and in Swaziland. The sex (male = m, female = f), tooth wear class (A, B, C, or D), and locality code (1-12, see Appendix 5.1 for locality data) of individuals are indicated.

Table 5.18 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in cranial measurements of *Neoromicia africanus* from 12 localities in KwaZulu-Natal and the Eastern Cape Provinces in South Africa and Swaziland, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, *P* = significance of *F* values. * denote significance at $P < 0.05$. SS = sum of squares.

Levene's		**CIL**	**BH**	**ZB**	**BB**	**LIW**	**WFM**	**WAS**	**WOUC**	**WIUM1**	**WUPM4**	**LUM1**	**MAOT**
2-way	*F*	2.566	1.771	0.832	1.192	2.954	0.694	1.614	2.089	2.095	1.295	1.555	1.451
	df	7,27	7,27	7,27	7,27	7,27	7,27	7,27	7,27	7,27	7,27	7,27	7,27
	P	0.037 *	0.135	0.570	0.340	0.020 *	0.676	0.174	0.080	0.079	0.290	0.192	0.227
2-way ANOVA													
Sex	SS	0.192	0.013	0.051	0.001	0.016	0.001	0.005	0.005	0.002	2.39E-04	0.006	0.036
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	5.591	1.271	1.602	0.038	2.653	0.115	0.597	0.250	0.246	0.031	6.609	4.193
	P	0.025 *	0.270	0.216	0.846	0.115	0.737	0.446	0.621	0.624	0.862	0.016 *	0.050
	%	1.03	-	-	-	-	-	-	-	-	-	2.61	-
TW	SS	0.178	0.074	0.058	0.056	0.062	0.067	0.016	0.031	0.017	0.007	0.001	0.004
	df	3	3	3	3	3	3	3	3	3	3	3	3
	F	1.730	2.369	0.606	0.985	3.389	1.822	0.575	0.487	0.746	0.288	0.311	0.161
	P	0.184	0.093	0.617	0.415	0.032 *	0.167	0.636	0.694	0.534	0.834	0.817	0.921
	%	-	-	-	-	3.82	-	-	-	-	-	-	-
Sex×TW	SS	0.270	0.057	0.070	0.030	0.004	0.011	0.029	0.046	0.016	0.061	0.004	0.008
	df	3	3	3	3	3	3	3	3	3	3	3	3
	F	2.616	1.836	0.739	0.522	0.244	0.302	1.077	0.729	0.686	2.618	1.417	0.311
	P	0.071	0.164	0.538	0.671	0.865	0.823	0.376	0.544	0.568	0.071	0.259	0.817

specimens of both sexes and more than one tooth wear class, the plot of the first two principal component axes showed separation of the male and female specimens along the first principal component axis but no distinct pattern of separation of the tooth wear classes. On the first principal component axis, width between the inner surfaces of the upper first molars (WIUM1), width across the outer surfaces of the upper canines (WOUC), braincase breadth (BB) and moment arm of the temporal (MAOT) loaded highest, and width of the articular surface (WAS) loaded least. Moment arm of the temporal (MAOT) was also significantly sexually dimorphic in the two-way ANOVA tests. On the second principal component axis, width of the articular surface (WAS) and zygomatic breadth (ZB) loaded highest and width across the outer surfaces of the upper canines (WOUC) and width between the inner surfaces of the upper first molars (WIUM1) loaded least.

A two-group DFA of the sexes produced 82.86% *a posteriori* correct assignments of specimens to the different sexes [females (n = 12) - 83.33%, males (n = 23) - 82.61%]. A four-group DFA analysis of the tooth wear classes produced a 68.57% *a posteriori* correct assignment of specimens to the different tooth wear classes [tooth wear A (n = 3) 66.67%, tooth wear B (n = 8) - 100%, tooth wear C (n = 16) - 68.75%; tooth wear D (n = 8) - 37.5%]. A plot of the first two discriminant function axes of the four-group DFA (Fig. 5.31) shows no separation between the tooth wear classes. Two specimens, two males of tooth wear class A (TM39818) and B (DM5870) plotted as outliers on the second discriminant function axis.

5.3.1.12.2 External measurements

The univariate analyses were based on 40 specimens from 12 localities in the Eastern Cape and KwaZulu-Natal Provinces of South Africa and Swaziland (Fig. 5.15). With the exception of one locality (Ngome Forest) which occurs in the grassland biome, the rest of the localities occurred in the Savanna biome. Accounting for missing data, the multivariate analyses were based on 29 specimens from 11 localities and eight measurements. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendices 5.7 G1 and G2. Two-way ANOVA tests showed two (25%) measurements, hind foot (HFL) and forearm (FA) lengths, were significantly sexually dimorphic, with females 5.28 and 4.43% respectively larger than males (Table 5.19). No measurements were significantly different between the tooth wear classes or in the interaction between sex and tooth wear class. A two-way MANOVA of eight measurements (T, HFL, E, TIB, FA, TMETA, TRL, TRB), showed no significant variation between sexes (Wilks = 0.529, $F_{(8,15)}$ = 1.670, P = 0.186), tooth wear classes (Wilks = 0.320, $F_{(24,44.106)}$ = 0.883, P = 0.620) or in the interaction between sex and tooth wear class (Wilks = 0.774, $F_{(8,15)}$ = 0.548, P = 0.803).

In the analysis of eight measurements, the UPGMA phenogram and plot of the first two principal component axes separated localities differently. The phenogram (Fig. 5.32) based on eight measurements showed some clustering of specimens in relation to locality and sex but not tooth wear class, since two of the five major clusters were composed almost entirely of male specimens (83.33%) and there were pairs of specimens from Ngome (# 2), Ithala Game Reserve, Vuma Farm (# 5), Stainbank Nature Reserve (# 6), Port St Johns (# 10), and near Simunye in Swaziland (# 11). The two major clusters of the UPGMA phenogram separated specimens from Jozini Dam, Bonamanzi Game Reserve, Stainbank Nature Reserve and Umdoni Park from specimens near Simunye, Ithala Game Reserve, Empisini Nature Reserve, and Port St Johns. The PCA based on eight measurements (Fig. 5.32) identified an oblique separation along the first and second principal component axes, which explained 33.76% and 21.43% of the variation, respectively, that separated specimens on the smaller side of the first and second principal component axes from near Simunye in Swaziland (# 11), Ithala Game Reserve (# 3), Stainbank Nature Reserve (# 6), Renishaw (# 8) and Empisini (# 7), from specimens on the larger sides of the first and second principal component axes from Jozini Dam (# 1), Ngome Forest (# 2), Bonamanzi Game Reserve (# 4), Vuma Farm (# 5), Umdoni Park (# 9), and Port St Johns (#10). Although there was considerable overlap between the sexes in the PCA, more females were found on the larger sides of the first and second principal component axes, but there was little distinction in the PCA between tooth wear classes. On the first principal component axis, tragus breadth (TRB) and third metacarpal length (TMETA) loaded highest and lowest, respectively. On the second principal component, axis forearm (FA) and ear (E) lengths loaded highest and lowest, respectively. In neither analysis does the separation of localities relate to their longitudinal or latitudinal distribution.

A two-group DFA of the sexes produced a 79.31% *a posteriori* correct assignment of

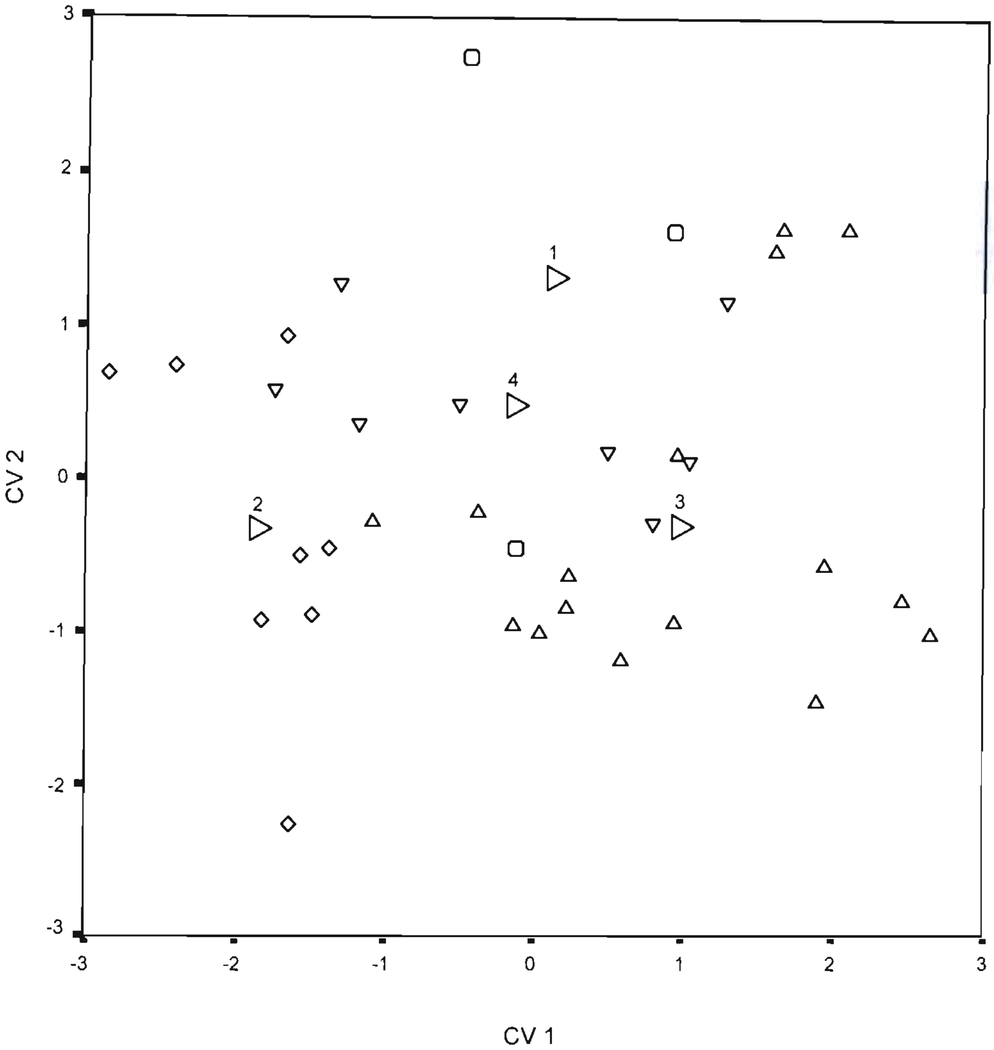
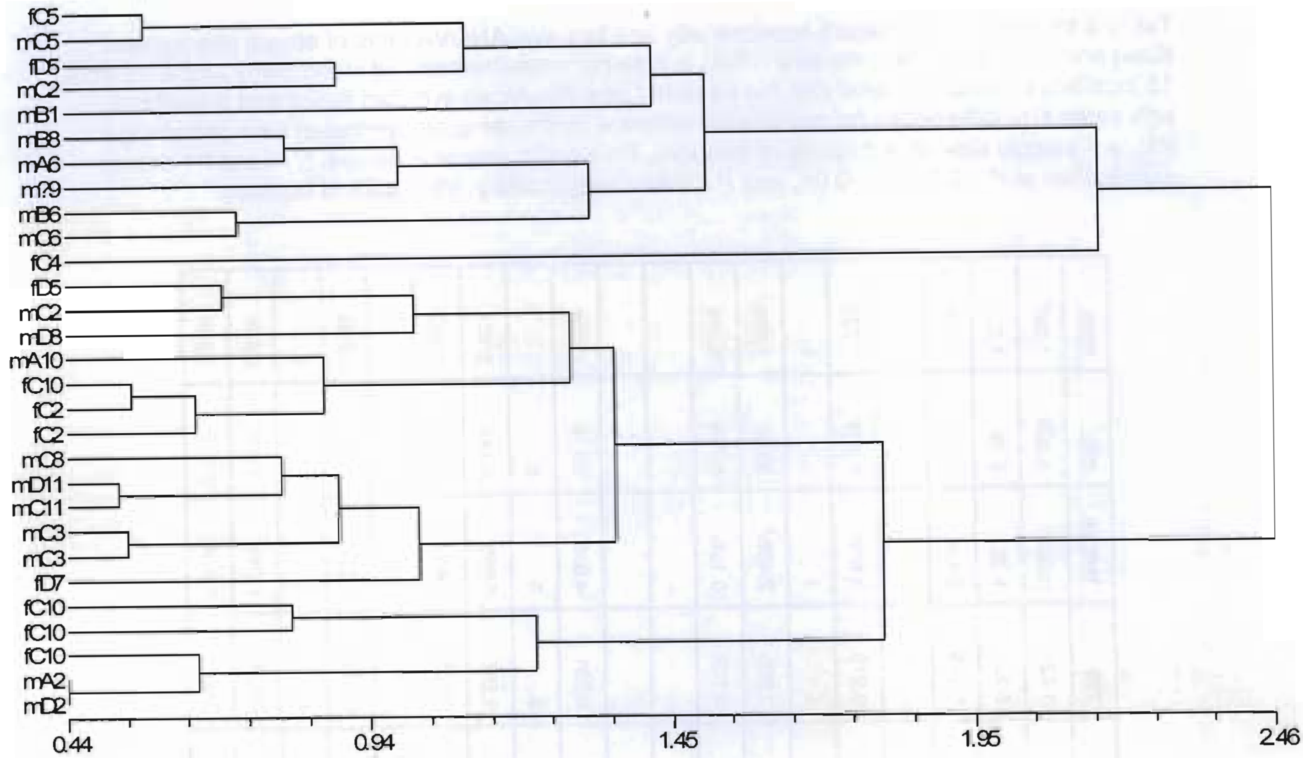


Figure 5.31 Plot of the first two discriminant functions of cranial measurements of four different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C; 4 and ▽ = tooth wear class D) of *Neoromicia africanus* from South Africa and Swaziland.

A)



Cophenetic correlation coefficient = 0.708.

B)

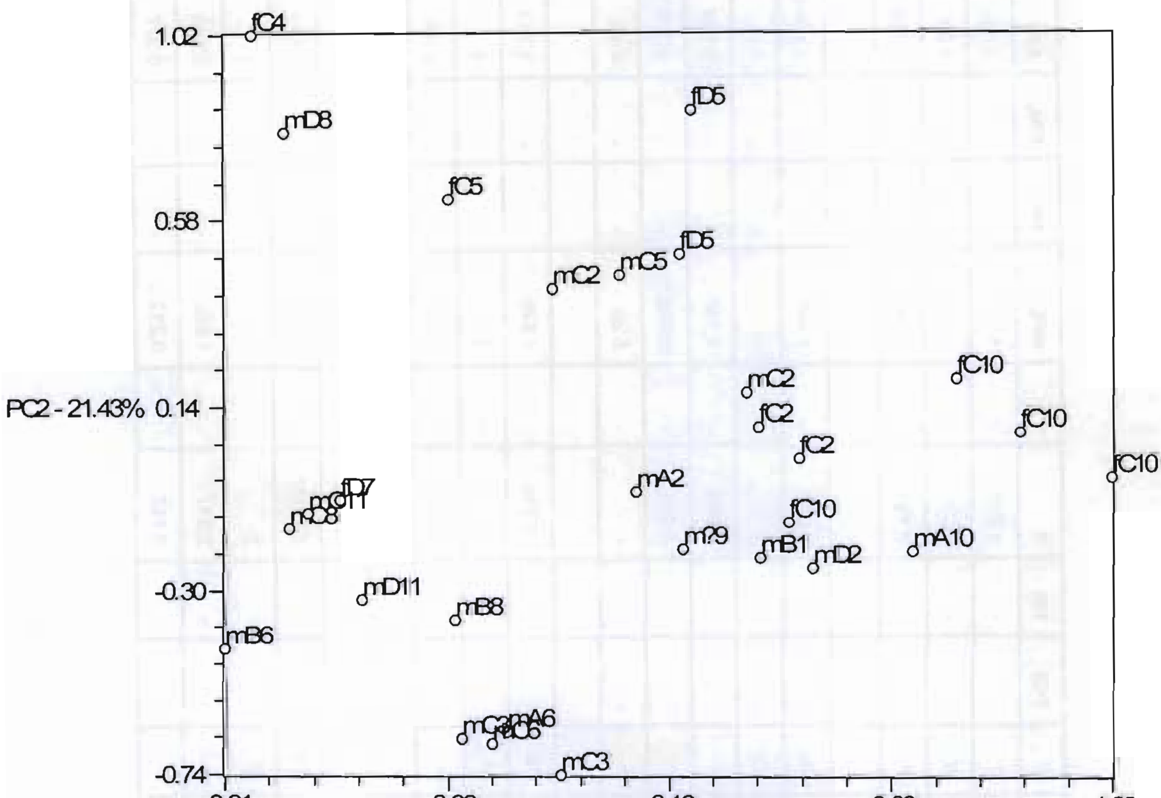


Figure 5.32 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of first two principal components of eight external measurements of *Neoromicia africanus* from 11 localities in the KwaZulu-Natal and Eastern Cape Provinces of South Africa, and in Swaziland. The sex (male = m, female = f), tooth wear class (A, B, C, D, or unknown = ?), and locality code (1-11, see Appendix 5.1 for locality data) of individuals are indicated.

Table 5.19 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in external measurements of *Neoromicia africanus* from 15 localities in KwaZulu-Natal and the Eastern Cape Provinces in South Africa and Swaziland, with mean size differences for significantly different measurements expressed as a percentage (%). *n* = sample size, df = degrees of freedom, *P* = significance of *F* values. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. SS = sum of squares.

Levene's		TOT	HB	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
2-way	*F*	-	-	1.815	-	1.203		-	0.482	1.419	1.828	1.050	1.207	1.057
	df	-	-	5,22	-	5,22		-	5,22	5,22	5,22	5,22	5,22	5,22
	P	-	-	0.151	-	0.340		-	0.786	0.256	0.149	0.414	0.339	0.410
2-way ANOVA														
Sex	SS	-	-	0.023	-	2.496	-	-	12.844	0.008	0.919	3.618	0.033	0.278
	df	-	-	1	-	1	-	-	1	1	1	1	1	1
	F	-	-	0.002	-	4.798	-	-	9.737	0.008	2.905	2.408	0.081	1.849
	P	-	-	0.963	-	0.039 *	-	-	0.005 **	0.931	0.102	0.135	0.778	0.188
	%	-	-	-	-	5.28	-	-	4.43	-		-	-	
TW	SS	-	-	37.755	-	1.645	-	-	1.711	4.078	0.281	4.035	0.178	0.428
	df	-	-	3	-	3	-	-	3	3	3	3	3	3
	F	-	-	1.212	-	1.054	-	-	0.432	1.368	0.297	0.895	0.145	0.951
	P	-	-	0.329	-	0.388	-	-	0.732	0.279	0.827	0.459	0.932	0.433
Sex×TW	SS	-	-	22.296	-	0.859	-	-	1.072	0.371	0.055	1.568	0.033	0.043
	df	-	-	1	-	1	-	-	1	1	1	1	1	1
	F	-	-	2.147	-	1.652	-	-	0.813	0.374	0.174	1.043	0.081	0.284
	P	-	-	0.157	-	0.212	-	-	0.377	0.547	0.681	0.318	0.778	0.599

specimens to the different sexes [females (n = 11) - 90.91%, males (n = 18) - 72.22%]. A four-group DFA of the tooth wear classes produced a 71.43% *a posteriori* correct assignments of specimens to the different tooth wear classes [tooth wear A (n = 3) - 66.67%, tooth wear B (n = 3) - 66.67%, tooth wear C (n = 16) - 68.75%; tooth wear D (n = 6) - 83.33%]. A plot of the first two discriminant function axes of the four-group DFA (Fig. 5.33) showed no separation between the tooth wear classes.

5.3.1.13 *Neoromicia africanus* – Malawi

5.3.1.13.1 External measurements

The univariate analyses were based on 34 specimens from three localities in Malawi (Fig. 5.15), occurring in the Tropical and Subtropical Grasslands, Savannas and Shrublands, and Montane Grasslands and Shrublands biomes (Olsen *et al.* 2001). Accounting for missing data, the multivariate analyses were based on nine measurements from 14 specimens. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendices 5.7 H1 and H2. Three (27.3%) measurements, hind foot (HF), forearm (FA), and third metacarpal (TMETA) lengths were significantly sexually dimorphic in the one-way ANOVA tests with females being 3.74 to 7.76% larger than males, and one (9.1%) measurement, tibia length (TIB) was significantly different between different tooth wear classes (Table 5.20). A post-hoc Tukey test identified two overlapping subsets of tooth wear classes B and D, and tooth wear classes D and C, which separated tooth wear classes B and C. The relative difference between tooth wear classes B and C was 8.0%. The smaller mean size of tibia for tooth wear class D was influenced by the small tibia length of a female (KM11716) from Zomba Plateau.

Two Kruskall-Wallis tests contradicted the ANOVA results (Appendix 5.5). In hind foot length (HFL), which showed both significant homogeneity between the sexes and significant non-normality in males, the Kruskall-Wallis test identified sexual dimorphism whereas the ANOVA test did not. In hind foot length (HF), which showed significant homogeneity between the sexes, the Kruskall-Wallis test did not find any significant sexual dimorphism, whereas the ANOVA test found significant sexual dimorphism. A one-way MANOVA of 14 specimens of 9 measurements (HB, E, HF, TIB, FA, TMETA, TRL, TRB, TL) showed significant sexual dimorphism (Wilks = 0.047, $F_{(4,9)}$ = 9.031, P = 0.024), but a one-way MANOVA of 10 specimens of 9 measurements (HB, E, HF, TIB, FA, TMETA, TRL, TRB, TL) found no significant difference between tooth wear classes B, C and D (Wilks = 0.036, $F_{(2,14)}$ = 0.614, P = 0.764).

The phenogram (Fig. 5.34) identified a single female (KM11707) of unknown tooth wear class from Zomba Plateau as an outlier, the remaining specimens split into two major clusters, the smaller of which contained three of the seven specimens from Zomba Plateau, of mixed sexes and tooth wear classes, whereas the other cluster showed little grouping of specimens in relation to sex, tooth wear class or locality. The PCA (Fig. 5.34) identified the same outlier (KM11707) as in the phenogram, as well as another female of unknown tooth wear class from Zomba Plateau (KM11712) which was larger on the second principal component axis than the other specimens. Among the remaining specimens, males were smaller than females on the first principal component axis which explained 37.44% of the variation, and there was some separation of specimens in relation to locality and different tooth wear class. On the first principal component axis, the lengths of the third metacarpal (TMETA) and ear (E) loaded highest and lowest, respectively, while on the second principal component axis which explained 19.04% of the variation, forearm length (FA) and tragus breadth (TRB) loaded highest and lowest, respectively. Forearm (FA) and third metacarpal (TMETA) lengths were also significantly sexually dimorphic in the one-way ANOVA tests.

A two-group DFA of the sexes and a three-group DFA of tooth wear classes each produced 100% *a posteriori* correct assignments of specimens to the different sexes and tooth wear classes. A plot of the first two discriminant function axes of the three-group DFA (Fig. 5.35) showed the separation between tooth wear classes B, C and D on the first discriminant function axis which described 57.7% of the variation. On the first discriminant function, axis forearm length (FA) loaded highest and tragus length (TRL) loaded least. The second discriminant function axis which described 42.3% of the variation separated tooth wear class D from tooth wear classes B and C. On the second discriminant function axis, forearm length (FA) and tragus length (TRL) loaded highest, and length of the third metacarpal (TMETA) loaded least. Forearm (FA) and third metacarpal (TMETA) lengths were also significantly sexually dimorphic in the one-way ANOVA tests and important in the separation on the first two principal component axes, yet the measurement that showed significant variation between the tooth wear classes in the one-way

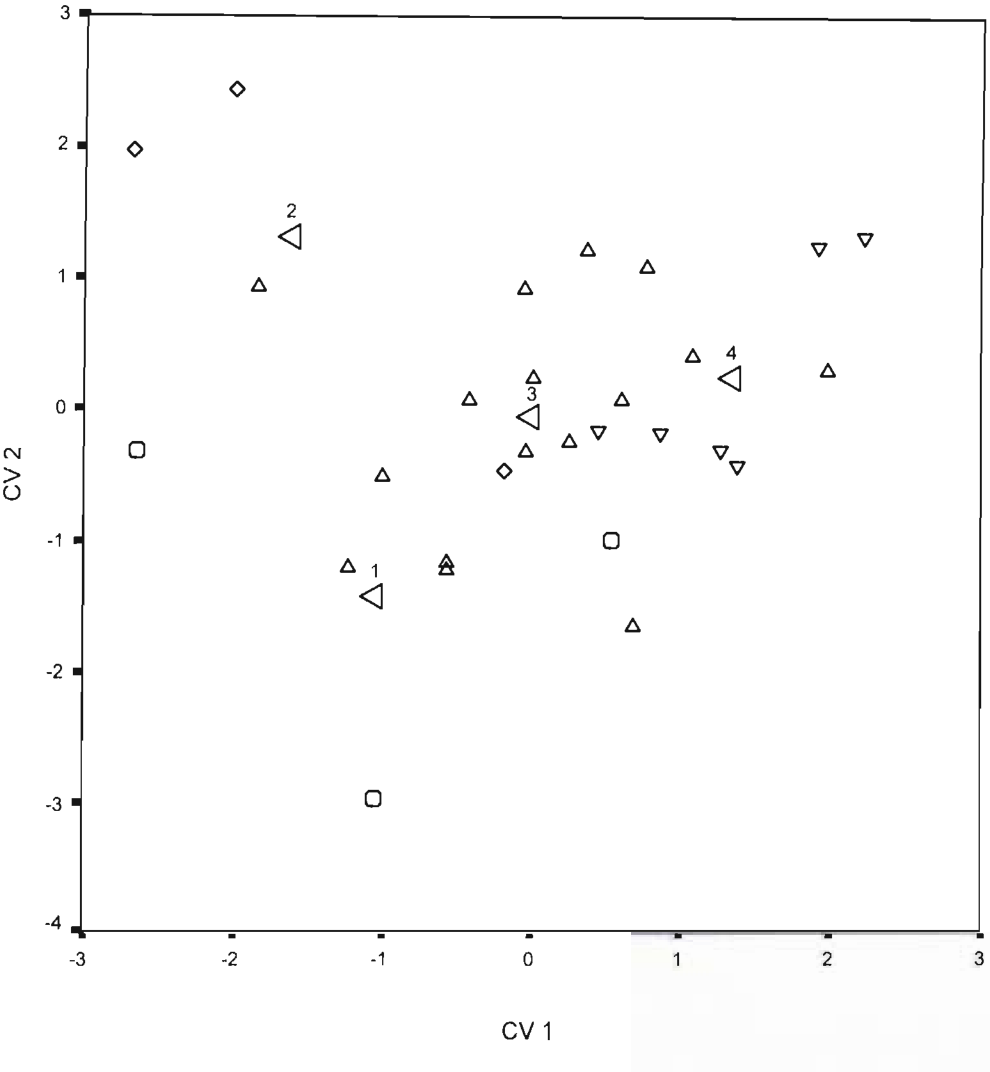


Figure 5.33 Plot of the first two discriminant functions of eight external measurements of four different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C; 4 and ▽ = tooth wear class D) of *Neoromicia africanus* from South Africa and Swaziland.

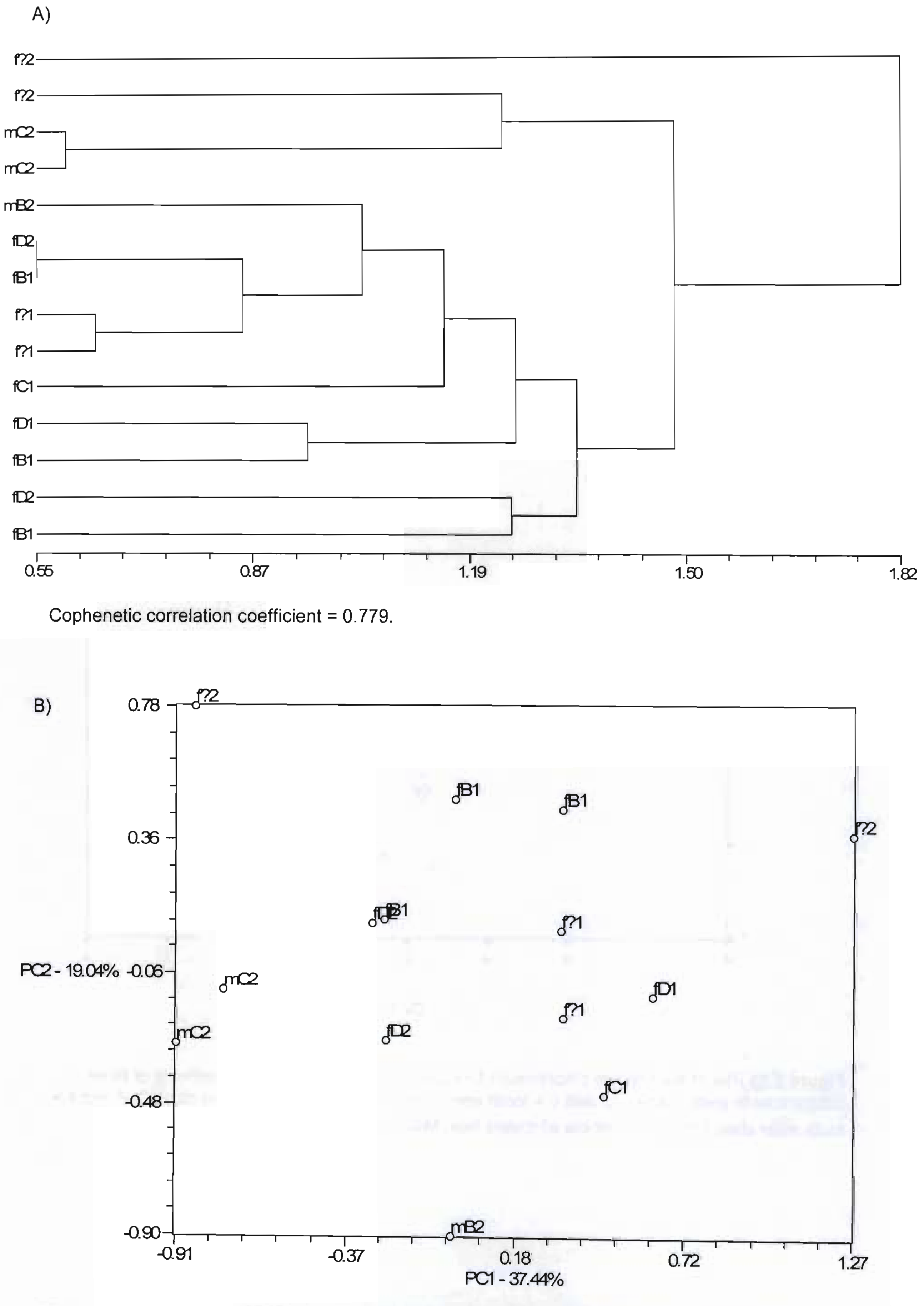


Figure 5.34 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of the first two principal components of nine external measurements of *Neoromicia africanus* from two localities in Malawi. The sex (male = m, female = f), tooth wear class (B, C, D, or unknown = ?), and locality code (1-2, see Appendix 5.1 for locality data) of individuals are indicated.

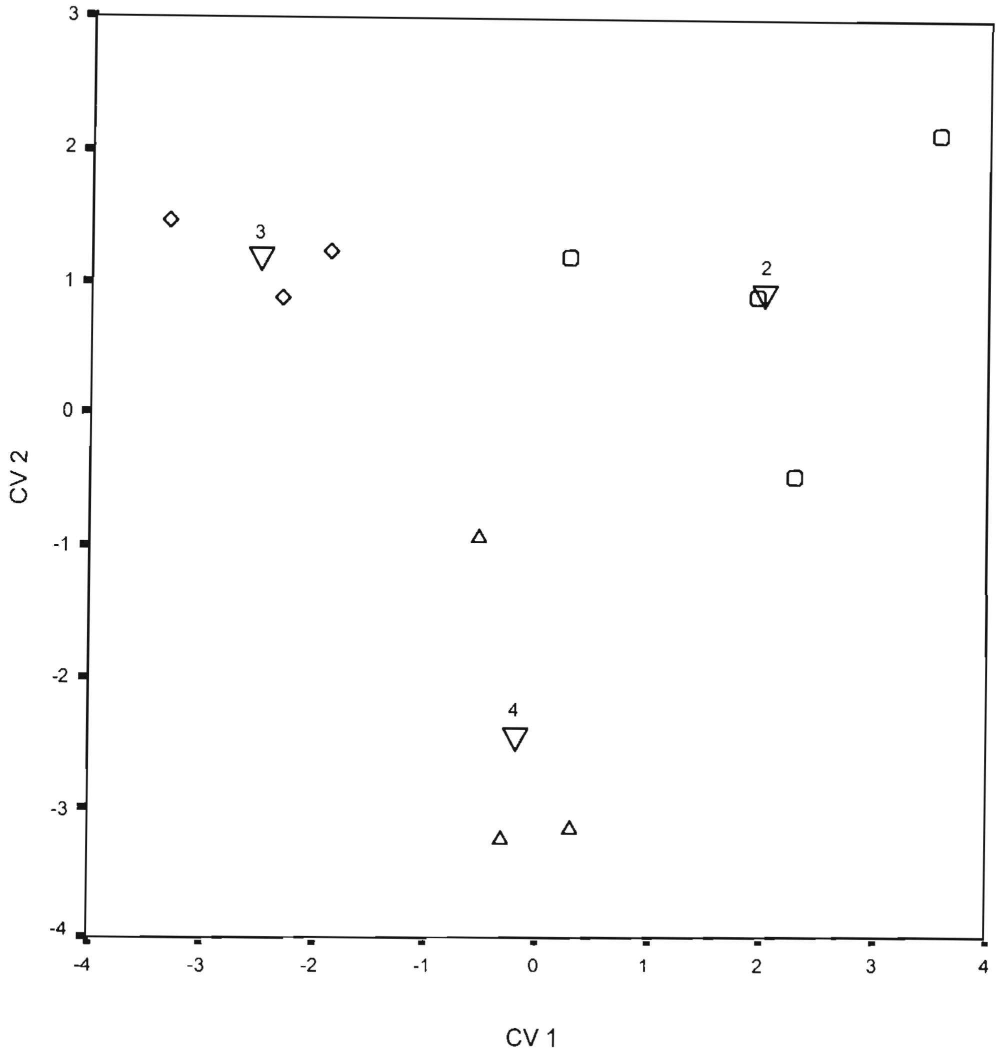


Figure 5.35 Plot of the first two discriminant functions of nine external measurements of three different tooth wear classes (2 and ○ = tooth wear class B; 3 and ◇ = tooth wear class C; 4 and △ = tooth wear class D) of *Neoromicia africanus* from Malawi.

Table 5.20 Results of Levene's homogeneity and one-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in external measurements of *Neoromicia africanus* from three localities in Malawi, with mean size differences for significantly different measurements expressed as a percentage (%). n = sample size, df = degrees of freedom, *P* = significance of *F* values. *, ** and *** denote significance at *P* < 0.05, *P* < 0.01, and *P* < 0.001, respectively. SS = sum of squares.

Levene's		**HB**	**T**	**TL**	**HFL**	**HF**	**FA**	**E**	**TIB**	**TMETA**	**TRL**	**TRB**
Sex	*F*	1.309	0.051	1.592	5.786	4.612	1.889	8.718	0.176	0.088	1.299	0.293
	df	1,23	1,22	1,28	1,23	1,30	1,32	1,23	1,27	1,32	1,24	1,26
	P	0.264	0.823	0.217	0.025 *	0.040 *	0.179	0.007 **	0.678	0.769	0.266	0.593
TW	*F*	1.678	0.615	2.234	0.391	2.146	1.384	0.658	2.229	0.554	1.119	1.346
	df	2,11	2,10	2,13	2,11	3,15	3,15	2,11	2,12	3,15	3,11	3,12
	P	0.231	0.560	0.147	0.686	0.137	0.286	0.537	0.150	0.653	0.383	0.306
ANOVA												
Sex	*n*	22:3	21:3	24:6	22:3	25:7	27:7	22:3	22:7	27:7	20:6	21:7
	SS	4.081	0.149	6.012	0.545	1.076	16.904	0.123	3.515E-02	7.263	0.694	1.630E-02
	df	1	1	1	1	1	1	1	1	1	1	1
	F	1,263	0.062	1.367	4.074	5.256	16.993	1.238	0.093	8.914	3.272	0.623
	P	0.273	0.805	0.252	0.055	0.029 *	2.48E-04 ***	0.277	0.763	0.005 **	0.083	0.437
	%	-	-	-	-	7.76	5.46	-	-	3.74	-	-
TW - females	*n*	-:3:6:5	-:3:6:4	-:5:7:4	-:3:6:5	1:5:8:5	1:5:8:5	-:3:6:5	-:5:6:4	1:5:8:5	1:5:5:4	1:4:5:6
	SS	5.867	6.058	1.256	1.429E-02	0.723	1.706	0.406	2.541	0.134	0.386	0.149
	df	2	2	2	2	3	3	2	2	3	3	3
	F	2.283	1.072	0.116	0.046	1.800	0.787	1.633	7.431	0.052	0.755	1.986
	P	0.148	0.379	0.891	0.955	0.190	0.520	0.239	0.008 **	0.984	0.542	0.170
	%	-	-	-	-	-	-	-	8.00	-	-	-

ANOVA tests, tibia length (TIB), was not important in this analysis.

5.3.1.14 *Neoromicia rueppellii* – Southern African
5.3.1.14.1 Cranial measurements

The analyses were based on seven specimens from seven localities in Botswana and Zimbabwe and South Africa (Fig. 5.36), all occurring in the Savanna biome. Since the number of specimens was less than the number of variables, only one-way univariate tests were performed. The summary statistics and results of the normality tests for sexes are given in Appendix 6 L. No measurements were significantly sexually dimorphic or significantly different between different tooth wear classes in the one-way ANOVAs (Table 5.21).

5.3.1.14.2 External measurements

The univariate analyses were based on 17 specimens from 11 different localities in Botswana, Zimbabwe and South Africa (Fig. 5.15), all occurring in the Savanna biome. Accounting for specimens with missing data, the multivariate analyses were based on eight measurements from eight specimens from three localities in Zimbabwe. The summary statistics and results of the normality tests for sexes are given in Appendix 5.7 I. No measurements were significantly different between the sexes or the different tooth wear classes in the one-way ANOVA tests (Table 5.22). The one-way MANOVA of eight specimens and eight measurements (TOT, T, HFL, E, FA, TMETA, TRL, TRB) showed no significant difference between the sexes (Wilks = 0.037, $F_{(6,1)}$ = 4.331, P = 0.352).

The phenogram (Fig. 5.37) showed no distinct clustering in relation to sex, tooth wear class or locality. The PCA (Fig. 5.37) showed considerable separation of the few specimens in the analysis on both the first and second principal component axes, which explained 38.54% and 23.69%, respectively. While the pattern of separation showed little relationship to differences tooth wear class and locality, males were larger and almost separated distinctly from females on the first principal component axis. On the first principal component axis, hind foot (HFL) and ear (E) lengths loaded highest and lowest, respectively, while on the second principal component axis tail length (T) loaded highest, and forearm (FA) and tragus (TRL) lengths loaded least.

There were too few specimens for a DFA of the different tooth wear classes. However, a two-group DFA of the sexes produced a 100% *a posteriori* correct assignment of specimens to the different sexes.

5.3.1.15 *Neoromicia rueppellii* – Zambia
5.3.1.15.1 External measurements

The univariate analyses were based on 17 specimens from a single locality, Balovale, in Zambia (Fig. 5.15), occurring in the Tropical and Subtropical Grasslands, Savannas, and Shrublands biomes (Olsen and Dinerstein, 1998). Accounting for missing data, the multivariate analyses were based on eight measurements from 16 specimens. The analyses of external measurements only assessed variation due to sexual dimorphism and not due to tooth wear class, as the crania of these specimens were too damaged for measurement, and not having measured the skulls tooth wear class information was not collected for these specimens. The summary statistics and results of the normality tests for sexes are given in Appendix 5.7 J. No measurements were significantly sexually dimorphic in the one-way ANOVAs (Table 5.23). A one-way MANOVA of 16 specimens and eight measurements (HB, T, HFL, E, TIB, FA, TMETA, TRB) showed no significant difference between the different sexes (Wilks = 0.333, $F_{(8,7)}$ = 1.752, P = 0.237).

Neither the phenogram (Fig. 5.38) nor the PCA (Fig. 5.38) showed distinct clustering or separation of the sexes. On the first principal component axis, which explained 49.28% of the variation, tibia (TIB) and forearm (FA) lengths loaded highest, and hind foot length (HFL) loaded least. On the second principal component axis, which explained 19.96% of the variation, tragus breadth (TRB) and hind foot length (HFL) loaded highest and lowest, respectively.

There were too few specimens for a DFA of the different tooth wear classes. However, a two-group DFA of the sexes produced an 87.5% *a posteriori* correct assignment of specimens to the different sexes [females (n = 8) - 100%, males (n = 8) - 75%].

5.3.1.16 *Neoromicia zuluensis* – South Africa, Mpumalanga and Limpopo Provinces
5.3.1.16.1 Cranial measurements

These analyses were based on 36 specimens from 20 different localities in the Limpopo

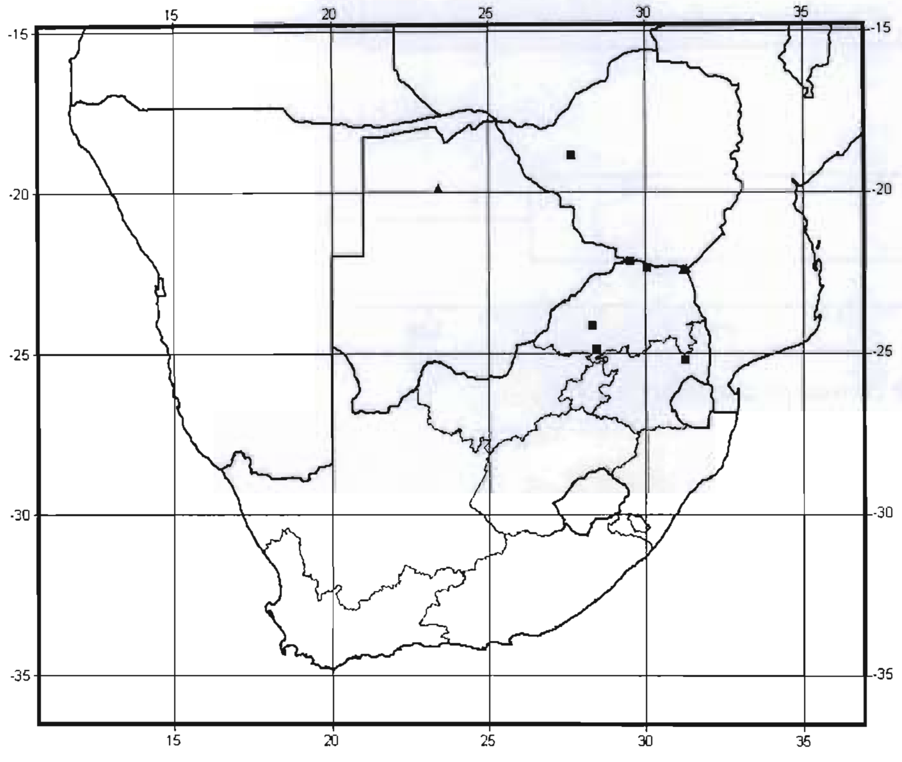
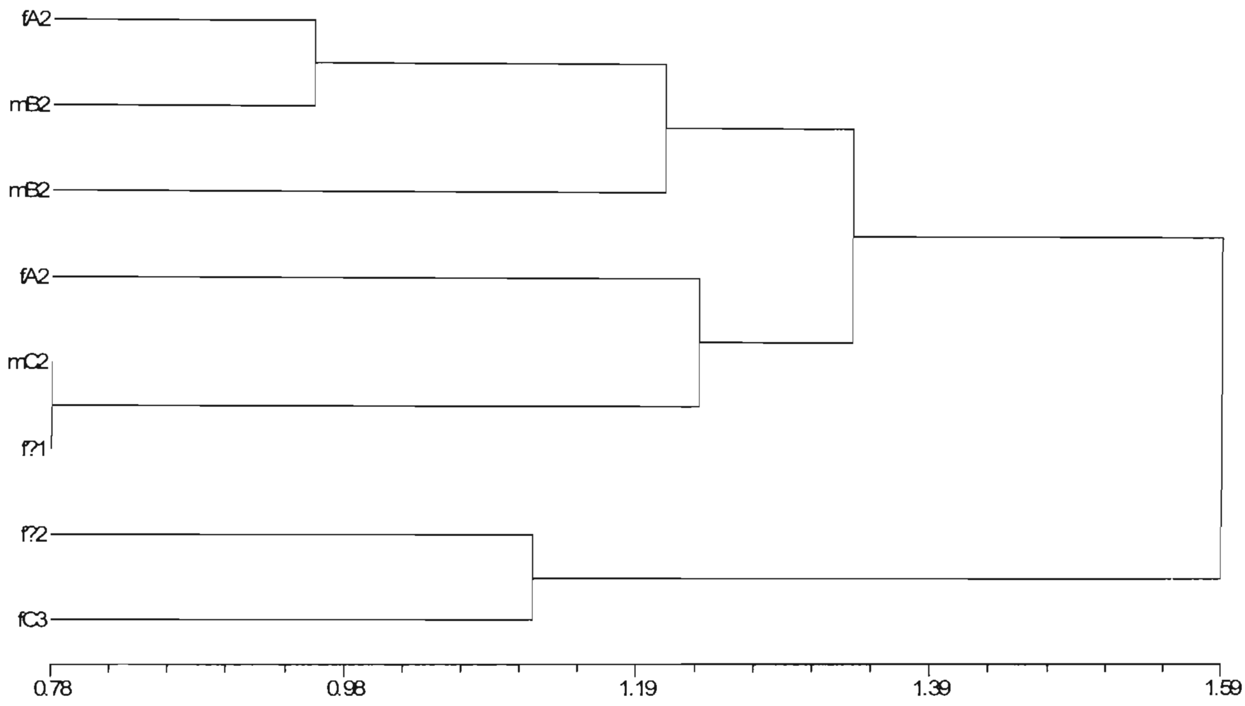


Figure 5.36 Map showing the distribution of specimens of *Neoromicia rueppellii* and *Pipistrellus rusticus* from Southern Africa used in the statistical analyses of cranial measurements. [*N. rueppellii* from Southern Africa = filled triangle; *P. rusticus* from Southern Africa = filled square.] Both *N. rueppellii* and *P. rusticus* occur at near Gwayi River in north-eastern Zimbabwe.

A)



Cophenetic correlation coefficient = 0.756

B)

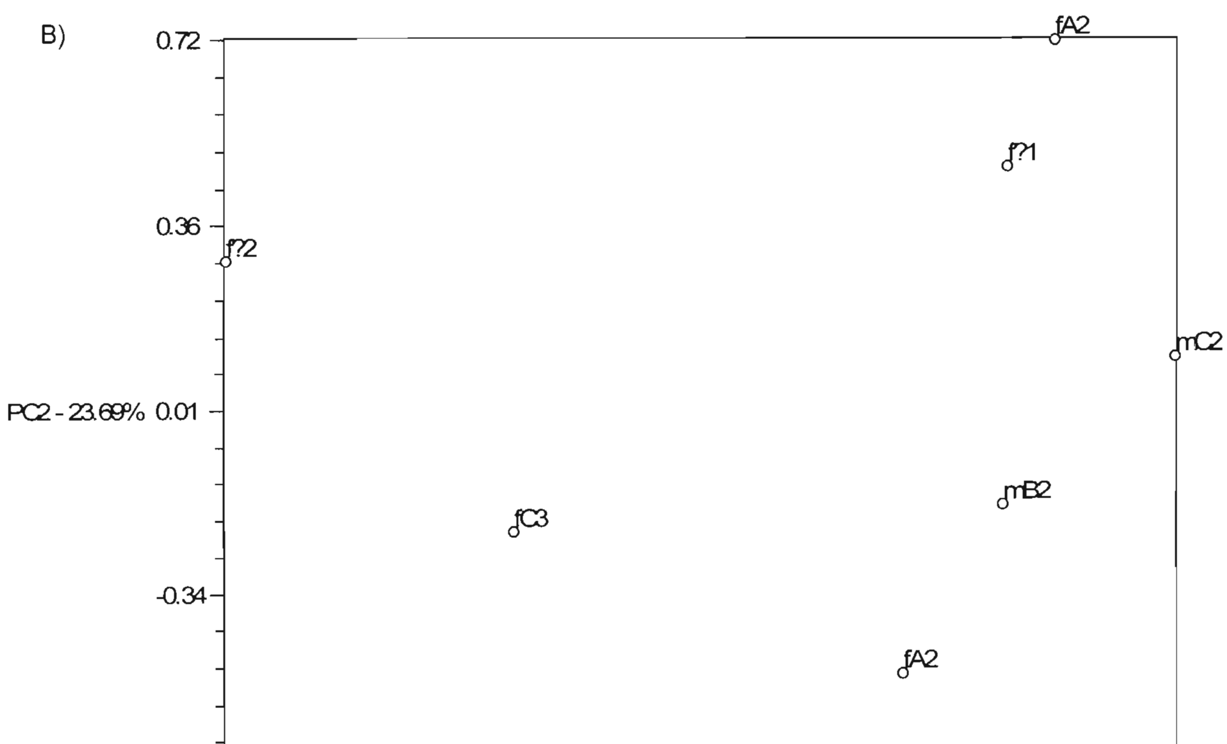
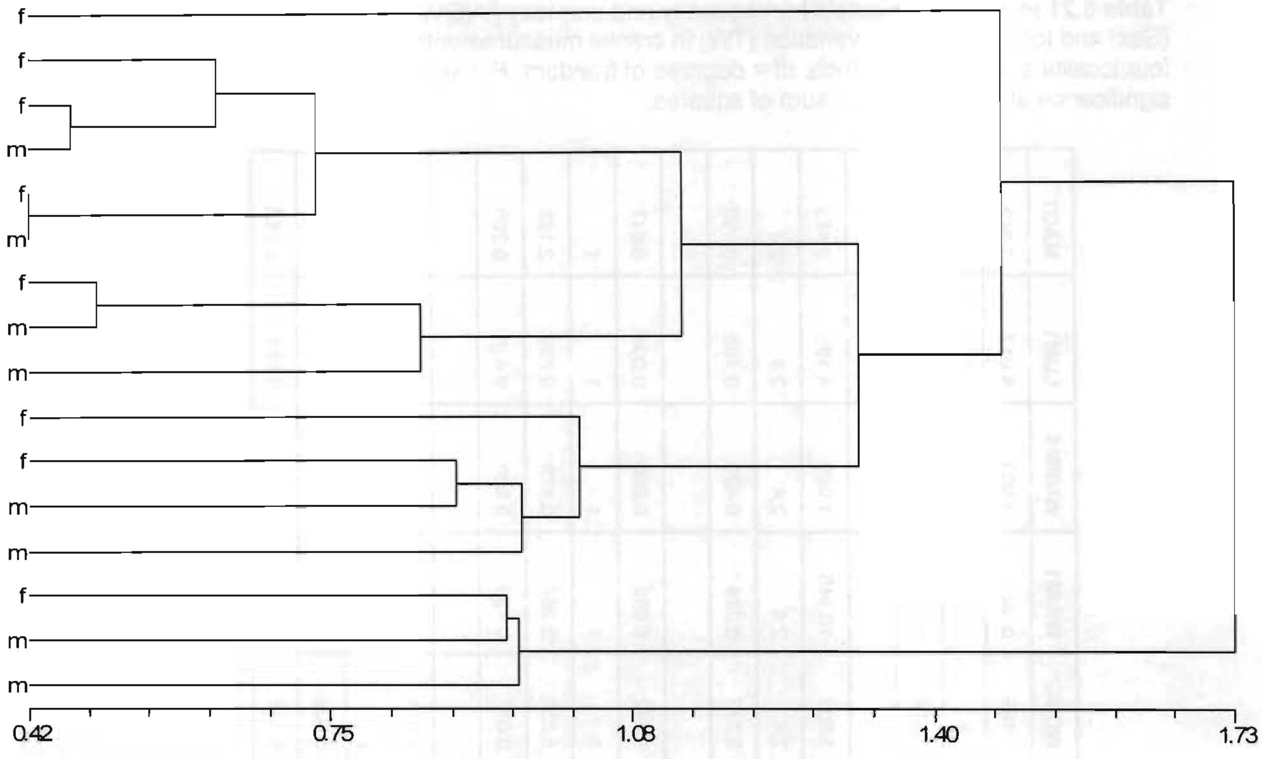


Figure 5.37 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of the first two principal components of eight external measurements of *Neoromicia rueppellii* from three localities in Southern Africa. The sex (male = m, female = f), tooth wear class (A, B, C, or unknown = ?), and locality code (1-3, see Appendix 5.1 for locality data) of individuals are indicated.

A)



Cophenetic correlation coefficient = 0.795.

B)

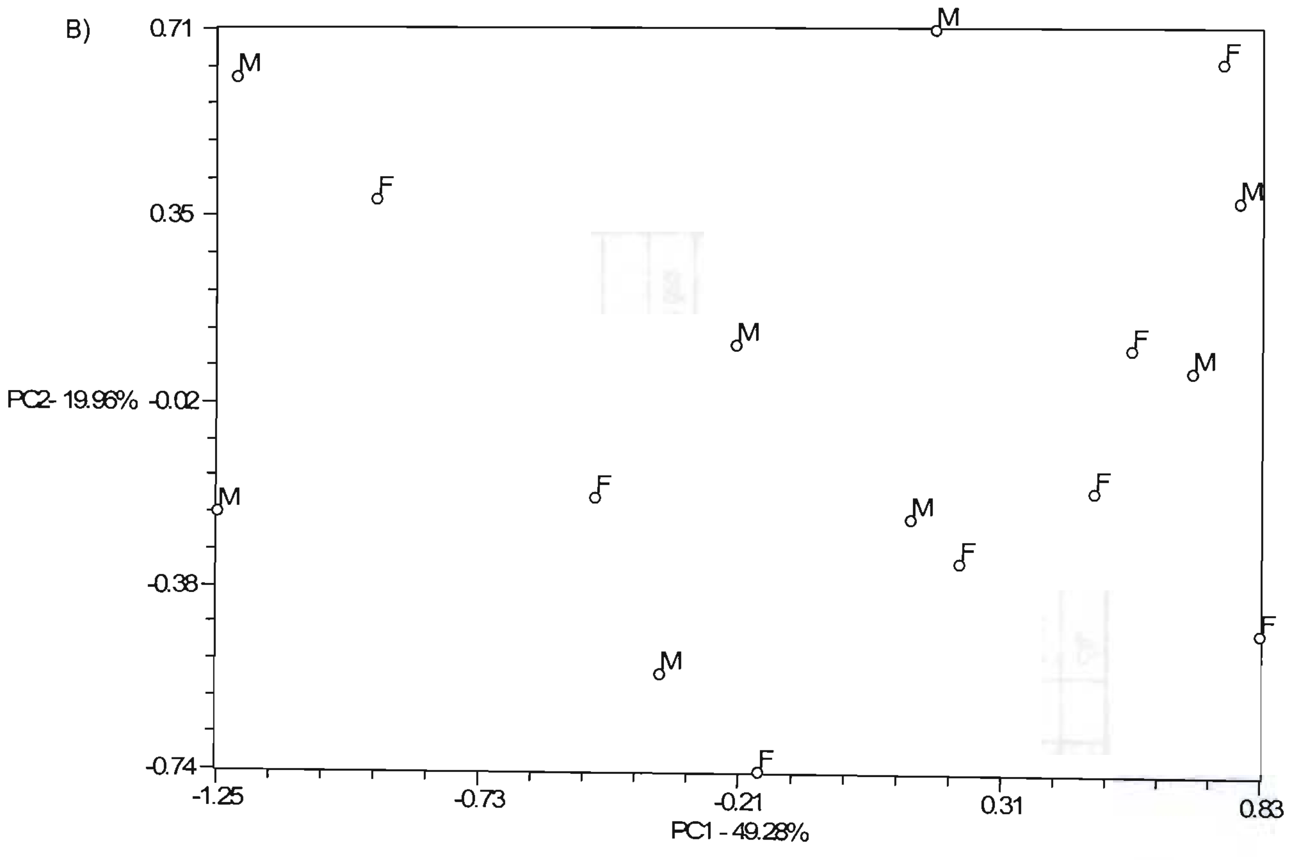


Figure 5.38 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of first two principal components of eight external measurements of *Neoromicia rueppellii* from Balovale in Zambia. The sex (male = m, female = f) of individuals are indicated.

Table 5.21 Results of Levene's homogeneity and one-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in cranial measurements of *Neoromicia rueppellii* from four localities in Southern Africa. df = degrees of freedom, *P* = significance of *F* values. * denotes significance at *P* < 0.05. SS = sum of squares.

Levene's		**CIL**	**BH**	**ZB**	**BB**	**LIW**	**WFM**	**WAS**	**WOUC**	**WIUM1**	**WUPM4**	**LUM1**	**MAOT**
Sex	*F*	2.364	0.180	1.953	4.083	0.413	1.633	4.710	0.199	0.593	0.863	5.017	3.842
	df	1,5	1,5	1,5	1,5	1,5	1,5	1,5	1,5	1,5	1,5	1,5	1,5
	P	0.185	0.689	0.221	0.099	0.549	0.257	0.082	0.674	0.476	0.396	0.075	0.107
TW	*F*	16.259	3.296	0.997	1.647	3.810	2.897	1.245	1.803	10.945	1.080	4.165	2.493
	df	2,4	2,4	2,4	2,4	2,4	2,4	2,4	2,4	2,4	2,4	2,4	2,4
	P	0.012 *	0.143	0.445	0.301	0.119	0.167	0.380	0.277	0.024 *	0.422	0.105	0.198
ANOVA													
Sex	SS	0.200	1.43E-04	0.048	0.082	0.043	0.011	0.004	0.142	0.060	0.005	0.004	0.047
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	2.892	0.017	1.061	5.815	1.059	0.461	0.427	5.250	3.367	0.479	0.789	2.175
	P	0.150	0.900	0.350	0.061	0.351	0.527	0.542	0.071	0.126	0.520	0.415	0.200
TW	SS	0.052	0.011	0.054	0.019	0.113	0.077	0.012	0.098	0.006	0.023	0.006	0.013
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	0.210	0.729	0.482	0.291	1.703	2.875	0.734	1.099	0.082	1.259	0.473	0.179
	P	0.819	0.537	0.649	0.762	0.292	0.168	0.535	0.417	0.923	0.377	0.654	0.842

Table 5.22 Results of Levene's homogeneity and one-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in external measurements of *Neoromicia rueppellii* from six localities in Southern Africa. *n* = sample size, df = degrees of freedom, *P* = significance of *F* values. * denotes significance at $P < 0.05$ respectively. SS = sum of squares.

Levene's		**TOT**	**T**	**TL**	**HFL**	**HF**	**FA**	**E**	**TIB**	**TMETA**	**TRL**	**TRB**
Sex	*F*	2.223	0.168	0.244	0.134	5.404	0.669	0.263	0.305	0.725	1.929	0.032
	df	1,11	1,11	1,7	1,11	1,10	1,15	1,10	1,8	1,14	1,13	1,12
	P	0.164	0.690	0.637	0.721	0.042 *	0.426	0.619	0.596	0.409	0.188	0.862
TW	*F*	1.591	3.819	2.302	1.956	-	1.595	2.897	-	1.498	2.195	5.446
	df	2,7	2,7	2,4	2,7	-	2,11	2,6	-	2,10	2,9	2,8
	P	0.269	0.076	0.216	0.212	-	0.246	0.132	-	0.270	0.167	0.032 *
ANOVA												
Sex	*n*	5:8	5:8	3:6	5:8	4:8	6:11	5:7	2:8	6:10	6:9	6:8
	SS	18.094	18.094	43.183	1.202	0.905	3.968	0.860	4.733	3.876E-02	0.145	0.243
	df	1	1	1	1	1	1	1	1	1	1	1
	F	0.440	1.376	3.214	0.740	1.831	3.095	0.390	0.275	0.014	0.067	2.795
	P	0.521	0.266	0.116	0.408	0.206	0.099	0.546	0.614	0.907	0.800	0.120
TW	*n*	4:3:3:-	4:3:3:-	3:1:3:-	4:3:3:-	-	7:4:3:-	4:3:3:-	-	7:3:3:-	6:4:2:-	5:4:2:-
	SS	37.483	63.517	32.980	1.650	-	0.218	1.556	-	3.560	5.853	0.230
	Df	2	2	2	2	-	2	2	-	2	2	2
	F	0.393	3.172	2.397	0.392	-	0.064	0.304	-	0.561	1.186	3.852
	P	0.689	0.105	0.207	0.690	-	0.939	0.748	-	0.588	0.349	0.067

Table 5.23 Results of Levene's homogeneity and one-way ANOVA tests of sexual dimorphism (Sex) in external measurements of *Neoromicia rueppellii* from Balovale in Zambia. *n* = sample size, df = degrees of freedom, *P* = significance of *F* values. ** denotes significance at $P < 0.01$. SS = sum of squares.

Levene's		HB	T	TL	HFL	HF	FA	E	TIB	TMETA	TRL	TRB
Sex	*F*	4.345	0.087	0.860	9.251	0.507	0.052	0.970	0.064	0.011	0.176	0.957
	df	1,15	1,15	1,13	1,15	1,15	1,15	1,15	1,15	1,14	1,8	1,14
	P	0.055	0.772	0.371	0.008 **	0.487	0.823	0.340	0.804	0.919	0.686	0.345
ANOVA												
Sex	*n*	8:9	8:9	8:7	8:9	8:9	8:9	8:9	8:9	8:8	5:5	8:8
	SS	2.042E-02	15.334	3.007	0.196	0.458	3.149	0.222	0.127	5.625E-03	4.00E-05	2.256E-03
	df	1	1	1	1	1	1	1	1	1	1	1
	F	0.010	3.462	0.468	3.802	1.040	1.405	1.286	0.162	0.002	3.57E-04	0.097
	P	0.923	0.082	0.506	0.070	0.324	0.254	0.275	0.693	0.968	0.985	0.760

and Mpumalanga Provinces of South Africa (Fig. 5.1), all occurring in the Savanna biome. The summary statistics and results of the normality tests, for sexes and tooth wear classes are given in Appendix 6 M1 - M4. In two-way ANOVA tests five (41.67%) measurements were sexually dimorphic, condylo-incisor length (CIL), zygomatic breadth (ZB), width across the outer surfaces of the upper canine teeth (WOUC), and moment arm of the temporal (MAOT), length of the upper first molar (LUM1) with females being 2.28 to 4.79% larger than males, and one (8.3%) measurement, width of the articular surface (WAS) was significantly different between different tooth wear classes (Table 5.24). A post-hoc Tukey test identified two overlapping subsets of tooth wear classes B, A and D, and tooth wear classes A, D and C, that separated tooth wear classes B and C. The relative difference between tooth wear classes B and C was 10.93%. The mean figures for the tooth wear classes showed a progression in size of width of the articular surface (WAS) from tooth wear class B, through tooth wear classes D and A, to tooth wear class C. This pattern of variation in size of width of the articular surface (WAS) is contrary to the assumed pattern of increasing size with age. Width of the articular surface (WAS) was smaller in four of ten specimens of tooth wear class B than the smallest of six specimens of tooth wear class A. No measurements showed a significant interaction between sex and tooth wear class in the two-way analysis. A two-way MANOVA found no significant variation between sexes (Wilks = 0.453, $F_{(12,17)} = 1.709$, $P = 0.152$) and tooth wear classes (Wilks = 0.199, $F_{(36,50.956)} = 1.030$, $P = 0.455$), and there was also no significant interaction between sex and tooth wear class (Wilks = 0.255, $F_{(36,50.956)} = 0.832$, $P = 0.716$).

The phenogram (Fig. 5.39) identified two clusters of six specimens as outliers to the bulk of the specimens analysed, that were composed mostly of males of mixed tooth wear classes (TW A, TW B, TW C) from four localities (Pafuri Fig Tree Camp, # 8; Tambotieskloof, # 16; Sheila No. 10, # 18; Farm Platbos # 19). The remainder of the specimens clustered into three major clusters, one of which was comprised almost entirely of females of mixed tooth wear classes and localities, otherwise, there was little evidence of clustering in relation to sex, tooth wear class or locality. In the PCA (Fig. 5.39), although males and females largely overlapped on the first principal component axis which explained 34.70% of the variation, males were smaller and females were larger. On the first principal component axis width across the outer surfaces of the upper canine teeth (WOUC), and width of the upper fourth premolar tooth (WUPM4) loaded highest and lowest, respectively. On the second principal component axis which explained 15.12% of the variation, tooth wear classes C and B separated within females, but not within males. There was no clear separation within either sex of specimens in relation to locality. On the second principal component axis, least inter-orbital width (LIW) and width of the fourth upper premolar (WUPM4) loaded highest and lowest, respectively. None of these measurements were significant in the one-way or two-way ANOVA tests of sexual dimorphism and variation between tooth wear classes.

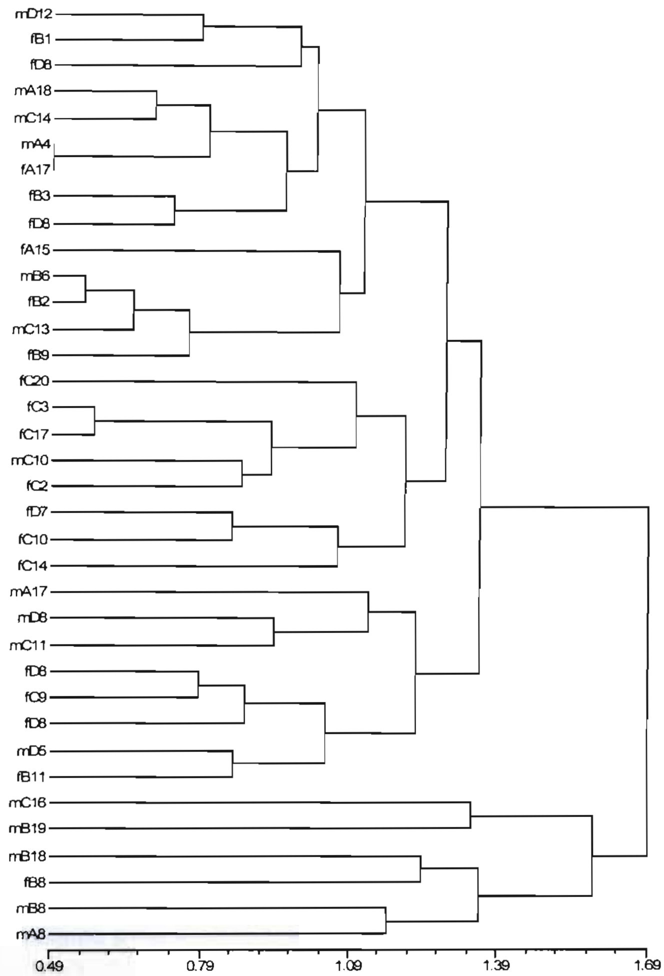
A two-group DFA of the sexes produced an 83.33% *a posteriori* correct assignment of specimens to the different sexes [females (n = 20) - 80%, males (n = 16) - 87.5%]. A four-group DFA of the tooth wear classes produced a 69.44% *a posteriori* correct assignment of specimens to the different sexes and tooth wear classes [tooth wear A (n = 6) 66.67%, tooth wear B (n = 10) - 60%, tooth wear C (n = 12) - 66.67%; tooth wear D (n = 8) - 87.5%]. A plot of the first two discriminant function axes of the four-group DFA (Fig. 5.40) showed no separation between the tooth wear classes.

5.3.1.16.2 External measurements

The univariate analyses were based on 16 specimens from 14 different localities in the Limpopo Province (Fig. 5.4), all occurring in the Savanna biome. To accommodate for missing data, the multivariate analyses were based on six measurements from 14 specimens from 13 localities. Only variation in external measurements between sexes was assessed as there were too few specimens to also assess variation between tooth wear classes. The summary statistics and results of the normality tests for sexes are given in Appendix 5.7 K. No measurements were significantly sexually dimorphic in the one-way ANOVAs (Table 5.25). The one-way MANOVA of 14 specimens and six measurements (HF, TIB, FA, TMETA, TRL, TRB) showed no significant differences between the different sexes (Wilks = 0.343, $F_{(6:7)} = 2.237$, P = 0.158).

The phenogram (Fig. 5.41) showed distinct clustering of sexes but not of localities. The PCA (Fig. 5.41) identified a single female from Anthrax Camp at Pafuri (TM37863) as an outlier to the rest of the specimens on the second principal component axis which explained 30.67% of the variation. The remainder of the specimens separated into three groups, two of which separated on the first principal component which identified 42.37% of the variation. On the first principal

A)



Cophenetic correlation coefficient = 0.691.

B)

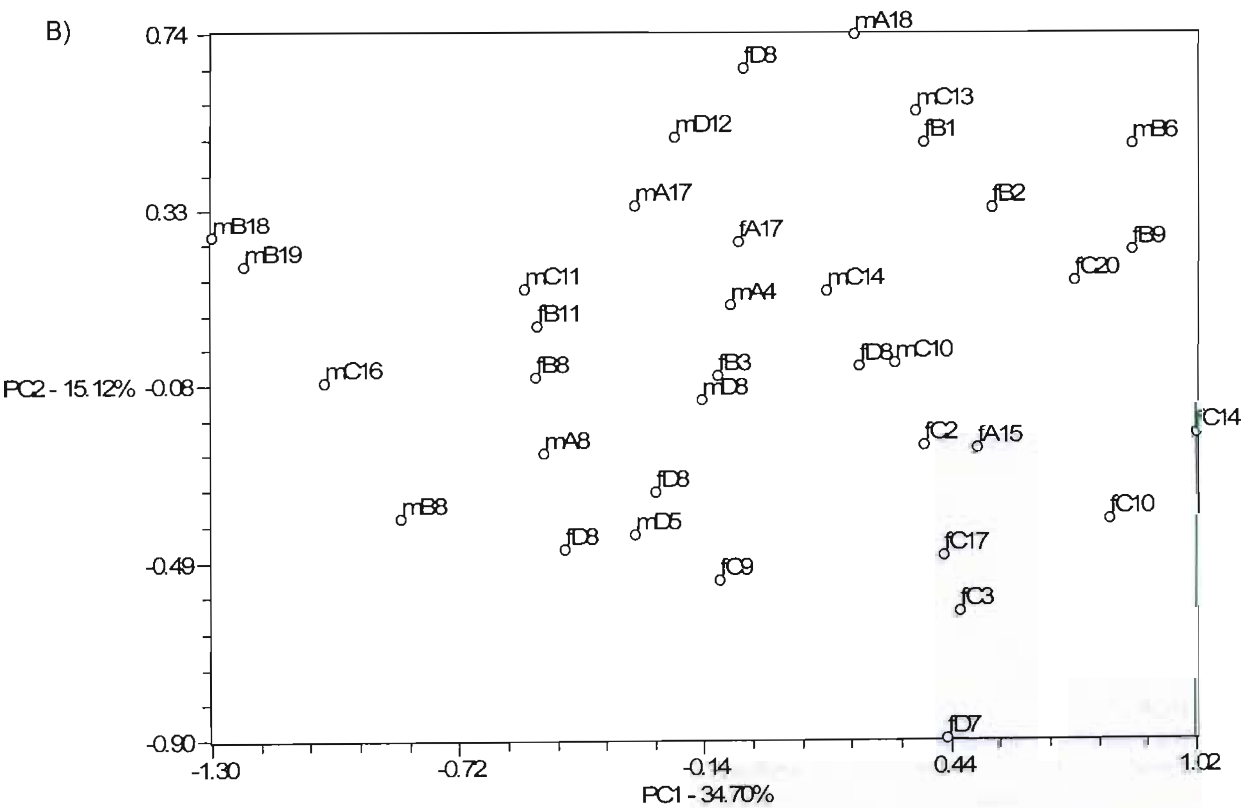


Figure 5.39 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of the first two principal components of 12 cranial measurements of *Neoromicia zuluensis* from 19 localities in the Mpumalanga and Limpopo Provinces in South Africa. The sex (male = m, female = f), tooth wear class (A, B, C, or D), and locality code (1-11, see Appendix 5.1 for locality data) of individuals are indicated.

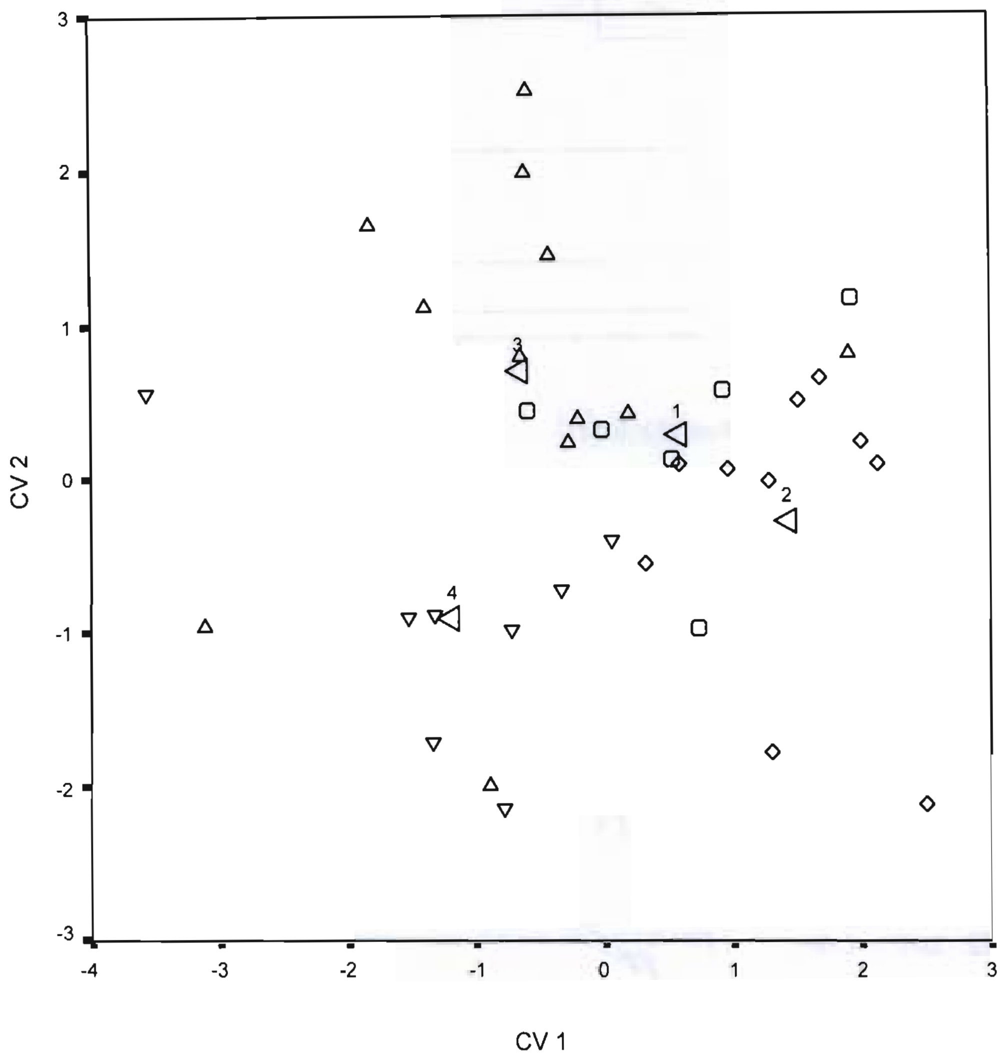
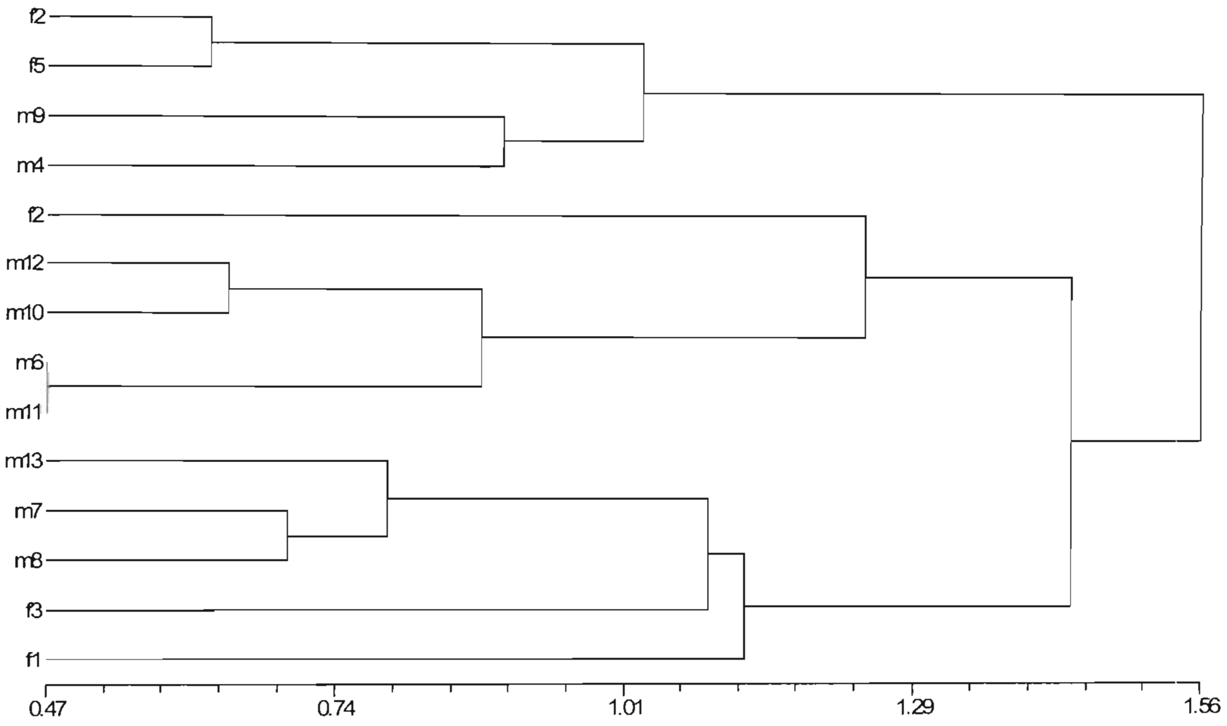


Figure 5.40 Plot of the first two discriminant functions of cranial measurements of four different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C; 4 and ▽ = tooth wear class D) of *Neoromicia zuluensis* from Limpopo and Mpumalanga Provinces in South Africa.

A)



Cophenetic correlation coefficient = 0.687.

B)

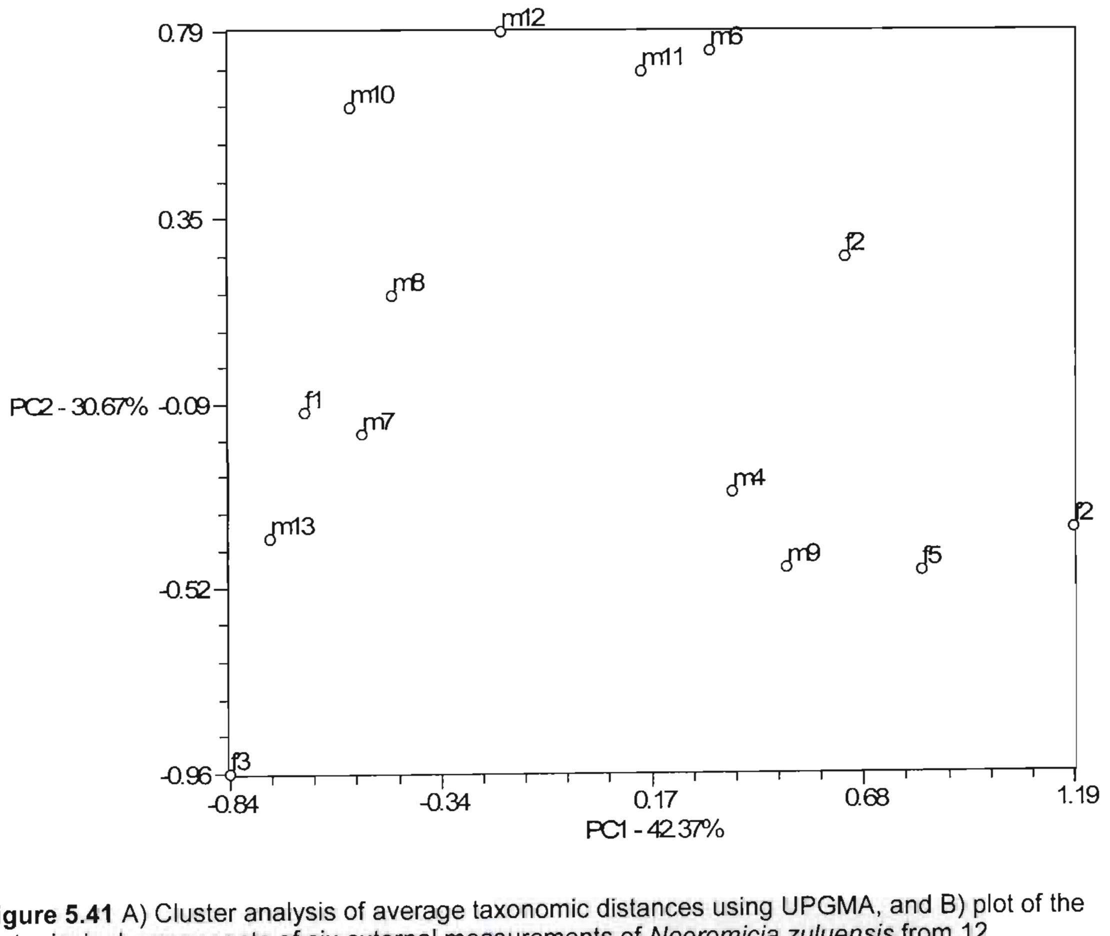


Figure 5.41 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of the first principal components of six external measurements of *Neoromicia zuluensis* from 12 localities in Mpumalanga and Limpopo Provinces in South Africa. The sex (male = m, female = f) and locality code (1-12, see Appendix 5.1 for locality data) of individuals are indicated.

Table 5.24 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in cranial measurements of *Neoromicia zuluensis* from 19 localities in Mpumalanga and Limpopo Provinces of South Africa, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, *P* = significance of *F* values. * and ** denote significance at *P* < 0.05 and *P* < 0.01 respectively. SS = sum of squares.

Levene's		**CIL**	**BH**	**ZB**	**BB**	**LIW**	**WFM**	**WAS**	**WOUC**	**WIUM1**	**WUPM4**	**LUM1**	**MAOT**
2-way	*F*	1.615	2.318	0.848	2.135	1.148	1.271	0.773	1.674	0.980	2.069	1.530	2.390
	df	7,28	7,28	7,28	7,28	7,28	7,28	7,28	7,28	7,28	7,28	7,28	7,28
	P	0.172	0.054	0.558	0.073	0.363	0.300	0.615	0.156	0.465	0.081	0.198	0.048 *
2-way ANOVA													
Sex	SS	0.621	0.000	0.216	0.005	0.002	4.76E-05	0.015	0.135	0.021	0.005	0.026	0.126
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	8.041	0.027	5.881	0.154	0.145	0.001	1.628	4.747	1.480	1.022	4.485	9.954
	P	0.008 **	0.871	0.022*	0.698	0.706	0.970	0.213	0.038 *	0.234	0.321	0.043*	0.004 **
	%	2.28	-	2.89	-	-	-	-	3.53	-	-	3.94	4.79
TW	SS	0.130	0.001	0.177	0.038	0.025	0.070	0.121	0.120	0.004	0.012	0.026	0.066
	df	3	3	3	3	3	3	3	3	3	3	3	3
	F	0.562	0.014	1.603	0.410	0.674	0.701	4.515	1.404	0.095	0.800	1.536	1.734
	P	0.644	0.998	0.211	0.747	0.575	0.560	0.011 *	0.262	0.962	0.505	0.227	0.183
	%	-	-	-	-	-	-	10.93	-	-	-	-	-
2-way Sex×TW	SS	0.007	0.048	0.051	0.148	0.041	0.039	0.016	0.027	0.017	0.010	0.016	0.016
	df	3	3	3	3	3	3	3	3	3	3	3	3
	F	0.028	1.160	0.461	1.599	1.108	0.393	0.586	0.314	0.405	0.662	0.925	0.412
	P	0.993	0.342	0.712	0.212	0.363	0.759	0.630	0.815	0.750	0.582	0.442	0.746

Table 5.25 Results of Levene's homogeneity and one-way ANOVA tests of sexual dimorphism (Sex) in external measurements of *Neoromicia zuluensis* from 11 localities in Mpumalanga and Limpopo Provinces of South Africa. *n* = sample size, df = degrees of freedom, *P* = significance of *F* values. * and ** denote significance at P < 0.05 and P < 0.01, respectively. SS = sum of squares.

Levene's		**TOT**	**T**	**TL**	**HFL**	**HF**	**FAL**	**FA**	**E**	**TIB**	**TMETA**	**TRL**	**TRB**
Sex	*F*	0.571	1.542	1.252	16.000	2.68E-04	0.046	11.013	16.000	6.9110.104	0.131	0.489	0.551
	df	1,4	1,4	1,5	1,4	1,14	1,3	1,14	1,4	1,14	1,14	1,13	1,14
	P	0.492	0.282	0.314	0.016 *	0.987	0.844	0.005 **	0.016 *	0.020 *	0.723	0.497	0.470
ANOVA													
Sex	*n*	3:3	3:3	4:3	3:3	6:10	3:2	6:10	3:3	6:10	6:10	6:9	6:10
	SS	1.500	4.167	21.341	2.667	1.838E-02	2.133	0.361	0.375	20.399	0.505	0.404	1.042E-03
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	0.273	0.357	5.278	4.000	0.167	3.840	0.289	1.000	2.678	0.326	1.773	0.059
	P	0.629	0.582	0.070	0.116	0.689	0.145	0.599	0.374	0.124	0.577	0.206	0.812

component axis, hind foot (HF) and forearm (FA) lengths loaded highest and lowest, respectively. The groups which separated along the first principal component axis were of mixed sex. However, in the group of larger individuals on the first principal component axis, females were larger than males along the first principal component axis. The third group, a male-only group, separated on the second principal component axis. On the second principal component axis, third metacarpal (TMETA) and tragus (TRL) lengths loaded highest and lowest, respectively. The different groups did not separate the localities according to their arrangement either latitudinally or longitudinally.

There were too few specimens for a DFA of the different tooth wear classes. However, a two-group DFA of the sexes produced an 92.86% *a posteriori* correct assignment of specimens to the different sexes [females (n = 5) - 100%, males (n = 9) - 88.89%].

5.3.1.17 *Pipistrellus hesperidus*

5.3.1.17.1 Cranial measurements

These analyses were based on 43 specimens from 20 different localities in KwaZulu-Natal Province of South Africa (Fig. 5.1). With the exception of one locality (Ngome Forest) which occurred in the grassland biome, the other localities occurred in the Savanna biome. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendices 6 N1 – N3. In a two-way ANOVA (Table 5.26), two (16.7%) measurements showed sexual dimorphism: condylo-incisor length (CIL) and width of the upper fourth premolar (WUPM4), with females being 2.17 and 7.10% larger than males. No measurements were significantly different between different tooth wear classes, and one (8.3%) measurement, width of the articular surface (WAS) showed a significant interaction between sexes and tooth wear classes. A two-way MANOVA showed no significant sexual dimorphism (Wilks = 0.645, $F_{(12,26)}$ = 1.194, P = 0.337), variation between tooth wear classes (Wilks = 0.650, $F_{(24,52)}$ = 0.522, P = 0.958), or interaction between sex and tooth wear class (Wilks = 0.398, $F_{(24,52)}$ = 1.267, P = 0.234).

The phenogram (Fig. 5.42) identified a female (DM6893) of tooth wear class B from Glenmore as an outlier. The remaining specimens cluster separated into two major clusters which showed some clustering of specimens in relation to sex and locality, but no apparent clustering in relation to tooth wear class. The most obvious groupings of specimens in relation to sex and locality was that 80% of male and female specimens from Dlinza Forest (# 7) largely clustered together in two clusters (40% each) that, with the exception of one female clustering with the male specimens, separated the sexes. All three specimens from Ndumu Game Reserve (# 1) clustered together with 50% of the specimens from Kosi Lake (# 2) and Ngome Forest Reserve (# 3), in a cluster with mixed sexes and three different tooth wear classes (TW A, TW B, TWC). This last cluster included all the most north-easterly occurring localities in the analysis.

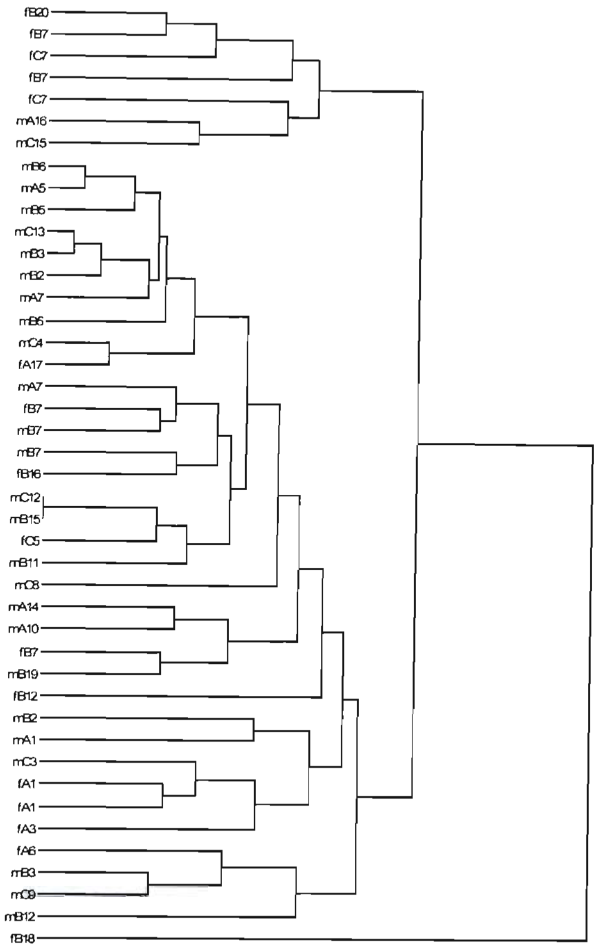
In the PCA (Fig. 5.42), although males and females largely overlapped, males were smaller and females larger on the first principal component axis, which explained 35.61% of the variation. On the first principal component axis, condylo-incisor length (CIL) and width across the outer surfaces of the upper canines (WOUC) loaded highest, and brain case height (BH) loaded least. Within each sex, most tooth wear classes overlapped, with the exception of tooth wear classes A and C within females, which separated on the second principal component axis. There was no apparent separation within the PCA of specimens in relation to different localities. The second principal component axis explained 13.89% of the variation, and width of the upper fourth premolar (WUPM4) and width of the foramen magnum (WFM) loaded highest and lowest, respectively on the second principal component axis. Condylo-incisor length (CIL) and width of the upper fourth premolar (WUPM4) were also significantly sexually dimorphic in the two-way ANOVA tests.

A two-group DFA of the sexes produced an 81.4% *a posteriori* correct assignment of specimens to the different sexes [females (n = 16) - 93.75%, males (n = 27) - 74.07%]. A three-group DFA of the tooth wear classes produced a 55.81% *a posteriori* correct assignment of specimens to the different tooth wear classes [tooth wear A (n = 12) - 58.33%, tooth wear B (n = 21) - 47.62%, tooth wear C (n = 10) - 70%]. A plot of the first two discriminant function axes of the three-group DFA (Fig. 5.43) shows no separation between the tooth wear classes. Four specimens, however, plotted as outliers to the rest of the specimens on the second discriminant function axis: two males of tooth wear class B (DM7143, TM40014), a female of tooth wear class B (DM6893), and a female of tooth wear class A (TM35207).

5.3.1.17.2 External measurements

The univariate analyses were based on 33 specimens from 18 different localities (Fig. 5.4).

A)



Cophenetic correlation coefficient = 0.747.

B)

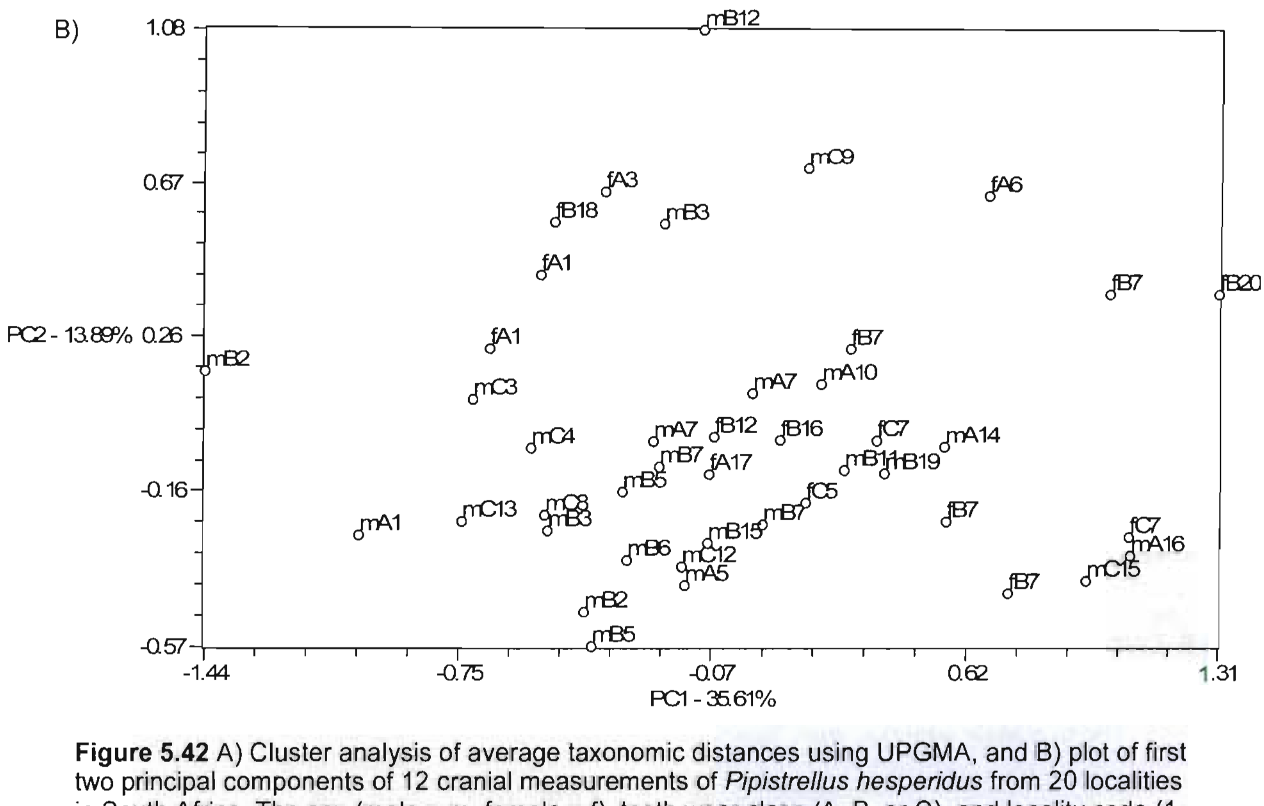


Figure 5.42 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of first two principal components of 12 cranial measurements of *Pipistrellus hesperidus* from 20 localities in South Africa. The sex (male = m, female = f), tooth wear class (A, B, or C), and locality code (1-20, see Appendix 5.1 for locality data) of individuals are indicated.

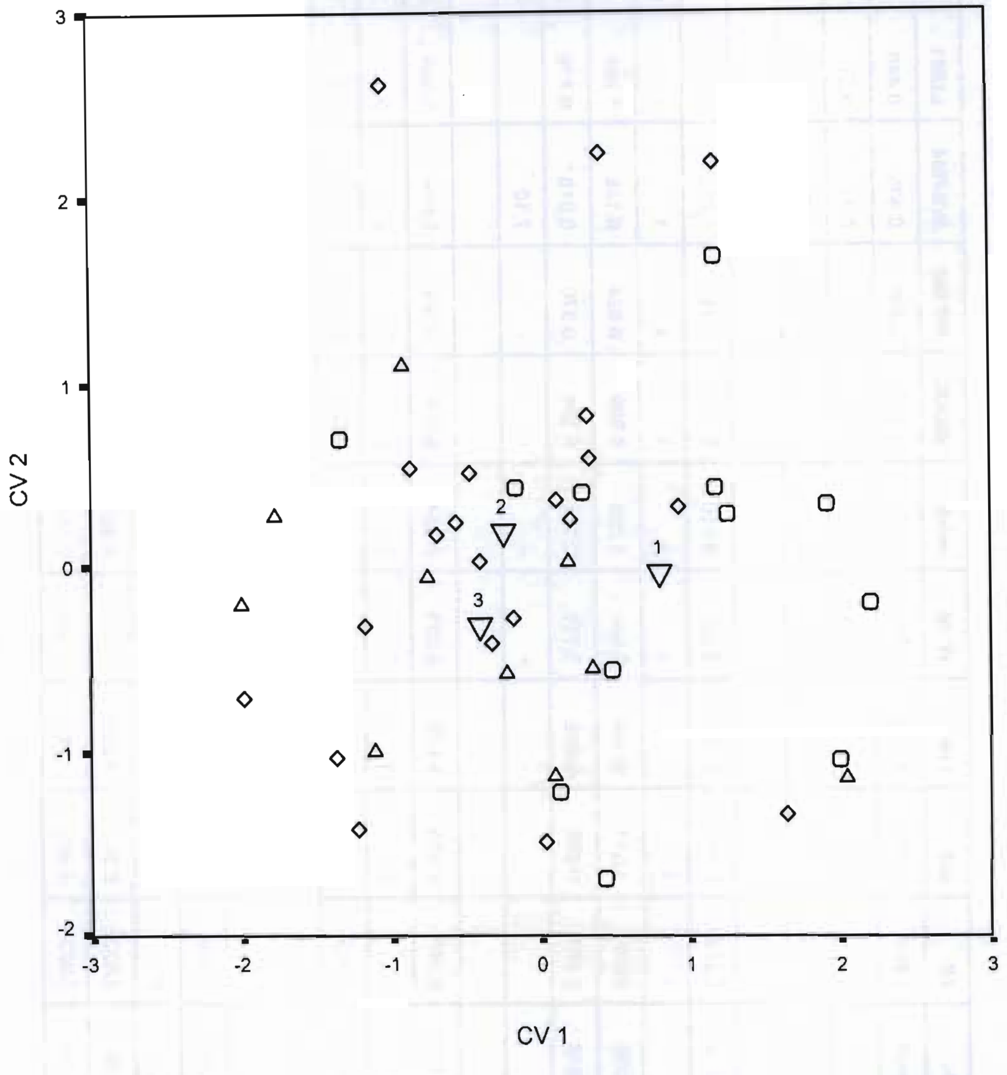


Figure 5.43 Plot of the first two discriminant functions of cranial measurements of three different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C) of *Pipistrellus hesperidus* from KwaZulu-Natal in South Africa.

Table 5.26 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in cranial measurements of *Pipistrellus hesperidus* from 20 localities in the KwaZulu-Natal Province of South Africa, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, P = significance of F values. * and ** denote significance at $P < 0.05$ and $P < 0.01$ respectively. SS = sum of squares.

Levene's		**CIL**	**BH**	**ZB**	**BB**	**LIW**	**WFM**	**WAS**	**WOUC**	**WIUM1**	**WUPM4**	**LUM1**	**MAOT**
2-way	*F*	1.429	2.686	0.659	0.991	1.028	0.585	3.463	1.828	0.240	0.635	0.446	1.973
	df	5,37	5,37	5,37	5,37	5,37	5,37	5,37	5,37	5,37	5,37	5,37	5,37
	P	0.237	0.036 *	0.656	0.436	0.416	0.711	0.011 *	0.131	0.942	0.674	0.813	0.106
2-way ANOVA													
Sex	SS	0.583	0.024	0.079	0.041	0.003	0.002	0.019	0.017	0.012	0.032	0.011	0.056
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	6.861	0.253	2.048	1.517	0.194	0.087	1.038	0.809	0.824	6.138	3.258	3.864
	P	0.013 *	0.618	0.161	0.226	0.662	0.770	0.315	0.374	0.370	0.018 *	0.079	0.057
	%	2.17	-	-	-	-	-	-	-	-	7.10	-	-
TW	SS	0.090	0.122	0.145	0.015	0.002	0.013	0.024	0.026	0.002	0.014	0.003	0.005
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	0.529	0.649	1.881	0.270	0.056	0.321	0.675	0.627	0.057	1.361	0.478	0.178
	P	0.593	0.528	0.167	0.765	0.946	0.728	0.515	0.540	0.944	0.269	0.624	0.837
Sex×TW	SS	0.492	0.216	0.218	0.012	0.008	0.071	0.165	0.122	0.037	0.020	0.004	0.043
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	2.896	1.150	2.832	0.212	0.239	1.757	4.587	2.946	1.266	1.888	0.638	1.508
	P	0.068	0.328	0.072	0.810	0.788	0.187	0.017 *	0.065	0.294	0.166	0.534	0.235

With the exception of one locality (Ngome Forest) which occurred in the grassland biome, the other localities occurred in the Savanna biome. Accounting for missing data, multivariate analyses were based on nine measurements from 23 specimens originating from 10 different localities. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendices 5.7 L1 – L4. Four (44.44%) measurements, tail (T), ear (E), tibia length (TIB) and tragus breadth (TRB) were significantly sexually dimorphic in the two-way ANOVA, with females being 0.96 to 7.92% larger than males (Table 5.27). Two (22.22%) measurements were significantly different between tooth wear classes: tragus breadth (TRB), and third metacarpal length (TMETA). Post-hoc Tukey tests identified two overlapping subsets in the significantly different tooth wear classes of length of the third metatarsal (TMETA), of tooth wear classes A and B and tooth wear classes B and C, which separated tooth wear classes A and C. The relative difference between tooth wear classes A and C was 4.31%. Whereas, no subsets of different tooth wear classes were identified by post-hoc Tukey tests within tragus breadth (TRB), although mean measurements of each tooth wear class indicated that as in the post-hoc test of the two-way ANOVA, tragus breadth (TRB) of tooth wear class A was larger than in either tooth wear class B or C. The relative difference between tooth wear classes A and B was 5.80%. A two-way MANOVA showed significant sexual dimorphism (Wilks = 0.193, $F_{(9,9)} = 4.193$, $P = 0.022$) and significant interaction between sex and tooth wear class (Wilks = 0.069, $F_{(18,18)} = 2.804$, $P = 0.017$), but not a significant difference between the tooth wear classes (Wilks = 0.130, $F_{(18,18)} = 1.768$, $P = 0.118$).

The phenogram (Fig. 5.44) identified three major clusters, one of which was a single male (DM1063) of tooth wear class A from St Lucia (# 2), whereas the other two clusters were predominantly of the sexes. Within each of the clusters of predominantly males or females, there was an indication of some clustering in relation to tooth wear class and locality. In a pattern similar to that in the phenogram based on cranial measurements of *P. hesperidus* (Fig. 5.42), specimens from Dlinza Forest (# 3) clustered together in clusters that clustered specimens of same tooth wear classes, and both female specimens of tooth wear class A from Ndumu Game Reserve (# 1) clustered together.

Although the PCA (Fig. 5.44) showed considerable overlaps of males and females, males were smaller and females larger on the first principal component axis, which comprised 39.83% of the variation. On the first principal component axis, tail (T) and tragus (TRL) lengths loaded highest and lowest, respectively. Within males, there was an overlap of the different tooth wear classes, whereas in females, probably due to there being only two specimens of tooth wear class A and two specimens of tooth wear class C, these tooth wear classes separated from each other on the first principal component axis, and from specimens of tooth wear class B on the second principal component axis which explained 17.14% of the variation. On the second principal component axis total (TOT) and hind foot (HFL) lengths loaded highest, and tibia breadth (TIB) loaded least. There was no obvious separation within the PCA of specimens in relation to different localities. Total (TOT) length was also significantly sexually dimorphic in the two-way ANOVA tests, and tail (T) length was also significantly sexually dimorphic in both the two-way ANOVA tests.

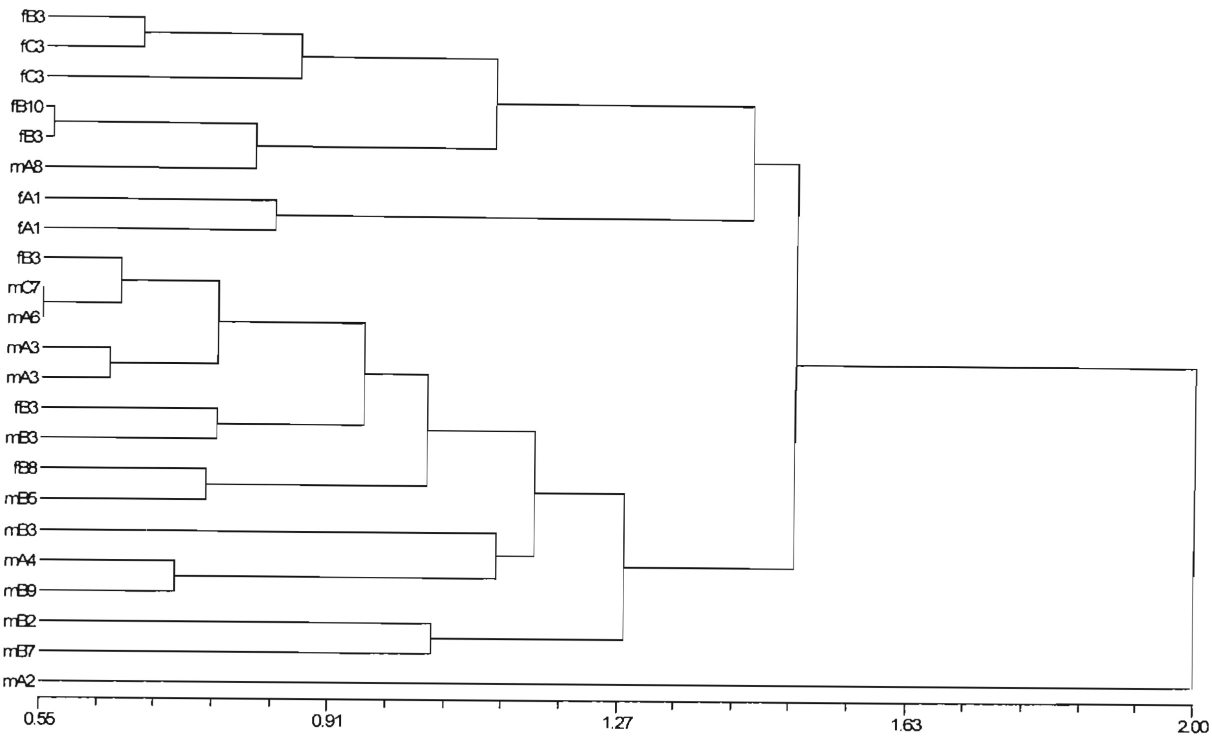
A two-group DFA of the sexes produced a 95.65% *a posteriori* correct assignments of specimens to the different sexes [females (n = 9) - 88.89%, males (n = 14) - 100%]. A three-group DFA of the tooth wear classes produced a 78.26% *a posteriori* correct assignments of specimens to the different sexes and tooth wear classes [tooth wear A (n = 8) - 75%, tooth wear B (n = 12) - 83.33%, tooth wear C (n = 3) - 66.67%]. A plot of the first two discriminant function axes of the three-group DFA (Fig. 5.45) showed the tooth wear classes did not separate. Although tooth wear class C almost separated from tooth wear classes A and B on the second discriminant function axis, there was an overlap of a male of tooth wear class C (DM5384) with specimens of tooth wear class A and B.

5.3.1.18 *Pipistrellus rusticus*

5.3.1.18.1 Cranial measurements

These analyses were based on 35 specimens from six localities in the Limpopo Province of South Africa and Zimbabwe (Fig. 5.36) all occurring in the Savanna biome. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendices 5.6 O1 - O4. Two-way ANOVA tests found one measurement, braincase height (BH), was sexually dimorphic with females being 1.60% larger than males, no measurements were significantly different between the tooth wear classes, but one measurement, braincase height

A)



Cophenetic correlation coefficient = 0.758.

B)

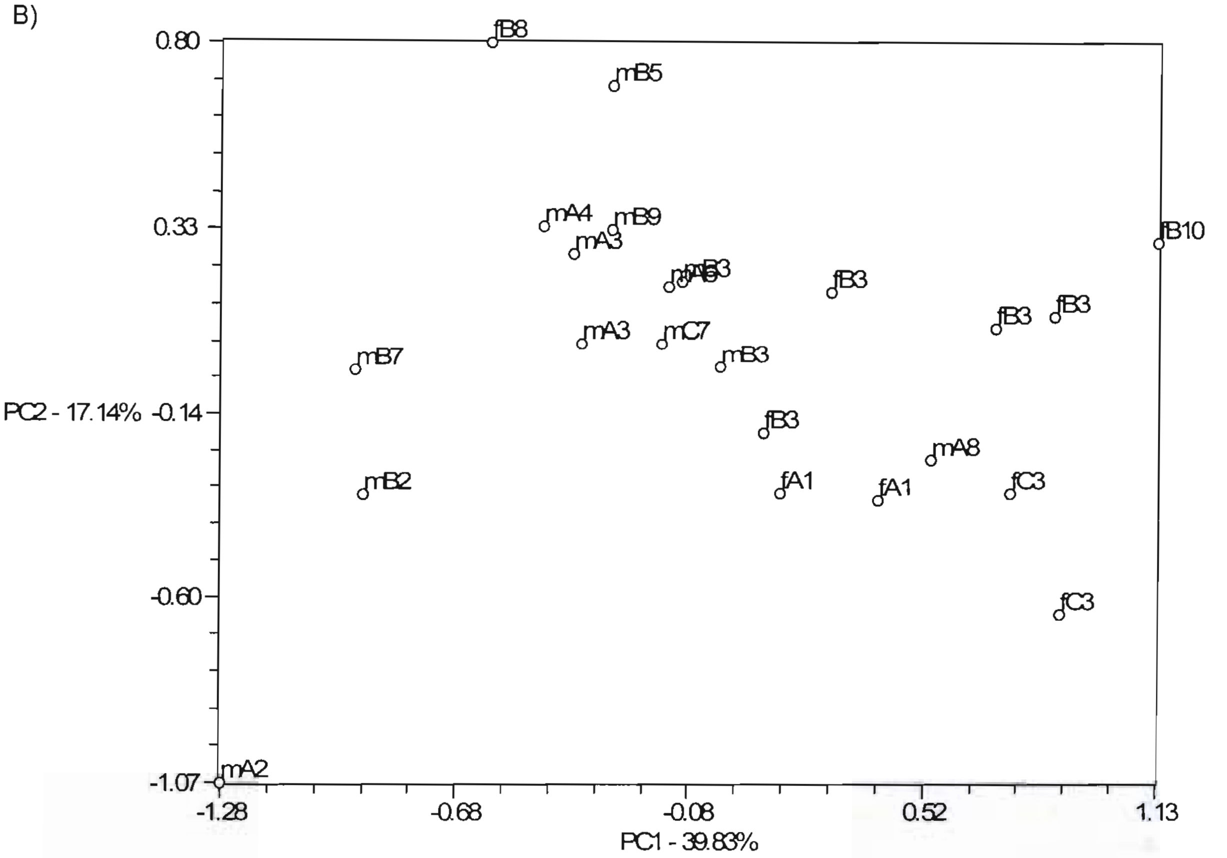


Figure 5.44 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of the first two principal components of nine external measurements of *Pipistrellus hesperidus* from 10 localities in South Africa. The sex (male = m, female = f), tooth wear class (A or B), and locality code (1, 6, 8, 10-14, 16-17; see Appendix 5.1 for locality data) of individuals are indicated.

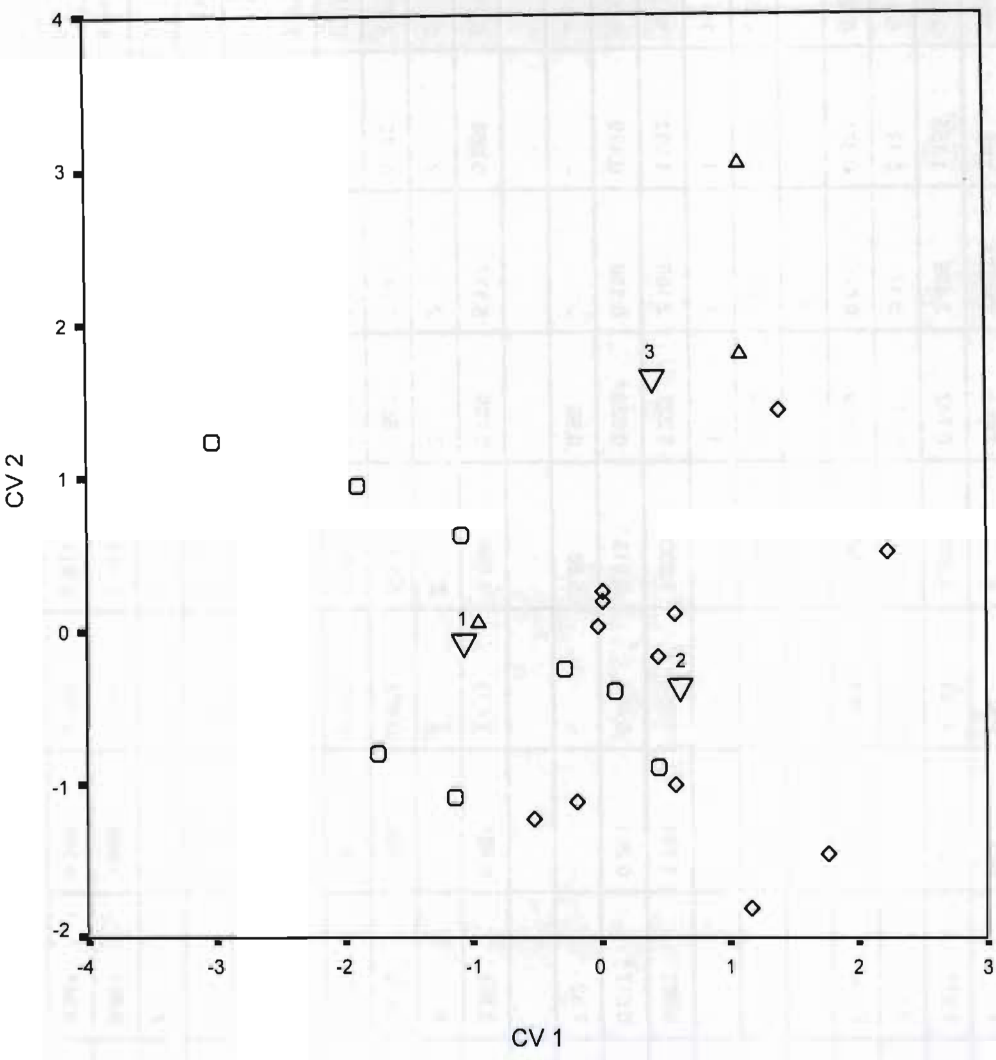


Figure 5.45 Plot of the first two discriminant functions of external measurements of three different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C) of *Pipistrellus hesperidus* from KwaZulu-Natal in South Africa.

Table 5.27 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in external measurements of *Pipistrellus hesperidus* from 17 localities in the KwaZulu-Natal and Eastern Cape Provinces of South Africa, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, P = significance of F values. * and ** denote significance at $P < 0.05$ and $P < 0.01$ respectively. SS = sum of squares.

Levene's		TOT	T	HFL	FAL	E	TIB	TMETA	TRL	TRB
2-way	*F*	0.983	1.977	2.230	1.161	1.468	0.747	2.459	1.155	2.555
	df	5,17	5,17	5,17	5,17	5,17	5,17	5,17	5,17	5,17
	P	0.456	0.134	0.099	0.368	0.252	0.599	0.075	0.371	0.067
ANOVA										
Sex	SS	24.544	36.100	0.544	0.462	2.844	2.560	1.487	0.376	0.237
	df	1	1	1	1	1	1	1	1	1
	F	1.500	6.961	1.354	0.560	7.635	6.227	2.168	1.962	10.339
	P	0.237	0.017 *	0.261	0.464	0.013 *	0.023 *	0.159	0.179	0.005 **
	%	-	7.92	-	-	5.88	0.96	-	-	4.31
TW	SS	30.831	6.952	0.487	1.436	0.559	0.709	5.137	0.066	0.219
	df	2	2	2	2	2	2	2	2	2
	F	0.942	0.670	0.605	0.871	0.750	0.862	3.744	0.172	4.773
	P	0.409	0.525	0.557	0.437	0.487	0.440	0.045 *	0.843	0.023 *
	%	-	-	-	-	-	-	4.31	-	5.80
Sex×TW	SS	17.476	0.629	0.809	1.832	0.140	1.950	7.596	0.232	0.190
	df	2	2	2	2	2	2	2	2	2
	F	0.534	0.061	1.006	1.111	0.188	2.371	5.537	0.605	4.145
	P	0.596	0.941	0.386	0.352	0.831	0.123	0.014 *	0.558	0.034 *

(BH), showed a significant interaction between sex and tooth wear class (Table 5.28). A two-way MANOVA test showed no significant sexual dimorphism (Wilks = 0.679, $F_{(12,18)}$ = 0.709, P = 0.725), variation between tooth wear classes (Wilks = 0.318, $F_{(24,36)}$ = 1.162, P = 0.335), or interaction between sex and tooth wear class (Wilks = 0.312, $F_{(24,36)}$ = 1.186, P = 0.315).

The phenogram (Fig. 5.46) identified that although there was considerable mixing of sexes, tooth wear classes and localities in many sub-clusters, there was some clustering in relation to sex or tooth wear class and locality. The most obvious of these being the cluster of mixed sexes and tooth wear classes of specimens largely from Farm Klipfontein (# 2). There was also a cluster of mostly females, of tooth wear class B, from Messina Nature Reserve (# 1), another cluster of three females only of mixed tooth wear classes and localities, and a cluster of two males of tooth wear class B from Messina Nature Reserve (# 1).

Although the PCA (Fig. 5.46) showed considerable overlap of the different sexes, tooth wear classes and localities, on the first principal component axis which explained 40.13 % of the variation, males were smaller and females were larger, and specimens from Messina Nature Reserve (# 1) were generally smaller than specimens from Klipfontein Farm in the Waterberg area (# 2). On the first principal component axis width between the inner surfaces of the upper first molars (WIUM1) and width across the outer surfaces of the upper canines (WOUC) loaded highest, and width of the articular surface (WAS) loaded least. On the second principal component analysis which explained 12.60% of the variation, females of tooth wear class C were generally larger than specimens of tooth wear class B. On the second principal component axis, width of the upper fourth premolar (WUPM4) and zygomatic breadth (ZB) loaded highest and lowest, respectively. Width across the outer surfaces of the upper canines (WOUC) was also significantly sexually dimorphic in the two-way ANOVA tests, and width of the upper fourth premolar (WUPM4) was also significantly different between tooth wear classes in the two-way ANOVA tests.

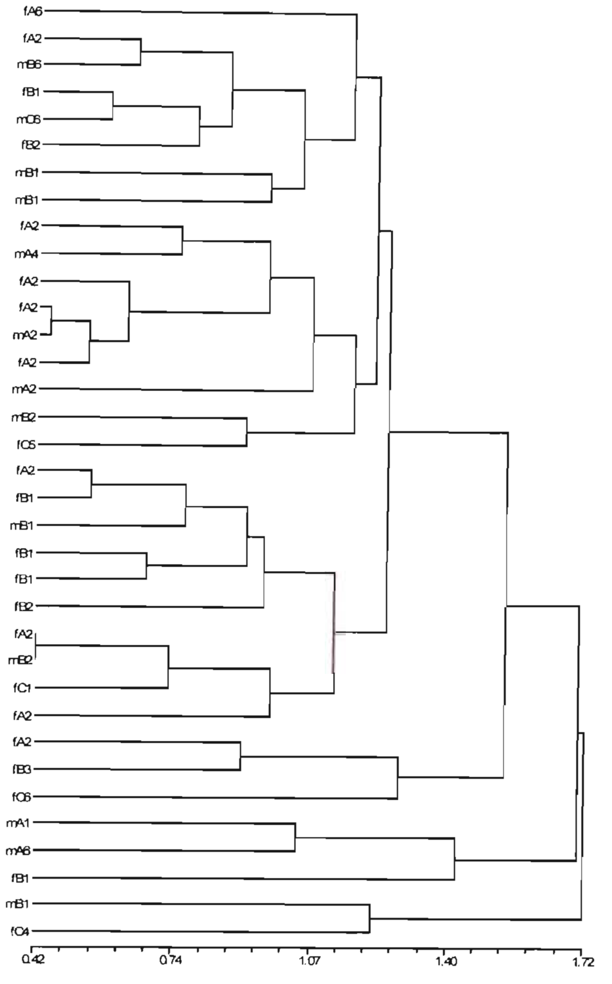
A two-group DFA of the sexes produced a 74.29% *a posteriori* correct assignments of specimens to the different sexes [females (n = 22) - 77.27%, males (n = 13) - 69.23%]. A three-group DFA of the tooth wear classes produced a 77.14% *a posteriori* correct assignments of specimens to the different sexes and tooth wear classes [tooth wear A (n = 15) - 80%, tooth wear B (n = 15) - 80%, tooth wear C (n = 5) - 60%]. A plot of the first two discriminant function axes of the three-group DFA (Fig. 5.47) shows no separation between the tooth wear classes. However, three specimens of tooth wear class B plotted as outliers on the second discriminant function axis: two females (DM5407 and TM40291) and one male (DM5391).

5.3.1.18.2 External measurements

The univariate analyses were based on 24 specimens from three different localities (Fig. 5.7), all occurring in the Savanna biome. Accounting for missing data, the multivariate analyses were based on nine measurements from 16 specimens from two localities. The summary statistics and results of the normality tests for sexes and tooth wear classes are given in Appendices 5.7 M1 – M2. No measurements were significantly sexually dimorphic in the one-way ANOVAs. However, four (33.3%) measurements, hind foot (HFL), both forearm (FAL, FA), and tibia (TIB) lengths were significantly different between the different tooth wear classes (Table 5.29). These significant differences may have resulted from the bias between the number of specimens in each of the different tooth wear classes (tooth wear class A - n = 2-7; tooth wear class B - n = 10-11; tooth wear class C - n = 2).

A post-hoc Tukey test identified two overlapping subsets between the significantly different tooth wear classes of forearm length (FAL), of tooth wear classes B and C and tooth wear classes C and A, separating tooth wear classes B and A. The relative difference between tooth wear classes B and A was 5.56% (Table 5.29). Tooth wear class B is smallest and tooth wear class A largest, which is contrary to the assumption of growth increasing with age. The larger mean of forearm length for tooth wear class A is due to the large forearm length (FAL) of a female (TM20655) of tooth wear class A from Rissik Private Nature Reserve, whereas the smaller mean of tooth wear class B is due to the small forearm length (FAL) of a female (DM5407) from Messina Nature Reserve. A post-hoc Tukey test of forearm length measured from the dry skins (FA) identified two separate groups separating tooth wear class B from tooth wear classes C and A. The relative difference between tooth wear classes B and A was 7.7 % (Table 5.29). This pattern of forearm length (FA) of tooth wear class B being smaller than the forearm lengths (FA) of tooth wear classes A and C is the same as that observed for the forearm lengths (FAL) taken from specimen records. The two specimens that influenced sizes of the tooth wear classes of

A)



Cophenetic correlation coefficient = 0.701.

B)

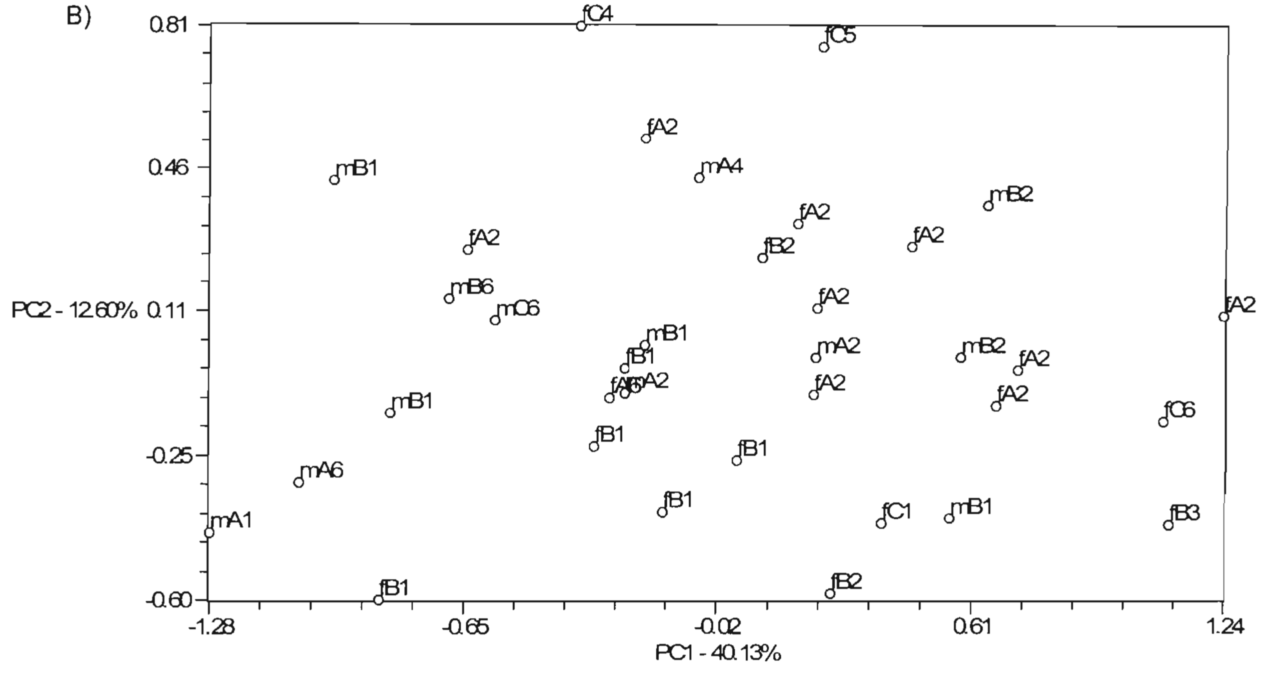


Figure 5.46 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of the first two principal components of 12 cranial measurements of *Pipistrellus rusticus* from six localities in South Africa. The sex (male = m, female = f), tooth wear class (A or B), and locality code (1-6, see Appendix 5.1 for locality data) of individuals are indicated.

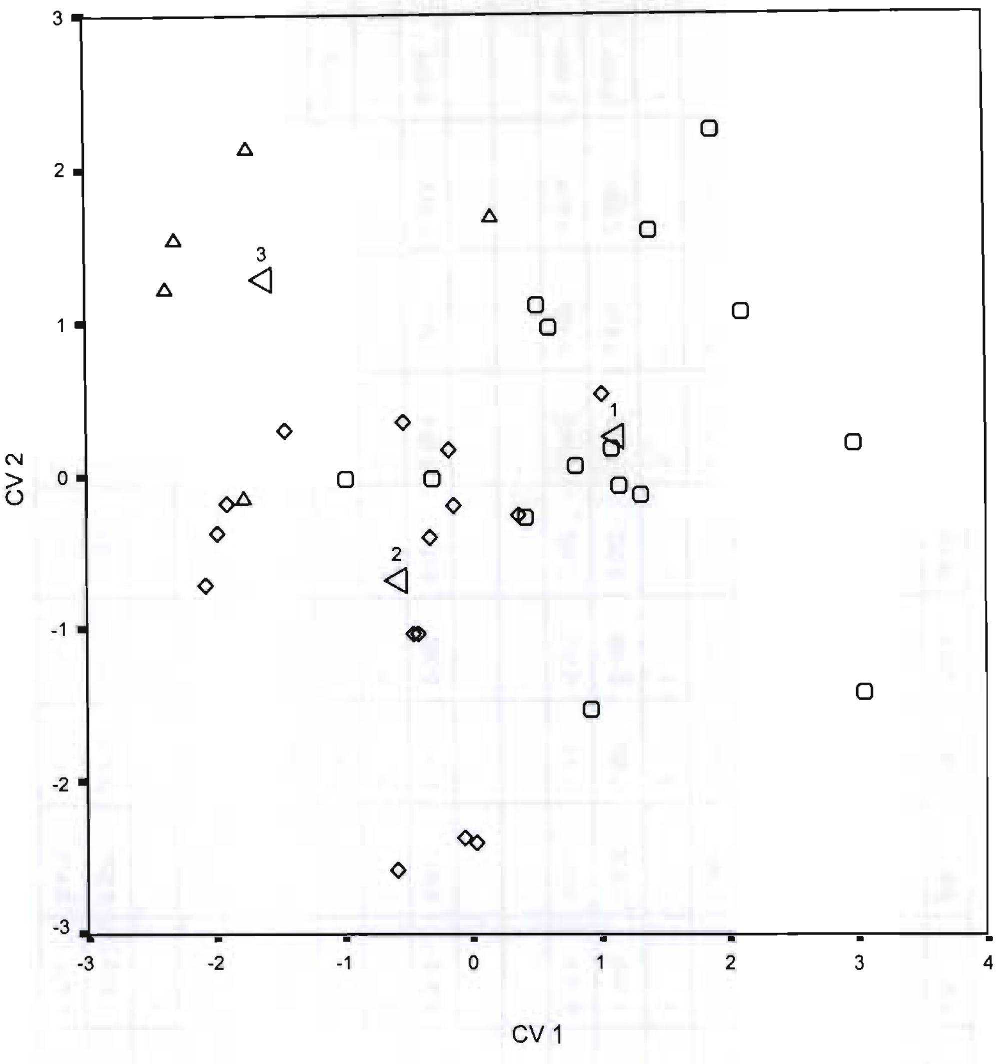


Figure 5.47 Plot of the first two discriminant functions of cranial measurements of three different tooth wear classes (1 and ○ = tooth wear class A; 2 and ◇ = tooth wear class B; 3 and △ = tooth wear class C) of *Pipistrellus rusticus* from South Africa and Zimbabwe.

Table 5.28 Results of Levene's homogeneity and two-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in cranial measurements of *Pipistrellus rusticus* from six localities in Zimbabwe and South Africa, with mean size differences for significantly different measurements expressed as a percentage (%). df = degrees of freedom, *P* = significance of *F* values. * and ** denote significance at *P* < 0.05 and *P* < 0.01 respectively. SS = sum of squares.

Levene's		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
2-way	*F*	0.756	1.034	2.839	3.473	0.973	1.663	2.997	0.384	1.392	1.207	1.609	0.606
	df	5,29	5,29	5,29	5,29	5,29	5,29	5,29	5,29	5,29	5,29	5,29	5,29
	P	0.589	0.416	0.033 *	0.014 *	0.450	0.175	0.027 *	0.856	0.256	0.331	0.189	0.696
2-way ANOVA													
Sex	SS	0.053	0.044	0.163	0.091	0.029	0.057	0.019	0.101	0.053	2.94E-04	0.005	0.028
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	0.583	4.270	1.868	3.858	1.625	2.409	0.862	3.162	2.855	0.045	2.040	0.930
	P	0.451	0.048 *	0.182	0.059	0.213	0.132	0.361	0.086	0.102	0.834	0.164	0.343
	%	-	1.60	-	-	-	-	-	-	-	-	-	-
TW	SS	0.141	0.044	0.073	0.011	0.002	0.035	0.032	0.044	0.008	0.033	0.004	0.037
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	0.775	2.119	0.421	0.235	0.046	0.746	0.718	0.694	0.203	2.494	0.698	0.614
	P	0.470	0.138	0.660	0.792	0.956	0.483	0.496	0.508	0.817	0.100	0.506	0.548
Sex×TW	SS	0.280	0.126	0.019	0.039	0.079	0.060	0.046	0.025	0.016	0.015	4.48E-04	0.011
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	1.537	6.093	0.110	0.821	2.213	1.282	1.014	0.385	0.442	1.163	0.086	0.178
	P	0.232	0.006 **	0.896	0.450	0.128	0.293	0.375	0.684	0.647	0.327	0.918	0.838

Table 5.29 Results of Levene's homogeneity and one-way ANOVA tests of sexual dimorphism (Sex) and tooth wear class variation (TW) in external measurements of *Pipistrellus rusticus* from three localities in the Limpopo Province of South Africa, with mean size differences for significantly different measurements expressed as a percentage (%). n = sample size, df = degrees of freedom, *P* = significance of *F* values. * and ** denote significance at *P* < 0.05 and *P* < 0.01 respectively. SS = sum of squares.

Levene's		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Sex	*F*	0.00E-17	0.140	0.215	5.119	3.196	0.001	0.625	6.760	0.422	5.228	0.827	0.535
	df	1,14	1,14	1,19	1,14	1,22	1,14	1,22	1,14	1,22	1,22	1,22	1,22
	P	1.000	0.714	0.648	0.040 *	0.088	0.974	0.438	0.021 *	0.523	0.032 *	0.373	0.472
TW	*F*	5.254	0.404	11.348	0.475	0.019	7.212	1.043	11.251	0.469	0.067	4.129	1.802
	df	2,11	2,11	2,15	2,11	2,17	2,11	2,17	2,11	2,17	2,17	2,17	2,17
	P	0.025 *	0.677	0.001 **	0.634	0.981	0.010 *	0.374	0.002 **	0.633	0.935	0.035 *	0.195
ANOVA													
Sex	*n*	8:8	8:8	10:11	8:8	11:12	8:8	11:13	8:8	11:13	11:13	11:13	11:13
	SS	6.250	6.250	4.710	2.250	0.338	7.562E-02	0.935	0.563	3.151	1.692	3.921E-04	1.701E-02
	df	1	1	1	1	1	1	1	1	1	1	1	1
	F	0.250	1.691	0.593	3.231	1.224	0.086	0.357	1.615	3.447	1.141	0.002	0.098
	P	0.625	0.214	0.451	0.094	0.281	0.774	0.556	0.224	0.077	0.297	0.968	0.758
TW	*n*	2:10:2:-	2:10:2:-	7:9:2:-	2:10:2:-	7:11:2:-	2:10:2:-	7:11:2:-	2:10:2:-	7:11:2:-	7:11:2:-	7:11:2:-	7:11:2:-
	SS	57.857	13.829	8.634	4.029	0.988	6.556	24.576	1.457	8.344	2.574	1.077	0.201
	df	2	2	2	2	2	2	2	2	2	2	2	2
	F	1.288	1.828	0.565	4.103	1.712	8.451	9.041	2.357	8.590	0.704	2.890	0.521
	P	0.314	0.206	0.580	0.047 *	0.210	0.006 **	0.002 **	0.141	0.003 **	0.509	0.083	0.603
	%	-	-	-	20.29	-	5.56	7.78	-	16.21	-	-	-

forearm length (FA) to be contrary to the usual assumption of increasing growth were the same as those that caused forearm lengths (FAL), taken from the specimen records, to be contrary to the usual assumptions about increasing growth with increasing age. These specimens were a female (TM20655) of tooth wear class A from Rissik Private which had a large forearm length (FA), and a female (DM5407) of tooth wear class B from Messina Nature Reserve which had a small forearm length (FA). Although, eight other specimens of tooth wear class B had forearm lengths (FA) that were smaller than the smallest forearm length (FA) in tooth wear class A. A post-hoc Tukey test of tibia length (TIB) identified two overlapping subsets of tooth wear classes B and A, and tooth wear classes A and C, which separated tooth wear classes B and C. The relative difference between tooth wear classes A and C was 16.21% (Table 5.29). Similarly, contrary to the assumption of growth increasing with age, tibia length of tooth wear class B was shorter than the tibia lengths of tooth wear class A and C, due to the small tibia lengths of two females (DM5407 and DM5866) from Messina Nature Reserve. The post-hoc Tukey test of hind foot length (HFL) found no separate subsets within the significantly different tooth wear classes. However, observations of the means for each tooth wear class indicated that contrary to the findings in the other significant measurements, hind foot length (HFL) of tooth wear class B was largest, tooth wear class C smallest, and tooth wear class A intermediate between the two. The relative difference between tooth wear classes B and C was 20.29% (Table 5.29). A one-way MANOVA of 16 specimens and nine measurements (TOT, T, HFL, FAL, E, TIB, TMETA, TRL, TRB) showed no significant difference between the different sexes (Wilks = 0.262, $F_{(6,9)}$ = 1.878, P = 0.228), whereas a one-way MANOVA of 14 specimens and the same nine measurements showed a significant difference between the different tooth wear classes (Wilks = 0.002, $F_{(6,18)}$ = 7.157, P = 0.011).

Both the phenogram and PCA showed separation of specimens due to geographic locality. The phenogram (Fig. 5.48) identified three major clusters, one of which separated the specimens from Rissik Private Nature Reserve (# 2) from the specimens from Messina Nature Reserve (# 1), which were divided into two clusters. Within the three major clusters there was no obvious separation in relation to sex or tooth wear class.

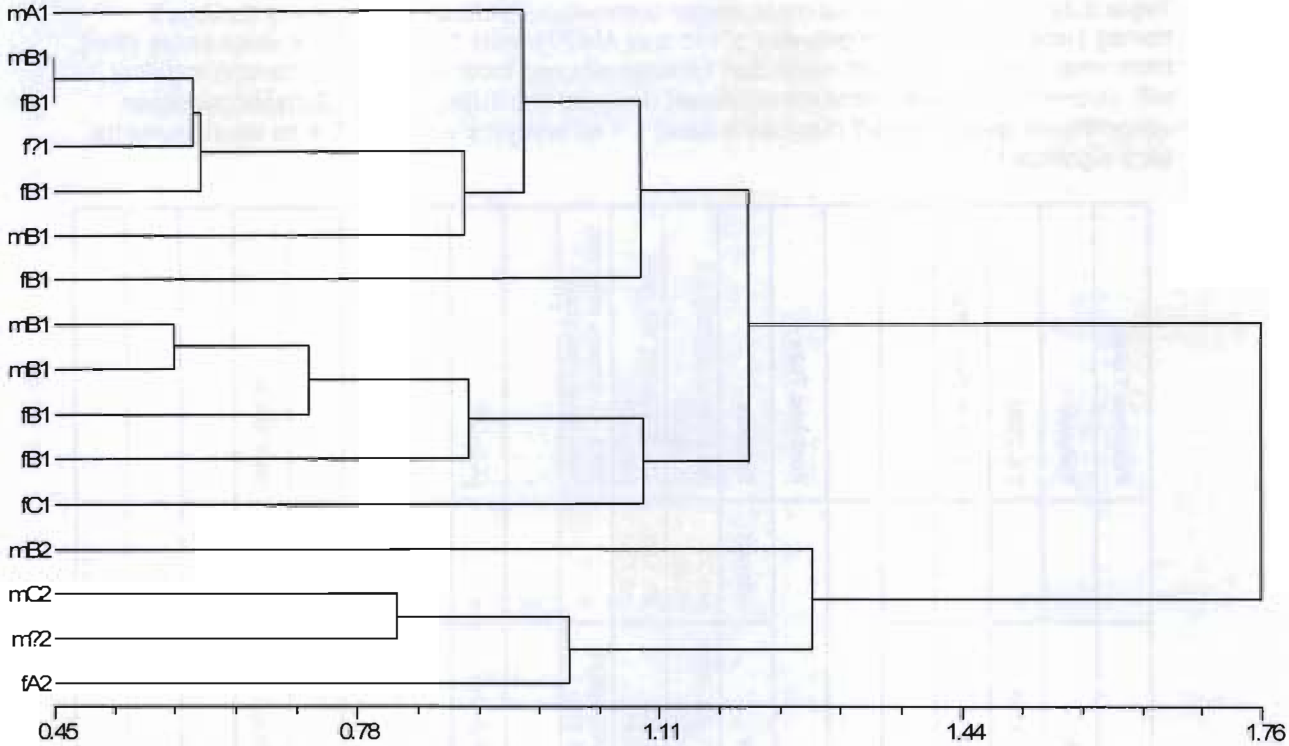
The PCA (Fig. 5.48) also separated specimens from Rissik Private Nature Reserve (# 2) and Messina Nature Reserve (# 1), with specimens from Rissik Private Nature Reserve being larger on the first principal component axis which explained 48.33% of the variation, than specimens from Messina Nature Reserve. On the first principal component axis ear (E) and tibia (TIB) lengths loaded highest, and hind foot length (HFL) loaded least. On the second principal component axis which explained 21.47% of the variation, although males and females overlapped considerably, females were larger and males were smaller. On the second principal component axis, tail length (T) and tragus breadth (TRB) loaded highest and lowest, respectively. Hind foot (HFL) and tibia (TIB) lengths also showed significant difference between tooth wear classes in the one-way ANOVA tests.

A two-group DFA of the sexes produced a 93.75% *a posteriori* correct assignment of specimens to the different sexes [females (n = 8) - 100%, males (n = 8) - 87.5%]. There were too few specimens in each tooth wear classes with sufficient measurements for a DFA of variation between the tooth wear classes, and two-way ANOVA and MANOVA analyses of external measurements.

5.3.2 Summary across species

Tables 5.30 to 5.39 summarise the results of the different analyses across and within the different species tested, and it can be collated from these tables that the degree of sexual dimorphism and tooth wear class variation in external and cranial measures of size varied both across species and within species. In addition, the different tests gave different results, while one-way and two-way ANOVA, MANOVA and DFA often showed considerable sexual dimorphism and tooth wear class variation. PCA scatterplots and UPGMA phenograms did not clearly separate the different sexes and tooth wear classes, and the results of DFA were often contradictory to the other tests. Given the variation in results between the different tests the identification of which species or group within a species showed more or less sexual dimorphism or tooth wear class variation often depended on which test was being evaluated. There were more similarities between the species in measurements showing sexual dimorphism than measurements showing significant tooth wear class variation. The cranial and external measurements commonly important between and within the different species in sexual dimorphism and tooth wear class variation were different.

A)



Cophenetic correlation coefficient = 0.860.

B)

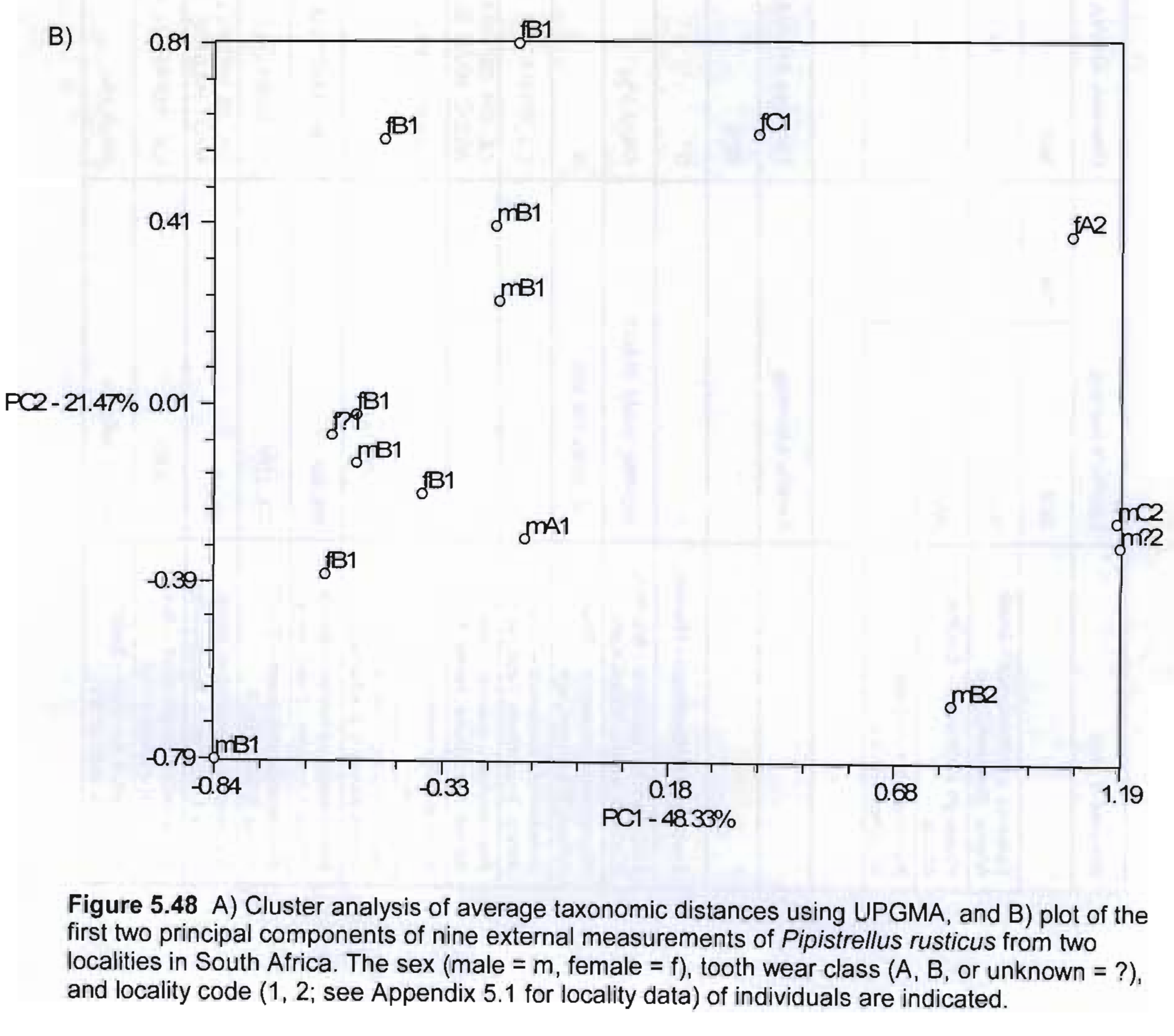


Figure 5.48 A) Cluster analysis of average taxonomic distances using UPGMA, and B) plot of the first two principal components of nine external measurements of *Pipistrellus rusticus* from two localities in South Africa. The sex (male = m, female = f), tooth wear class (A, B, or unknown = ?), and locality code (1, 2; see Appendix 5.1 for locality data) of individuals are indicated.

Table 5.30 Summary of cranial measurements showing significant homogeneity (Levene's homog.) and significance in one-way or two-way ANOVA tests for variation between sexes (Sex), tooth wear classes (TW) and interaction between sex and tooth wear class (Interact), together with percentage of measurements significant and post-hoc Tukey results (Subsets) for seven vespertilionid species tested (Species & area). - = no analyses were run, 0 = no measurements were significant.

Species & area	**Levene's homog.**		**One-way ANOVA**			**Post-hoc Tukey**
	SEX	**TW**	**SEX**	**TW**		**Subsets**
***Eptesicus hottentotus* - South Africa, Western Cape**	WUPM4	CIL, WAS	BH, BB, WIUM1 (25%)	LUM1 (8.3%)		[DC][CB]
***Hypsugo anchietae* – Southern Africa**	WUPM4	BB,WIUM1, WUPM4	LUM1, MAOT (16.7%)	LIW (8.3%)		D smaller than A,B&C
***Neoromicia rueppellii* – Southern Africa**	0	CIL, WIUM1	0	0		-
	Levene's homog.		**Two-way ANOVA**			**Post-hoc Tukey**
			SEX	**TW**	**Interact**	**Subsets**
***Eptesicus hottentotus* - Namibia**	0		0	BH, BB, WAS (23%)	MAOT (8.3%)	BH & WAS: [B][CD]; BB: [BC][CD]
***Neoromicia capensis* – Namibia & South Africa, Nama-Karoo**	WUPM4, LUM1, MAOT		CIL (8.3%)	ZB, BB (16.7%)	ZB, LIW (16.7%)	ZB: [BA][ACD]; BB: [BA] [AD][DC]
***Neoromicia capensis* – South Africa, Western Cape**	CIL, WAS, WIUM1		0	WAS, MAOT (16.7%)	0	WAS: no subsets even with SNK; MAOT [AB][DC]
***Neoromicia capensis* – South Africa, Free State, Grassland**	0		CIL, BH (16.7%)	0	0	-
***Neoromicia capensis* – South Africa, Free State, Nama-Karoo**	0		CIL, BH, ZB, WAS, WOUC, MAOT (50%)	ZB (8.3%)	0	[A][BCD]
***Neoromicia capensis* – Zimbabwe**	0		WUPM4 (8.3%)	0	0	-
***Neoromicia* cf. *melckorum* – South Africa & Zimbabwe**	CIL, LIW, LUM1		0	0	0	-
***Neoromicia africanus* - South Africa, Limpopo, Pafuri area**	WIUM1		LUM1, MAOT (16.7%)	0	0	-
***Neoromicia africanus* – South Africa & Swaziland**	CIL, LIW		CIL, LUM1 (16.7%)	LIW (8.3%)	0	[BDC][DCA]
***Neoromicia zuluensis* - South Africa Limpopo & Mpumalanga**	MAOT		CIL, ZB, WOUC, LUM1, MAOT (41.67%)	0	0	-
***Pipistrellus hesperidus* – South Africa, KwaZulu-Natal**	BH, WAS		CIL, WUPM4 (16.7%)	0	WAS (8.3%)	-
***Pipistrellus rusticus* - South Africa & Zimbabwe**	BB, ZB, WAS		BH (8.3%)	0	BH (8.3%)	-

Table 5.31 Summary of external measurements showing significant homogeneity (Levene's homog.) and significance in one-way or two-way ANOVA tests for variation between sexes (Sex) and tooth wear classes (TW), together with percentage of measurements significant and post-hoc Tukey results (Subsets) for nine vespertilionid species tested (Species & area). Kruskall-Wallis tests giving contradictory results to the ANOVA tests are indicated by square brackets in the ANOVA results. - = no analyses were run, 0 = no measurements were significant.

Species & area	Levene's homog.		One-way ANOVA			Post-hoc Tukey
	Sex	TW	Sex	TW		Subsets
Eptesicus hottentotus **- Namibia**	0	T	FA, TMETA (18.2%)	0		0
Hypsugo anchietae **– Southern Africa**	T	-	TMETA (8.3%)	-		-
Neoromicia capensis **– Namibia, Savanna**	-	TMETA	HB, T, E, HF, FA, TMETA, TL (58.3%)	FAL (8.3%)		D LARGER THAN C
Neoromicia capensis **– South Africa, Free State, Grassland**	E, TRB	TRL	TOT, T, FAL, [E], FA, TMETA (50%) [41.7 %]	E, TMETA (16.7%)		[BC][D]
Neoromicia capensis **– South Africa, Eastern Cape**	T	FA	HB, T, FA, TMETA (33.3%)	0 [but in males only- TMETA (8.3%)]		[DB][BC]
Neoromicia **cf.** ***melckorum*** **– South Africa & Zimbabwe**	TRL	0	FA, TMETA (28.6%)	0		-
Neoromicia africanus **- Malawi**	HFL, E, HF	-	[HF], FA, TMETA (27.3%) [HFL – 27.3 %]	TIB (9.1%)		[BD][DC]
Neoromicia rueppellii **– Southern Africa**	HF	TRB	0	0		-
Neoromicia rueppellii **- Zambia**	HFL	-	0	-		-
Neoromicia zuluensis **- South Africa, Limpopo & Mpumalanga**	HFL, E, FA, TIB	Not tested	0	-		-
Pipistrellus rusticus **- South Africa & Zimbabwe**	HFL, E, TMETA	TOT, FAL, E, TRL, TL	0	HFL, FAL, TIB, FA (33.3%)		HFL: none; FAL: [BC][CA]; TIB: [BA][AC]; FA: [B][CA]
	Levene's homog.		**Two-way ANOVA**			**Post-hoc Tukey**
			SEX	**TW**	**Interact**	**Subsets**
Neoromicia capensis **– South Africa, Free State, Nama-Karoo**	T, TMETA		TOT, T, FAL, TIB, TMETA (55.56%)	TMETA, TRL (22.22%)	0	TMETA: [ACD][DCB] TRL: [AC][BD]
Neoromicia nanus **- South Africa & Swaziland**	0		HFL, FA (25%)	0	0	-
Pipistrellus hesperidus **– South Africa, KwaZulu-Natal**	0		T, E, TIB, TRB (44.44%)	TMETA, TRB (22.22%)	TMETA, TRB (22.22%)	TMETA: [AB][BC] TRB: no subsets

Table 5.32 Summary of percent differences between means of significantly different cranial measurements in one or two-way ANOVA analyses of sexual dimorphism and tooth wear class variation in vespertilionid species. Numbers in bold type is the only result where males were larger than females.

	Species & area	CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Sex	*Eptesicus hottentotus* - South Africa, Western Cape	-	5.81	-	3.28	-	-	-	-	6.41	-	-	-
	Hypsugo anchietae – Southern Africa	-	-	-	-	-	-	-	-	-	-	5.07	5.37
	Neoromicia capensis – Namibia, Savanna	4.42	-	6.41	-	-	-	12.84	5.46	7.78	-	-	-
	Neoromicia capensis – Namibia & South Africa, Nama-Karoo	2.55	-	-	--	-	-	-	-	-	-	-	-
	Neoromicia capensis – South Africa, Western Cape	3.03	-	-	-	-	-	-	-	-	-	-	-
	Neoromicia capensis – South Africa, Free State, Grassland	2.48	**2.52**	-	-	-	-	-	-	-	-	-	-
	Neoromicia capensis – South Africa, Free State, Nama-Karoo	2.07	2.19	3.04	-	-	-	3.77	3.28	-	-	-	4.85
	Neoromicia capensis – Zimbabwe	-	-	-	-	-	-	-	-	-	9.58	-	-
	Neoromicia cf. *melckorum* – South Africa & Zimbabwe	-	-	-	-	-	-	-	3.38	-	-	-	-
	Neoromicia africanus - South Africa, Limpopo, Pafuri area	-	-	-	-	-	-	-	-	-	-	6.17	3.05
	Neoromicia africanus - South Africa & Swaziland	1.03	-	-	-	-	-	-	-	-	-	2.61	-
	Neoromicia zuluensis. - South Africa, Limpopo & Mpumalanga	2.28	-	2.89	-	-	-	-	3.53	-	-	3.94	4.79
	Neoromicia zuluensis. - Namibia	-	-	-	-	-	-	-	-	-	-	-	7.82
	Pipistrellus. hesperidus – South Africa, KwaZulu-Natal	2.17	-	-	-	-	-	-	-	-	7.10	-	-
	Pipistrellus. rusticus. - South Africa & Zimbabwe	-	1.60	-	-	-	-	-	-	-	-	-	-
TW													
	Eptesicus hottentotus - South Africa, W. Cape	-	-	-	-	-	-	-	-	-	-	11.30	-
	Eptesicus hottentotus- Namibia	-	6.76	-	4.50	-	-	8.11	-	-	-	-	-
	Hypsugo anchietae – Southern Africa	-	-	-	-	8.17	-	-	-	-	-	-	-
	Neoromicia capensis – Namibia & South Africa, Nama-Karoo	-	-	4.37	4.06	-	-	-	-	-	-	-	-
	Neoromicia capensis – South Africa, Western Cape	-	-	-	-	-	-	8.87	-	-	-	-	-
	Neoromicia capensis – South Africa, Free State, Grassland	-	-	-	-	-	-	-	-	-	-	10.14	-
	Neoromicia capensis – South Africa, Free State, Nama-Karoo	-	-	6.53	-	-	-	-	-	-	-	-	-
	Neoromicia cf. *melckorum* – South Africa & Zimbabwe	4.10	-	-	-	-	-	-	-	-	-	-	-
	Neoromicia africanus - South Africa & Swaziland	-	-	-	-	3.82	-	-	-	-	-	-	-
	Neoromicia zuluensis - South Africa, Limpopo & Mpumalanga	-	-	-	-	-	-	10.93	-	-	-	-	-

Table 5.33 Summary of percent differences between means of significantly different external measurements in one or two-way ANOVA analyses of sexual dimorphism and tooth wear class variation in vespertilionid species.

	Species & area	TOT	HB	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Sex	*Eptesicus hottentotus* - Namibia	-	-	-	-	-	-	-	5.21	-	-	6.78	-	-
	Hypsugo anchietae	-	-	-	-	-	-	-	-	-	-	6.11	-	-
	Neoromicia capensis – Namibia, Savanna	-	10.03	12.76	13.84	-	10.40	-	7.27	12.38	-	8.98	-	-
	Neoromicia capensis – South Africa, Free State, Grassland	5.95	-	10.65	-	-	-	5.23	4.54	10.15	-	5.79	-	-
	Neoromicia capensis – South Africa, Free State, Nama-Karoo	3.32	-	6.12	-	-	-	3.97	-	-	4.25	5.50	-	-
	Neoromicia capensis – South Africa, Eastern Cape	-	10.89	11.58	-	-	-	-	7.82	-	-	8.38	-	-
	Neoromicia cf. *melckorum* – South Africa & Zimbabwe	-	-	-	-	-	-	-	5.61	-	-	2.46	-	-
	Neoromicia africanus - South Africa & Swaziland	-	-	-	-	5.28	-	-	4.43	-	-	-	-	-
	Neoromicia africanus - Malawi	-	-	-	-	-	7.76	-	5.46	-	-	3.74	-	-
	Pipistrellus hesperidus – South Africa, KwaZulu-Natal	-	-	7.92	-	-	-	-	-	5.88	0.96	-	-	4.31
TW	*Neoromicia capensis* – Namibia, Savanna	-	-	-	-	-	-	6.43	-	-	-	-	-	-
	Neoromicia capensis – South Africa, Free State, Grassland		-	-	-	-	-	-	-	25.4	-	11.63	-	-
	Neoromicia capensis – South Africa, Free State, Nama-Karoo	-	-	-	-	-	-	-	-	-	-	6.24	8.68	-
	Neoromicia africanus - Malawi	-	-	-	-	-	-	-	-	-	8.00	-	-	-
	Pipistrellus hesperidus – South Africa, KwaZulu-Natal	-	-	-	-	-	-	-	-	-	-	4.31	-	5.80
	Pipistrellus rusticus - South Africa & Zimbabwe	-	-	-	-	20.29	-	5.56	7.78	-	16.21	-	-	-

Table 5.34 Summary of results of the Box's M test for the assumption of homogeneity of group covariance matrices, and of one–way and two-way MANOVA tests of variation in cranial measurements between sexes (Sex), tooth wear classes (TW) and in the two-way analyses interaction between sex and tooth wear class (Interact) in eight vespertilionid species tested (Species & area). S = significant; NS = not significant; - = no analysis run; 0 = analysis not computed; *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Species & area	Two-way MANOVA				One-way MANOVA		One-way MANOVA	
	Box's M	SEX	TW	Interact	Box's M	SEX	Box's M	TW
Eptesicus hottentotus **- Namibia**	0	NS	S ***	S *	-	-	-	-
Hypsugo anchietae **– Southern Africa**	-	-	-	-	0	NS	0	NS
Neoromicia capensis **– Namibia, Savanna**	0	NS	NS	NS	-	-	-	-
Neoromicia capensis **– Namibia & South Africa, Nama-Karoo**	0	NS	NS	NS	-	-	-	-
Neoromicia capensis **– South Africa, Western Cape**	0	NS	NS	NS	-	-	-	-
Neoromicia capensis **– South Africa, Free State, Grassland**	0	NS	NS	NS	-	-	-	-
Neoromicia capensis **– South Africa, Free State, Nama-Karoo**	0	S	NS	NS	-	-	-	-
Neoromicia capensis **– Zimbabwe**	0	NS	NS	NS	-	-	-	-
Neoromicia **cf.** ***melckorum*** **– South Africa & Zimbabwe**	0	NS	NS	NS	-	-	-	-
Neoromicia africanus **- South Africa, Limpopo, Pafuri area**	0	NS	NS	NS	-	-	-	-
Neoromicia africanus **- South Africa & Swaziland**	0	NS	NS	NS	-	-	-	-
Neoromicia zuluensis **- South Africa, Limpopo & Mpumalanga**	0	NS	NS	NS	-	-	-	-
Neoromicia zuluensis **- Namibia**	-	-	-	-	0	NS	0	NS
Pipistrellus hesperidus **– South Africa, KwaZulu-Natal**	0	NS	NS	NS	-	-	-	-
Pipistrellus rusticus **– South Africa & Zimbabwe**	0	NS	NS	NS	-	-	-	-

Table 5.35 Summary of results of the Box's M test for the assumption of homogeneity of group covariance matrices, and of one–way and two-way MANOVA tests of variation in external measurements between sexes (Sex), tooth wear classes (TW) and in the two-way analyses interaction between sex and tooth wear class (Interact) in eight vespertilionid species tested (Species & area). S = significant; NS = not significant; - = no analysis run; 0 = analysis not computed; *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Species & area	Two-way MANOVA				One-way MANOVA		One-way MANOVA	
	Box's M	SEX	TW	Inter	Box's M	SEX	Box's M	TW
Eptesicus hottentotus - Namibia	-	-	-	-	0	NS	-	-
Hypsugo anchietae – Southern Africa	-	-	-	-	0	NS	-	-
Neoromicia capensis – Namibia, Savanna	-	-	-	-	0	S **	0	S *
Neoromicia capensis – South Africa, Free State, Grassland	-	-	-	-	0	NS	0	NS
Neoromicia capensis – South Africa, Free State, Nama-Karoo	0	S **	NS	NS	-	-	-	-
Neoromicia capensis – South Africa, Eastern Cape	-	-	-	-	-	S*	0	NS
Neoromicia cf. *melckorum* – South Africa & Zimbabwe	-	-	-	-	0	NS	0	NS
Neoromicia africanus - South Africa & Swaziland	0	NS	NS	NS	-	-	-	-
Neoromicia africanus - Malawi	-	-	-	-	0	S *	0	NS
Neoromicia rueppellii– Southern Africa	-	-	-	-	0	NS	-	-
Neoromicia rueppellii - Zambia	-	-	-	-	0	NS	-	-
Neoromicia zuluensis - South Africa, Limpopo & Mpumalanga	-	-	-	-	0	NS	-	-
Pipistrellus hesperidus – South Africa, KwaZulu-Natal	0	S *	NS	S*	-	-	-	-
Pipistrellus rusticus - South Africa & Zimbabwe	-	-	-	-	0	NS	0	S *

Table 5.36 Summary of percent correct assignments in DFA between sexes (Sex), and tooth wear classes (TW) using cranial measurements, giving the total (Total) and breakdown figures for each sex (females = F, males = M) and tooth wear class (A, B, C, D) in eight vespertilionid species tested (Species & area). Together with a breakdown of the tooth wear classes separated on the first (DF1) and second DF (DF2) axes of three group DFA. - = no analyses were run; 0 = no tooth wear classes were separated.

Species & area	Sex			TW						
	Total	F	M	Total	A	B	C	D	DF1	DF2
Eptesicus hottentotus - Namibia	100	100	100	100	-	100	100	100	[B][C][D]	[C][BD]
Neoromicia capensis – Namibia, Savanna	100	100	100	88.00	-	75.00	71.43	100	[B][CD]	[B][C]
Neoromicia capensis – Namibia & South Africa, Nama-Karoo	95.65	88.89	100	91.30	83.33	100	100	83.33	[AB][CD]	0
Neoromicia capensis – South Africa, Western Cape	95.83	94.12	100	87.50	100	100	62.50	100	[AB][CD]	[C][D]
Neoromicia capensis – South Africa, Free State, Grassland	92.00	92.86	90.91	86.96	100	90.91	75	-	[A][BC]	0
Neoromicia capensis – South Africa, Free State, Nama-Karoo	91.11	100	88.57	75.56	100	100	70.37	75.00	0	0
Neoromicia capensis – Zimbabwe	100	100	100	100	100	100	100	-	[AB][C]	0
Neoromicia cf. *melckorum*– South Africa & Zimbabwe	94.12	88.89	100	100	100	100	100	-	[A][C][B]	[C][D]
Neoromicia africanus - South Africa, Limpopo, Pafuri area	89.66	85.71	100	75.86	66.67	75.00	88.89	-	0	0
Neoromicia africanus - South Africa & Swaziland	82.86	83.33	82.16	68.57	66.67	100	68.75	37.50	0	0
Neoromicia zuluensis - South Africa, Limpopo & Mpumalanga	83.33	80.00	87.50	69.44	66.67	60.00	66.67	87.50	0	0
Pipistrellus hesperidus – South Africa, KwaZulu-Natal	81.40	93.75	74.07	55.81	58.33	47.62	70.00	-	0	0
Pipistrellus rusticus - South Africa & Zimbabwe	74.29	77.27	69.23	77.14	80.00	80.00	60.00	-	0	0

Table 5.37 Summary of percent correct assignments in DFA between sexes (Sex), and tooth wear classes (TW) using external measurements, giving the total (Total) and breakdown for each sex (females = F, males = M) and tooth wear class (A, B, C, D) in eight vespertilionid species tested (Species & area). - = no analyses were run. Together with a breakdown of the tooth wear classes separated on the first (DF1) and second DF (DF2) axes of three group DFA. - = no analyses were run; 0 = no tooth wear classes were separated.

Species & area	**Sex**			**TW**						
	Total	**F**	**M**	**Total**	**A**	**B**	**C**	**D**	**DF1**	**DF2**
***Eptesicus hottentotus* - Namibia**	100	100	100	-	-	-	-	-	-	-
***Neoromicia capensis* – Namibia, Savanna**	96.67	100	66.67	90	-	100	80	91.67	[B][CD]	0
***Neoromicia capensis* – South Africa, Free State, Grassland**	83.33	88.89	77.78	93.33	-	88.89	100	-	-	-
***Neoromicia capensis* – South Africa, Free State, Nama-Karoo**	89.80	92.31	88.89	48.98	100	50.00	34.62	60.00	0	0
***Neoromicia capensis* – South Africa, Eastern Cape**	100	100	100	90.91	-	85.71	-	100	-	-
***Neoromicia* cf. *melckorum* – South Africa & Zimbabwe**	100	100	100	100	100	-	100	-	-	-
***Neoromicia africanus* - South Africa & Swaziland**	79.31	90.91	72.22	71.43	66.67	66.67	68.75	83.33	0	0
***Neoromicia africanus* - Malawi**	100	100	100	100	-	100	100	100	[B][C][D]	[BC][D]
***Neoromicia rueppellii*– Southern Africa**	100	100	100	-	-	-	-	-	-	-
***Neoromicia rueppellii* - Zambia**	87.50	100	75.00	-	-	-	-	-	-	-
***Neoromicia zuluensis* - South Africa, Limpopo & Mpumalanga**	92.86	100	88.89	-	-	-	-	-	-	-
***Pipistrellus hesperidus* – South Africa, KwaZulu-Natal**	95.65	88.89	100	78.26	75.00	83.33	66.67	-	0	0
***Pipistrellus rusticus* - South Africa & Zimbabwe**	93.75	100	87.50	-	-	-	-	-	-	-

Table 5.38 Summary of cranial measurements significantly different between sexes (Sex) and tooth wear classes (TW) in the one-way (1-way) and two-way ANOVAs (2-way), and the measurements contributing most to the separation on the first and second principal components of PCA (PC1, PC2) of both sexes and tooth wear classes, and the first and second discriminant function axes (DF1, DF2) of tooth wear classes, in seven vespertilionid species. Kruskall-Wallis tests giving contradictory results to the ANOVA tests are indicated by square brackets in the ANOVA results.

Species & area	PC1	PC2	1-way Sex	2-way Sex	1-way TW	2-way TW	DF1	DF2
Eptesicus hottentotus **- Namibia**	WOUC; WIUM1; CIL; WUPM4	WFM; LUM1	-	0	-	BH; BB; WAS	WAS; MAOT; WOUC	BH; WOUC; CIL
Neoromicia capensis **– Namibia, Savanna**	ZB; CIL; WFM	WFM; WAS	-	ZB; WAS	-	0	CIL; WOUC; BB; LUM1	WAS; CIL; ZB
Neoromicia capensis **– Namibia & South Africa, Nama-Karoo**	CIL; ZB; WOUC; WUPM4	LUM1; LIW	-	CIL	-	ZB; BB	BB; WFM	LUM1; MAOT; WIUM1
Neoromicia capensis **– South Africa, Western Cape**	ZB; WOUC; WUPM4	WUPM4; WFM	-	0	-	WAS; MAOT	MAOT; LIW; WOUC	CIL; LIW
Neoromicia capensis **– South Africa, Free State, Grassland**	WIUM1; WUPM4	BH; ZB; WOUC	-	CIL; BH	-	0	MAOT; BB	WIUM1; WFM
Neoromicia capensis **– South Africa, Free State, Nama-Karoo**	ZB; WOUC; WFM	BB; WFM; WUPM4	-	CIL; BH; ZB; WAS; WOUC; MAOT	-	ZB	MAOT; ZB; WOUC	ZB;CIL
Neoromicia capensis **– Zimbabwe**	CIL; WAS; LIW	BB; WOUC	-	WUPM4	-	0	LIW; BB	WOUC; WIUM1
Neoromicia **cf.** ***melckorum*** **– South Africa & Zimbabwe**	ZB; LUM1	LUM1; WIUM1; BB, LIW; BH	-	0	-	0	LUM1; WOUC	LIW; WIUM1; ZB
Neoromicia africanus **- South Africa, Limpopo, Pafuri area**	BB; CIL; WUPM4	WAS; LIW	-	LUM1; MAOT	-	0	ZB; CIL	WIUM1; BB
Neoromicia africanus **- South Africa & Swaziland**	WIUM1; WOUC; BB; MAOT; WAS	WAS; ZB; WOUC; WIUM1	-	LUM1	-	LIW	LIW; CIL	WIUM1; MAOT
Neoromicia zuluensis **- South Africa, Limpopo & Mpumalanga**	WOUC; WUPM4	LIW; WUPM4	-	CIL; ZB; WOUC; LUM1; MAOT	-	0	LUM1; WOUC	LUM1; WIUM1
Neoromicia zuluensis **- Namibia**	WOUC; LIW	WFM; LIW	MAOT	-	0	-	-	-
Pipistrellus hesperidus **– South Africa, KwaZulu-Natal**	CIL; WOUC; BH	WUPM4; WFM	-	CIL; WUPM4	-	0	WFM; BH	BB; WOUC
Pipistrellus rusticus. **- South Africa & Zimbabwe**	WIUM1; WOUC; WAS	WUPM4; ZB	-	BH	-	0	WOUC; BH	CIL; WOUC

Table 5.39 Summary of external measurements significantly different between sexes (Sex) and tooth wear classes (TW) in the one-way (1-way) and two-way ANOVAs (2-way), and the measurements contributing most to the separation on the first and second principal components of PCA (PC1, PC2) of both sexes and tooth wear classes, and the first and second discriminant function axes (DF1, DF2) of tooth wear classes, in eight vespertilionid species. - = no analyses were run; 0 = no measurements were significant. Kruskall-Wallis tests giving contradictory results to the ANOVA tests are indicated by square brackets in the ANOVA results.

Species & area	PC1	PC2	1-way Sex	2-way Sex	1-way TW	2-way TW	DF1	DF2
Eptesicus hottentotus **- Namibia**	TMETA; FA; TIB; TRB	HF; TRL	FA; TMETA	-	0	-	-	-
Neoromicia capensis **– Namibia, Savanna**	T; HB; TRB	E; HB; HFL	HB; T; E; HF; FA; TMETA; TL	-	FAL	-	E; HFL; HB; TRB	HB; T
Neoromicia capensis **– South Africa, Free State, Grassland**	T; TMETA, FA; TRL	TRL; HFL; E; TRB	TOT; T; FAL; [E]; FA; TMETA	-	E; TMETA	-	-	-
Neoromicia capensis **– South Africa, Free State, Nama-Karoo**	FAL; TIB; TRL	TRB; T; E	-	TOT; T; FAL; TIB; TMETA	-	TMETA; TRL	TRL; TOT	E; HFL
Neoromicia capensis **– South Africa, Eastern Cape**	TMETA; FA; HFL	T; TRL	HB; T; FA; TMETA	-	0 [but in males only-TMETA]	-	-	-
***Neoromicia* cf. *melckorum* – South Africa & Zimbabwe**	FA; TMETA; TRL	TRL; TIB	FA, TMETA	-	0	-	-	-
Neoromicia africanus **- South Africa & Swaziland**	TRB; TMETA	FA; E	-	HFL; FA	-	0	T; E	TMETA; TIB; FA
Neoromicia africanus **- Malawi**	TMETA; E	FA; TRB	[HF]; FA; TMETA; [HFL]	-	TIB	-	FA; TRL	FA; TRL; TMETA
Neoromicia rueppellii **– Southern Africa**	HFL; E	T; FA; TRL	0	-	0	-	-	-
Neoromicia rueppellii **- Zambia**	TIB; FA; HFL	TRB; HFL	0	-	-	-	-	-
Neoromicia zuluensis **- South Africa, Limpopo & Mpumalanga**	HF; FA	TMETA; TRL	0	-	-	-	-	-
Pipistrellus hesperidus **– South Africa, KwaZulu-Natal**	T; TRL	TOT; HFL;TIB	-	T; E; TIB; TRB	-	TMETA; TRB	TMETA; FAL	TMETA; TRB; HFL; TRL
Pipistrellus rusticus **- South Africa & Zimbabwe**	E; TIB; HFL	T; TRB	0	-	HFL; FAL; TIB; FA	-	-	-

5.3.2.1 Sexual dimorphism

Taking into account all the tests, *N. capensis* showed the greatest amount of sexual dimorphism. The cranial measurements most commonly involved in the distinction of different sexes across the different species were condylo-incisor skull length (CIL), width across the outer surfaces of the upper canine teeth (WOUC), and width between the inner surfaces of the upper first molars (WIUM1), whereas the external measurements most commonly involved in the distinction of different sexes across the different species were third metacarpal (TMETA) and forearm (FA) lengths.

Within the different analyses of *N. capensis* condylo-incisor skull length (CIL) was most common in the separation between the sexes, whereas within *N. africanus* and *N. zuluensis*, moment arm of the temporal (MAOT) was the common measurement showing sexual dimorphism. The external measurements most commonly important in sexual dimorphism in *N. capensis* were forearm (FA), third metacarpal (TMETA), and tail (T) lengths, while in *N. africanus*, forearm length (FA) was most common in the separation between the sexes.

5.3.2.2 Tooth wear class variation

Accounting for the results of all the tests, *E. hottentotus* showed the greatest amount of tooth wear class variation in cranial measurements, whereas *P. rusticus* showed the greatest amount of tooth wear class variation in external measurements. The cranial measurements most commonly involved in the distinction of different tooth wear classes across the different species were braincase height (BH) and breadth (BB), and width of the articular surface (WAS), whereas external variables most commonly involved in the distinction of different tooth wear classes across the different species were forearm (FAL) and tibia (TIB) lengths. The cranial measurement most commonly important within the different analyses of *N. capensis* was zygomatic breadth (ZB).

5.3.2.3 Geographic variation

Inevitably, geographic variation was introduced into the analyses due to the pooling of specimens from different localities. In the analyses of cranial measurements, four groups showed clustering in relation to locality in the UPGMA phenograms although this was not as apparent in the PCA scatterplot (*N. capensis* from Zimbabwe; *N.* cf. *melckorum* from South Africa and Zimbabwe; *N. africanus* from South Africa and Swaziland; and *P. hesperidus* from KwaZulu-Natal in South Africa). In analyses of external measurements, four groups also showed clear indications of geographic variation in both the UPGMA phenogram and PCA scatterplot. These were *E. hottentotus* from Namibia; *N. capensis* from the Grassland biome of the Free State Province in South Africa; *N. africanus* from South Africa and Swaziland; and *P. rusticus* from South Africa and Zimbabwe. One group showed clustering in the UPGMA phenogram which was not, however, apparent in the PCA scatter plot (*P. hesperidus* from KwaZulu-Natal in South Africa).

The geographic variation introduced into the analyses of cranial measurements was less than that observed in the external measurements and it is possible that the geographic variation may not have substantially influenced the assessment of sexual and tooth wear class variation in the cranial measurements of these groups. However, the same cannot be concluded for the analyses of external measurements, and hence the results of the analyses of external measurements that showed geographic variation should be considered bearing in mind that they may have been influenced by the extent of geographic variation in the analyses.

5.4 DISCUSSION

What degree of individual variation constitutes sexual dimorphism or age variation, and whether these should be measured within a population or across the geographic range of a species are not clear-cut issues as can be gathered from the published literature (Bogdanowicz and Owen, 1996; Burnett, 1983; Carpenter *et al.*, 1978; Kitchener *et al.*, 1986; Kitchener *et al.*, 1987; Kitchener and Caputi, 1985; Monadjem, 2001; Williams and Findlay, 1979; Willig and Hollander, 1995). In this analysis, which attempted to assess variation without the influence of geographic variation, both cranial and external measurements of the nine species tested showed some degree of sexual dimorphism in one or several of the statistical tests, with females being slightly larger than males in all but one test of cranial measurements. Fewer species showed significant tooth wear class variation in cranial and external measurements, and it appeared that tooth wear was not a very useful relative measure of age given the number of measurements across all nine species in which the means of different tooth wear classes did not follow the assumed pattern of growth with age, and the results of most statistical tests failed to demonstrate this assumption.

Although this analysis did not study the influence of diet, environment, habitat and or health on the degree of tooth wear (Pessoa and Dos Reis, 1991a and b), it is possible that these or other factors influenced tooth wear together with, rather than age alone. Young bats appear to be like shrews which have largely reached adult cranial dimensions by the time specimens are trappable and find their way into museum collections, than rodents which often continue to grow cranially after they have become adults (Dippenaar and Rautenbach, 1986). Unlike the observation made for rodents (Chimimba and Dippenaar, 1994) that older individuals showed greater cranial deformations, there were few observed cranial deformities in individuals of tooth wear class D, although individuals of tooth wear class D with the most worn teeth were sometimes smaller than individuals of tooth wear class C.

In contrast to the result of the shape morphometric analysis (Chapter 3) which found no sexual dimorphism in centroid size and shape in a population of *N. capensis* from Jagersfontein in the Free State Province of South Africa, this analysis found specimens of *N. capensis* from the Nama-Karoo biome in the Free State Province of South Africa (of which specimens from Jagersfontein formed the largest component) to have the greatest degree of sexual dimorphism. These results also contradicted the suspected sexual dimorphism in *H. anchietae*, with females being significantly larger than males (Monadjem, 2001), which was based on the reported forearm lengths of males and females being different by more than 2 mm in Taylor (2000), since forearm length of *H. anchietae* was not significantly sexually dimorphic in this analysis. However, of nine external measurements of *H. anchietae* tested in one-way ANOVA analyses, length of the third metacarpal was significantly sexually dimorphic, whereas of 12 cranial measurements tested in one-way ANOVA analyses in *H. anchietae* two measurements (16.7%) were significantly sexually dimorphic. The results of this analysis were, however, consistent with the results of intra-specific shape morphometric analysis in *E. hottentotus* (Chapter 3) which found a significant difference in dorsal and ventral skull centroid size between tooth wear classes, with specimens of tooth wear class B being significantly smaller than tooth wear classes C and D. In this analysis, the differences in sexually dimorphic cranial measurements ranged from 1.03 to 12.84% in cranial measurements and from 0.96 to 17.22% in external measurements. These differences were larger than those recorded from centroid size which ranged from 2.27 to 4.24% (Chapter 3). They were also larger than the differences recorded for *E. fuscus* which range from 1.3 to 3.8% (Burnett,1983), and those recorded in an analysis of plecotine bats, where the difference only exceeded 2.3% in one case, when female *Otonycteris hemprichi* were 4.4% larger than males (Bogdanowicz and Owen, 1996).

Although this analysis did not test the selective forces influencing the patterns of variation in sexual dimorphism, but merely documented patterns of change, it is interesting to consider the suggestions that have previously been made as to what selective forces may have been implicated in sexual dimorphism in bats, where females are often larger than males (see also Discussion in Chapter 3). Ralls (1978) "big mother hypothesis" suggested female bats were larger than males in bats as an ecological response to optimising the efficiency of motherhood. Rall's (1978) rationale being that larger mothers may have larger offspring that are more likely to survive, larger mothers may produce more and/or better milk allowing faster growth, and larger mothers would be better at maternal care such as carrying and defending the young. Myers (1978) suggested sexual dimorphism in vespertilionid bats related to the extra mass females carry during pregnancy and lactation, hence, a large female can reduce the proportionate load of the foetus, reduce the cost of milk production, and increase the quantity and size of insects ingested. Although Williams and Findlay (1979) agreed, increased weight loading of pregnant females might be important in the selection of larger size this hypothesis was not supported by their data. They suggested instead that increased energy demands during pregnancy might be the primary factor in selecting larger size in females, whereby larger females could maintaining homoeothermy during gestation and hence timing of birth more efficiently, could store more fat and potentially have a greater array of prey available to them.

Both proposals by Myers (1978) and Williams and Findlay (1979) incorporated elements of the resource utilisation argument (Selander, 1966 and 1972). Such partitioning allows the selection of different size prey by males and females, since larger predators utilise sizes of food unavailable to smaller predators, which in turn confers a competitive size advantage to larger animals within definable limitations of predator prey size. Although Williams and Findlay (1978) did not find a significant correlation between litter size and degree of dimorphism, Burnett (1983) found a positive correlation between the degree of sexual dimorphism and litter size and moisture, as well as a negative correlation between the degree of sexual dimorphism and temperature. This suggested wing-loading, moisture stress and thermoregulation were all important factors contributing to the sexual dimorphism. Sexual selection (Darwin, 1859; Trivers, 1972) has also been suggested as a mechanism whereby larger size in females could be the result of female competition for mates. Burnett (1983) suggested sexual selection may have driven the sexual dimorphism favouring male *E. fuscus* at low latitudes, where populations do not hibernate and males may gain sole mating access to a female. There are also several evolutionary theories (Daly and Wilson, 1978; Selander, 1957) that have linked sexual dimorphism to polygamous mating systems, unequal sex ratios, and dissimilar resource utilisation.

Although this analysis attempted to assess sexual dimorphism and tooth wear class variation excluding the influence of geographic variation, some geographic variation was inevitably introduced into the analyses as a result of pooling specimens from different localities. Geographic variation was more apparent in analyses of external measurements than cranial measurements. In most of the analyses where geographic variation was apparent, there was also the possibility that the results were further influenced by small and uneven sample sizes of the different samples of sexes and tooth wear classes. The results indicated that the degree of sexual dimorphism and tooth wear class variation may have been reduced by geographic variation in combination with small and uneven sample sizes. Unfortunately, not only did the museum collections rarely have large series of specimens from single localities, but where series from single or closely related localities of a species did exist, they were rarely of even numbers of males and females and different tooth wear classes. It is not clear whether this is an artefact of collecting or a natural occurrence for the vespertilionid species analysed here. However, unequal sex ratios with females generally outnumbering males in any given age class have been recorded for several other vespertilionid species (Humphrey and Cope, 1977; Wilson, 1971). While most of the museum collections used in this study also showed females to outnumber males, in the largest known collection of *N. capensis* specimens (n = 57) collected over two days from Jagersfontein Commonage in the Free State Province, males outnumbered females in the ratio 3.38:1.

Although many studies assume the patterns of intra-population sexual variation and tooth attrition observed for a single population apply over a broad geographic range, an analysis of *E. fuscus* in America from 13 diverse localities and including various subspecies indicated that the degree and direction of sexual dimorphism was geographically variable (Burnett, 1983). The results of this analysis also identified geographic variation within species in the degree of sexual dimorphism and tooth wear class variation, and one case of geographic variation in the direction of sexual dimorphism, since braincase height in *N. capensis* from the Grassland biome in the Free State Province of South Africa was larger in males, contrary to the direction of larger female size in braincase height in all other groups of *N. capensis*, and all other measurements tested. Localised stabilizing selection regimes, i.e. localized environments and diets (Bronner, 1996a; Miller-Butterworth *et al.* 2003) are a possible explanation for intra-specific geographic variation in intra-population sexual dimorphism and tooth wear class variation. Ralls (1976) suggested sexual dimorphism requires an assessment of what physiological circumstances it is possible and advantageous to be larger or smaller, hence Burnett (1983) identified that in arid areas the wing-loading advantage that females obtain from larger size may be offset by evaporation, and hence in arid areas there may be a reduction in sexual dimorphism relative to other areas in the geographic range of a species if the physiological requirements of reduced evaporation are sufficiently important. Other potentially stabilizing selection regimes are roost site, colony size and sex ratio which in the case of *N. capensis* in this analysis may have had the greatest influence on the geographic variation noted in the analyses of sexual dimorphism. A study of Australian *Eptesicus* species found sexual dimorphism varied with roost type, and that sexual dimorphism was greater for forest-roosting than cave-roosting individuals (Carpenter *et al.*, 1978).

Although the actual roost site was not known for many of the specimens examined in this analysis, it appears *N. capensis* has become more abundant their success being assisted in more recent history by their use of man-made roosts, which has led to a change in the recorded roost sizes of this species since earlier accounts indicated they roost singly, which appears to be the case when they rest in natural roosts. However, the species is currently often found roosting in buildings in larger groups (around twenty) of males and females. Aside from one specimen from Alma, the rest of the specimens in the group of *N. capensis* from the Nama-Karoo biome in the Free State Province of South Africa which showed the greatest degree of sexual dimorphism, were collected (according to the museum records) over two days (12 and 16 February 1990) from a single colony in a shaft next to water works at a disused mine at Jagersfontein Commonage. This large colony from Jagersfontein Commonage (n = 57) also showed the fairly unusual sex ratio for vesper species of males outnumbering females. A possibility that would require further testing is that larger colonies roosting in man-made structures have undergone a change in mating system (Bradbury, 1977) which has been accompanied by a greater degree of sexual dimorphism.

Willig and Hollander (1995) on the other hand, have suggested that significant constraints exist on the expression of sexual dimorphism between populations of the same species, and that populations within a species would express dimorphism via a consistent suite of morphometric characters because the groups are linked to the degree to which they share the same gene pool. In an analysis of 12 different vespertilionid species from two different biomes, Willig and Hollander (1995) found correlations among patterns of important characters that they suggested were expected if phylogenetic constraints were in operation, and that patterns in the exhibition of inter-sexual variation appeared to be species-specific and relatively unrelated to systematic arrangements at the generic level or higher. In this analysis, although there were some similarities within species in the measurements that showed sexual dimorphism and tooth wear class differences, there were also similarities between species as well as variations both between and within the species in the measurements that showed sexual dimorphism and tooth wear class differences across the different statistical tests.

Besides documenting patterns of variation between sexes and tooth wear class in localized populations of nine species, it was also the aim of this study to identify whether specimens of different sexes and ages of the different species needed to be treated separately or could be pooled for intra- and inter-specific analyses. For this reason, while the result of all tests were taken into consideration, it was the degree of separation of the sexes or tooth wear classes in the PCA that was considered decisive in pooling data. If the PCA overlap of sex and tooth wear classes was insufficient to obscure intra- and inter-specific analyses it would have been counter-productive to further reduce sample size by treating them as separate data sets. Since the degree of sexual dimorphism was sufficiently small in all but one analysis, these results indicate that with the exception of *N. capensis* from the Nama-Karoo biome in the Free State Province of South Africa which should initially be tested as separate sexes in intra- and inter-specific analysis, the sexes of the other species were sufficiently similar to allow pooling for intra and inter-specific analysis. The only analysis in which tooth wear class variation was sufficiently large to merit the suggestion of separate treatments for different tooth wear classes, or the use of only some and not other tooth wear classes for intra- and inter-specific analysis, was in *E. hottentotus* from Namibia, in which tooth wear classes B and D were sufficiently different in size.

In spite of small sample sizes which in some cases led to the introduction of geographic variation in these analyses, this analysis provides the first indication of patterns of variation of sexual dimorphism and tooth wear class variation in nine species of vesper bats occurring in southern Africa, which were useful for making decisions about pooling sexes and different tooth wear classes for intra- and inter-specific analyses.

Appendix 5.1

Southern African vespertilionid specimens used in analysis of sexual dimorphism and tooth wear class variation

Within each species localities are arranged in order of occurrence from north to south. Locality numbers were used as labels in the PCA plots and UPGMA phenograms. Information is also included about the vegetation biomes in which the localities occur.

Acronyms: BM - The Natural History Museum, London, United Kingdom; DM - Durban Natural Science Museum, South Africa; KM - Amathole Museum, King William's Town, South Africa (formerly Kaffrarian Museum); MM - McGregor Museum, Kimberley, South Africa; TM - Transvaal Museum, Pretoria, South Africa; NMB - National Museum, Bloemfontein, South Africa; NMBZ - National Museum, Bulawayo, Zimbabwe. ZM - Iziko South African Museum, Cape Town, South Africa.

Eptesicus hottentotus

South Africa, Western Cape

Cranial
SOUTH AFRICA: WESTERN CAPE PROVINCE:
- Cederberg, Algeria State Forest, Camp Site (32°22'S, 19°03'E): ZM41418, TM35150, TM38411, TM38412, TM40630, TM40631, ZM41419. [Fynbos]
- Cederberg, Pakhuis Pass, Kliphuis Camp Site (32°08'S, 19°00'E): ZM41416. [Fynbos]

Namibia

Cranial
NAMIBIA:
(1) Omaruru, Ombu, Erongo Mts. (21°40'S, 15°44'E): TM9480, TM9481, TM9482, TM9484, TM9485, TM9486, TM9488, TM9491, TM9493. [Savanna]
(2) 70 km W of Maltahohe, Zwartmodder (101) (24°54'S, 16°17'E): TM37588, TM37624. [Savanna]
(3) 3 km W of Aus, Klein Aus (8) (26°39'S, 16°13'E): TM37540, TM37551, TM37552, TM37553, TM37554, TM37555. [Desert]
(4) 35 km SSW of Keetmanshoop, Rheinsvels Farm (26°57'S, 17°56'E): TM32566. [Nama-Karoo]
(5) Bethanie, Huns (106) (ca. 27°23'S, 17°23'E): TM32695. [Nama-Karoo]

External
NAMIBIA:
(1) Omaruru, Ombu, Erongo Mts. (21°40'S, 15°44'E): TM9480, TM9482, TM9484, TM9486, TM9488, TM9492. [Savanna]
- Gobabeb Desert Research Station (22°33'S, 15°03'E): NMBZ64056. [Desert]
(2) 70 km W of Maltahohe, Zwartmodder (101) (24°54'S, 16°17'E): TM37588, TM37624. [Savanna]
- Farm Kanaan (25°52'S, 16°07'E): TM27418. [Nama-Karoo]
(3) 3 km W of Aus, Klein Aus (8) (26°39'S, 16°13'E): TM37540, TM37552, TM37554, TM37560. [Desert]
(4) 35 km SSW of Keetmanshoop, Rheinsvels Farm (26°57'S, 17°56'E): TM32566. [Nama-Karoo]

Hypsugo anchietae
Cranial [Savanna]
SOUTH AFRICA: LIMPOPO PROVINCE:
- Kruger National Park (KNP), Skukuza Staff Village (24°59'S, 31°35'E): TM39767.
- KNP, 1.5 km NW of Skukuza, dense woodland of western reservoir (24°59'S, 31°35'E): TM39768.

KWAZULU-NATAL PROVINCE:
- St. Lucia, Nibela Peninsula, Sobhengu Lodge (27°59'S, 32°24'E): DM6885.
- St Lucia, False Bay (28°01'S, 32°21'E): DM2269.
- Harold Johnson Nature Reserve (29°12'S, 31°25'E): DM5353, DM5357.
- 17.5 km SW of Richmond, Hella-Hella, Game Valley Estates (29°54'S, 30°05'E): DM5362.
- Umkomaas, Empisini Nature Reserve (30°12'S, 30°48'E): DM5358, DM5377.

ZIMBABWE:

Appendix 5.1 continued

- Near Gwayi River, Volunteer Farms (18°49'S, 27°38'E): NMBZ31965.

External [Savanna]
SOUTH AFRICA: LIMPOPO PROVINCE:
- Kruger National Park (KNP), Skukuza (24°59'S, 31°35'E): TM30061.
- KNP, 1.5 km NW of Skukuza, dense woodland of western reservoir (24°59'S, 31°35'E): TM39768.

KWAZULU-NATAL:
- St Lucia, False Bay (28°01'S, 32°21'E): DM2269.
- Harold Johnson Nature Reserve (29°12'S, 31°25'E): DM5353, DM5357, DM5364.
- 17.5 km SW of Richmond, Hella-Hella, Game Valley Estates (29°54'S, 30°05'E): DM5362.
- Umkomaas, Empisini Nature Reserve (30°12'S, 30°48'E): DM5358, DM5377.

Neoromicia capensis

Namibia and South Africa, Nama-Karoo

Cranial
NAMIBIA:
(1) 35 km SSW Keetmanshoop, Rheinsvels Farm (26°57'S, 17°56'E): TM32547, TM32548, TM32567.
SOUTH AFRICA: NORTHERN CAPE PROVINCE:
(2) 6 km SE Nossob, Kalahari Gemsbok National Park, Marie se Gat (25°38'S, 20°38'E): TM35584, TM35585, TM35586, TM35587, TM35588, TM35589, TM35591, TM35592, TM35593,TM35594,TM35595, TM35596, TM35597, TM35598, TM35599, TM35600, TM35601, TM35602.
(3) Kalahari Gemsbok National Park, Mata Mata Camp (25°45'S, 19°59'E): MM7070, MM7071.

South Africa, Western Cape

Cranial
SOUTH AFRICA: WESTERN CAPE PROVINCE:
(1) Cederberg, Algeria State Forest Campsite (32°21'S, 19°03'E): ZM41452, ZM41457, TM38413. [Fynbos]
(2) Clanwilliam, Olifants River (32°21'S, 18°57'E): MM7036, MM7037. [Succulent Karoo]
(3) Piketburg, SE Elandsbaai, Farm Groote Drift (ca. 32°38'S, 18°38'E): KM29004, KM29005, KM29007, KM29009, KM29010, KM29011. [Fynbos]
(4) 16 km N Hopefield, Kersefontein Farm (32°54'13"S, 18°19'51"E): DM7192, DM7193, DM7196, DM7199, DM7200, DM7204, DM7205, DM7206, DM7207, DM7208, TM2281, TM2283, TM2284. [Fynbos]

South Africa, Free State, Grassland

Cranial
SOUTH AFRICA: FREE STATE PROVINCE:
(1) Vredefort, Helena (780) (ca. 26°53'S, 27°23'E): NMB3171.
(2) Bethlehem, Orange River Confluence (28°14'S, 28°18'E): BM1902.4.3.1.
(3) Brandfort (ca. 28°38'S, 26°23'E): TM17041, TM17042, TM17043, TM17045, TM17046.
(4) Brandfort, Florisbad (686) (28°46'S, 26°05'E): NMB7751, NMB7752, NMB7762-7777.

External
SOUTH AFRICA: FREE STATE PROVINCE:
(1) Brandfort (ca. 28°38'S, 26°23'E): TM17041, TM17043, TM17045.
(2) Brandfort, Florisbad (686) (28°46'S, 26°05'E): NMB7752, NMB7762-7770, NMB7772-7777.

South Africa, Free State, Nama-Karoo

Cranial
SOUTH AFRICA: FREE STATE PROVINCE:
(1) Clocolan District, Alma (ca. 29°38'S, 25°08'E): TM7847.
(2) Jagersfontein Commonage, Disused Mine (ca. 29°39'S, 25°23'E): NMB7578, NMB7579, NMB7584, NMB7585, NMB7595, NMB7600, NMB7601, NMB7603, NMB7604, NMB7605, NMB7606, NMB7609, NMB7611, NMB7617, NMB7618, NMB7619, NMB7625, NMB7629, NMB7633, NMB7634, NMB7635, NMB7636, NMB7639, NMB7642, NMB7643, NMB7646,

Appendix 5.1 continued

NMB7647, NMB7675, NMB7677, NMB7680, NMB7681, NMB7682, NMB7683, NMB7685, NMB7686, NMB7688, NMB7689, NMB7691, NMB7692, NMB7693, NMB7694, NMB7695, NMB7697, NMB7699.

External
SOUTH AFRICA: FREE STATE PROVINCE:
- Jagersfontein Commonage, Disused Mine (ca. 29°39'S, 25°23'E): NMB7578, NMB7579, NMB7581, NMB7584, NMB7585, NMB7593, NMB7594,NMB7595, NMB7599, NMB7600, NMB7601, NMB7602, NMB7603, NMB7604, NMB7605, NMB7606, NMB7611, NMB7616, NMB7617, NMB7618, NMB7619, NMB7621, NMB7625, NMB7629, NMB7633, NMB7634, NMB7635, NMB7636, NMB7639, NMB7641, NMB7642, NMB7643, NMB7645, NMB7646, NMB7647, NMB7675, NMB7677, NMB7679, NMB7680, NMB7681, NMB7682, NMB7683, NMB7684, NMB7685, NMB7686, NMB7687, NMB7688, NMB7689, NMB7690, NMB7691, NMB7693, NMB7694, NMB7695, NMB7696, NMB7697, NMB7699.

Zimbabwe, Savanna

Cranial
ZIMBABWE:
(1) 25 km W Harare, Lion and Cheetah Park (17°23's, 31°17'E): TM34843, TM34844, TM34845.
(2) Harare, (syn. Salisbury), Thornpark (17°38'S, 31°08'E): NMBZ58818, NMBZ58822, NMBZ58827, NMBZ58828.
(3) Sengwa Wildlife Research Station (18°10'S, 28°13'E): TM34864, TM34865, TM34889, TM34890, TM34950, TM34951, TM34970, TM34971, TM34974, TM34975.
(4) Near Gwayi River, Volunteer Farms (18°49S, 27°38E): NMBZ31973, NMBZ31988, NMBZ31989, NMBZ31991.

South Africa, Eastern Cape

External
SOUTH AFRICA: EASTERN CAPE PROVINCE:
- Near Stutterheim (ca. 32°34'S, 27°25'E): KM19632. [Grassland]
- King William's Town (32°52'S, 27°23'E): KM12990, KM13281, KM18112, KM18135, KM19297, KM19369, KM1998, KM2000, KM2001, KM2002, KM2003, KM2004, KM2005, KM2006, KM2007, KM2011, KM24306, KM24307, KM24308, KM32636. [Savanna]

Neoromicia* cf. *melckorum
Cranial [Savanna]
SOUTH AFRICA: LIMPOPO PROVINCE:
(1) Kruger National Park (KNP), Pafuri, Anthrax Camp (22°25'S, 31°12'E): TM37943, TM37944, TM37945.
(2) KNP, Pafuri, Culling Camp (22°25'S, 31°15'E): TM37844, TM37937.
(3) KNP, Pafuri, Fig Tree Forest (22°25'S, 31°18'E): TM38599.
(4) KNP, Pafuri, Fig Tree Forest, 4.8 km downstream of bridge (22°25'S, 31°15'E): TM37680.
(5) KNP, Pafuri, New Fig Tree Forest (22°25'S, 31°18'E): TM37858, TM37906, TM38843.
(6) KNP, Pafuri, Manxeba Windmill (22°24'S, 31°14'E): TM38132.
(7) KNP, Pafuri, Mockford's Garden (22°25'S, 31°18'E): TM37852.
(8) KNP, Pafuri, Old Picnic Site (22°25'S, 31°18'E): TM37924, TM39506.
ZIMBABWE:
(9) Mana Pools National Park (15°43'S, 29°25'E): TM41860, TM41861, TM41862.

External [Savanna]
SOUTH AFRICA: LIMPOPO PROVINCE:
(1) Kruger National Park (KNP), Pafuri, Anthrax Camp (22°25'S, 31°12'E): TM37943, TM37944, TM37945.
(2) KNP, Pafuri, Culling Camp (22°25'S, 31°15'E): TM37844, TM37937.
(3) KNP, Pafuri, Fig Tree Forest (22°25'S, 31°18'E): TM38599.
(4) KNP, Pafuri, New Fig Tree Forest (22°25'S, 31°18'E): TM37858, TM37906.
(5) KNP, Pafuri, Manxeba Windmill (22°24'S, 31°14'E): TM38132.
(6) KNP, Pafuri, Mockford's Garden (22°25'S, 31°18'E): TM37852.
(7) KNP, Pafuri, Old Picnic Site (22°25'S, 31°18'E): TM37923, TM37924.

Appendix 5.1 continued

ZIMBABWE:
- Mana Pools National Park (15°43'S, 29°25'E): TM41860, TM41861, TM41862.

Neoromicia africanus

SA, Pafuri, Savanna

Cranial
SOUTH AFRICA: LIMPOPO PROVINCE:
(1) Kruger National Park (KNP), Pafuri, Fig Tree Camp (22°25'50"S, 31°11'50"E): TM36120, TM36709, TM39463.
(2) KNP, Pafuri, Anthrax Camp (22°25'S, 31°12'E): TM36647.
(3) KNP, Pafuri, Culling Camp (22°25'S, 31°15'E): TM37841, TM37842.
(4) KNP, Pafuri, Fig Tree Forest (22°25'S, 31°18'E): TM38604.
(5) KNP, Pafuri, Mockford's Garden (22°25'S, 31°18'E): TM37849, TM38523, TM38607, TM38608, TM38609, TM38610, TM38611, TM38612, TM39465, TM39466, TM39467.
(6) KNP, Pafuri, New Fig Tree Forest (22°25'S, 31°18'E): TM37856, TM37857, TM37907.
(7) KNP, Pafuri, Old Picnic Site (22°25'S, 31°18'E): TM37816, TM37817, TM37818, TM37820, TM37822, TM37919, TM43863.
(8) KNP, Pafuri, Picnic Site (22°25'S, 31°15'E): TM41731.

South Africa and Swaziland

Cranial
SOUTH AFRICA:
KWAZULU-NATAL PROVINCE:
(1) Pongola, Jozini, Jozini Dam, Dam Wall (27°25'S, 32°04'E): DM5367. [Savanna]
(2) Ngome, Ngome Forest Reserve (27°50'00"S, 31°24'45"E): TM39136, TM39137, TM39138, TM39199, TM39817, TM39818, TM39826, TM39827, TM39828. [Grassland]
(3) 9 km NE Louwsburg, Ithala (syn. Itala) Game Reserve, eastern side of reserve, Square Darvel and Craigadam (27°32'30"S, 31°22'23"E): DM5900, DM5901. [Savanna]
(4) Hluhluwe, Hluhluwe Game Reserve (ca. 28°05'S, 32°02'E): NM1408. [Savanna]
(5) Entumeni, Vuma Farm (28°53'S, 31°23'E): DM4551, DM4552, DM4553, DM4554, DM4555. [Savanna]
(6) Durban, Queensburgh, Malvern, 1 Rindle Rd. (ca. 29°53'S, 30°53'E): DM7019. [Savanna]
(7) Durban, Yellowwood Park, Stainbank Nature Reserve (29°54'S, 30°56'E): DM5869, DM5870, DM5871. [Savanna]
(8) Umkomaas (ca. 30°12'S, 30°48'E): BM1917.10.3.10, BM1917.10.3.5, BM1917.10.3.6. [Savanna]
(9) Umkomaas, Empisini Nature Reserve (30°12'S, 30°48'E): DM5373. [Savanna]
10) Renishaw (30°16'S, 30°44'E): DM5365, DM5402. DM5404, DM7012. [Savanna]
EASTERN CAPE PROVINCE:
(11) Port St Johns (31°38'S, 29°33'E): TM12362, TM12366, TM12368, TM12370. [Savanna]
SWAZILAND:
(12) 10 km N Simunye (26°07'S, 31°57'E): DM5880. [Savanna]

External
SOUTH AFRICA:
KWAZULU-NATAL PROVINCE:
- Manguzi (26°58'S, 32°44'E): NM72, NM73, NM74, NM75. [Savanna]
(1) Pongola, Jozini , Jozini Dam, Dam Wall (27°25'S, 32°04'E): DM5367. [Savanna]
(2) Ngome, Ngome Forest Reserve (27°50'00"S, 31°24'45"E): TM39137, TM39199, TM39818, TM39820, TM39826, TM39828. [Grassland]
(3) 9 km NE Louwsburg, Ithala (syn. Itala) Game Reserve, eastern side of reserve, Square Darvel (27°32'30"S, 31°22'23"E): DM5900, DM5901. [Savanna]
- Hluhluwe, Hluhluwe Game Reserve (ca. 28°05'S, 32°02'E): NM1407, NM1408, NM1409. [Savanna]
(4) Bonamanzi Game Reserve (28°06'S, 32°18'E): DM5405. [Savanna]
(5) Entumeni, Vuma Farm (28°53'S, 31°23'E): DM4552, DM4553, DM4554, DM4555. [Savanna]
- Durban, Malvern (ca. 29°53'S, 30°53'E): TM1085. [Savanna]
(6) Durban, Yellowwood Park, Stainbank Nature Reserve (29°54'S, 30°56'E): DM5869, DM5870, DM5871. [Savanna]

Appendix 5.1 continued

(7) Umkomaas, Empisini Nature Reserve (30°12'S, 30°48'E): DM5373. [Savanna]
(8) Renishaw (30°16'S, 30°44'E): DM5365, DM5402. DM5404. [Savanna]
(9) Umzinto, Umdoni Park (30°24'S, 30°41'E): TM30124, TM30125, TM30141. [Savanna]
EASTERN CAPE PROVINCE:
(10) Port St Johns (31°38'S, 29°33'E): TM1076, TM12361, TM12363, TM12365, TM12367, TM12369. [Savanna]
SWAZILAND:
(11) 10 km N Simunye (26°07'S, 31°57'E): DM5879, DM5880. [Savanna]

Malawi

External
MALAWI:
(1) Nkhota-kota District, W. Lake Malawi, Nkhota-kota (12°56'S, 34°18'E): KM11732-11746. [Savanna]
SOUTHERN REGION:
(2) Zomba District, Zomba Plateau (15°25'S, 35°19'E): KM11707-11721. [Grassland]
(3) Mulanje Mountain, Likhubula Mission (15°57'S, 35°24'E): TM41807, TM41809, TM41812, TM41786. [Grassland]

Neoromicia rueppellii

Southern African, Savanna

Cranial
BOTSWANA:
(1) Maun (ca. 19°53'S, 23°23'E): TM6546.
SOUTH AFRICA: LIMPOPO PROVINCE:
(2) KNP, Pafuri, Anthrax Camp (22°25'S, 31°12'E): TM38279.
(3) KNP, Pafuri, Fig Tree Camp (22°25'50"S, 31°11'50"E): TM36934.
(4) KNP, Pafuri, Fig Tree Forest, 4.8 km down stream of bridge (22°25'S, 31°15'E): TM36791.
(5) KNP, Pafuri, New Fig Tree Forest (22°25'S, 31°18'E): TM37908.
(6) KNP, 4 km W bridge, Levuvhu Hippo Pool (22°26'S, 31°11'E): TM36122.
ZIMBABWE:
(7) Near Gwayi River, Volunteer Farms (18°49S, 27°38E): NMBZ31995.

External
BOTSWANA:
- Maun (ca. 19°53'S, 23°23'E): TM6546.
SOUTH AFRICA: LIMPOPO PROVINCE:
- KNP, Pafuri, Anthrax Camp (22°25'S, 31°12'E): TM38279.
- KNP, Pafuri, Fig Tree Camp (22°25'50"S, 31°11'50"E): TM36609.
- KNP, Pafuri, Fig Tree Forest, 4.8 km down stream of bridge (22°25'S, 31°15'E): TM36791.
- KNP, Pafuri, New Fig Tree Forest (22°25'S, 31°18'E): TM37908.
- KNP, Pafuri, Old Picnic Site (22°25'S, 31°18'E): TM37074
- KNP, 4 km W bridge, Levuvhu Hippo Pool (22°26'S, 31°11'E): TM36122.
ZIMBABWE:
(1) Harare, Marlborough Sewerage Works (17°44'S, 31°00'E): NMBZ60460, NMBZ60466.
(2) Lake McIllwaire National Park (ca. 17°53'S, 30°53'E): NMBZ60455, NMBZ60456, NMBZ60457, NMBZ60458, NMBZ60459, NMBZ60461.
- Harare, Allantica East Research Station (ca. 17°53'S, 30°53'E): NMBZ60462.
(3) Pesu River Gorge (22°27'S, 31°12'E): NMBZ60464.

Zambia, Savanna

External
ZAMBIA:
Barotseland, Balovale (13°01'S, 22°44'E): KM1963, KM1968, KM1969, KM1970, KM1971, KM1972, KM1975, KM1976, KM1962, KM1964, KM1965, KM1967, KM1973, KM1974, KM1977, KM1978, KM1980.

Neoromicia zuluensis

South Africa, Limpopo and Mpumalanga, Savanna

Appendix 5.1 continued

Cranial
SOUTH AFRICA: LIMPOPO PROVINCE:
(1) 67 km W of Messina, Greefswald Farm 37 (syn. Mapungubwe), Shashi-Limpopo Confluence (22°13'S, 29°22'E): TM41408.
(2) Messina, Messina Nature Reserve (22°23'S, 30°03'E): DM5359, DM5375.
(3)Kruger National Park (KNP), Pafuri, Anthrax Camp (22°25'S, 31°12'E): TM36846, TM37863.
(4) KNP, Pafuri, Culling Camp (22°25'S, 31°15'E): TM37938.
(5) KNP, Pafuri, 4.8 km downstream of bridge (22°25'S, 31°15'E): TM37678.
(6) KNP, Pafuri, New Fig Tree Forest (22°25'S, 31°18'E): TM37905.
(7) KNP, Pafuri, Old Picnic Site (22°25'S, 31°18'E): TM36631.
(8) KNP, Pafuri, Fig Tree Camp (22°25'50"S, 31°11'50"E): TM36118, TM37017, TM38169, TM36778, TM36705, TM37001, TM37436, TM36759.
(9) KNP, 4 km W bridge, Levuvhu Hippo Pool (22°26'S, 31°11'E): TM30534, TM34213.
(10) KNP, Shashanga Windmill (22°40'S, 30°59'E): TM30672, TM30673.
(11) KNP, 12 km E of Phalaborwa gate, Erfplaas windmill (23°57'S, 31°07'E): TM36572, TM36574.
(12) KNP, 2 km E Letaba Olifants confluence, Lebombo Ironwood Forest (23°59'S, 31°50'E): TM39697.
(13) KNP, 2 km SE Roodewal Private Camp (24°08'S, 31°36'E): TM39684.
(14) KNP, 1.5 km NW of Skukuza, dense woodland of western reservoir (24°59'S, 31°35'E): TM39760, TM39761.
(15) Soutpansberg, 13 km W Vivo, Farm Urk 10, Blouberg Private Nature Reserve (23°02'S, 29°07'E): TM24087.
(16) Waterberg, 10 MI NE Ellisras, Tambotieskloof (607) (23°44'E, 27°55'S): TM19372.
(17) Waterberg, 65 km N Vaalwater, Lapalala Wilderness area (23°51'S, 28°09'E): TM39792, TM39794, TM39795.
(18) Leydsdorp, Sheila No. 10 (24°04'S, 31°09'E): TM6457, TM6458.
(19) Waterberg, 32 km NW Vaalwater, Farm Platbos (24°13'S, 27°52'E): TM24752.
MPUMALANGA:
(20) 11 km N of Newington, Acornhoek (24°45'E, 31°25'E): TM17293.

External
SOUTH AFRICA: LIMPOPO PROVINCE:
(1) 67 km W of Messina, Greefswald Farm 37 (syn. Mapungubwe), Shashi-Limpopo Confluence (22°13'S, 29°22'E): TM41408.
(2) Messina, Messina Nature Reserve (22°23'S, 30°03'E): DM5359, DM5375.
(3) Kruger National Park (KNP), Pafuri, Anthrax Camp (22°25'S, 31°12'E): TM37863.
(4) KNP, Pafuri, Culling Camp (22°25'S, 31°15'E): TM37938.
(5) KNP, Pafuri, Fig Tree Camp (22°25'50"S, 31°11'50"E): TM36778, TM37436.
- KNP, 4 km W bridge, Levuvhu Hippo Pool (22°26'S, 31°11'E): TM34213.
(6) KNP, Shashanga Windmill (22°40'S, 30°59'E): TM30672.
(7) KNP, 2 km E Letaba Olifants confluence, Lebombo Ironwood Forest (23°59'S, 31°50'E): TM39697.
(8) KNP, 1.5 km NW of Skukuza, dense woodland of western reservoir (24°59'S, 31°35'E): TM39761.
(9) Waterberg, 10 MI NE Ellisras, Tambotieskloof (607) (23°44'E, 27°55'S): TM19372.
(10) Waterberg, 65 km N Vaalwater, Lapalala Wilderness Area (23°51'S, 28°09'E): TM39794.
(11) Leydsdorp, Sheila No. 10 (24°04'S, 31°09'E): TM6458.
(12) Waterberg, 32 km NW Vaalwater, Farm Platbos (24°13'S, 27°52'E): TM24752.
(13) Barberton, Hectorspruit (25°26'S, 31°41'E): TM1072.

Pipistrellus hesperidus
Cranial
SOUTH AFRICA: KWAZULU-NATAL:
(1) Ndumu Game Reserve (26°53'S, 32°15'E): TM35184, TM35207, TM35232. [Savanna]
(2) Kosi Lake, Department of Health Camp (26°57'30"S, 32°49'30"E): TM40455, TM40457. [Savanna]
(3) Ngome, Ngome Forest Reserve (27°50'00"S, 31°24'45"E): TM39134, TM39135, TM39840, TM39854. [Grassland]

Appendix 5.1 continued

(4) Hluhluwe, Hluhluwe Game Reserve, Research Camp (28°04'S, 32°02'E): TM44399. [Savanna]
(5) St. Lucia, 2 km N of St Lucia Village, Ipheva Camp Site (28°21'S, 32°25'E): DM1063, DM1064, DM6895, DM6896. [Savanna]
(6) 6 km NNE Mtubatuba, Dukuduku Forest (28°23'S, 32°21'E): TM40406, TM40410. [Savanna]
(7) Eshowe, Dlinza Forest (28°53'S, 31°27'E): DM5356, DM5397, DM5352, DM5393, DM5406, DM5360, DM5372, DM5386, DM5363, DM5374. [Savanna]
(8) Mtunzini, Twin Streams Farm (28°57'S, 31°30'E): DM5872. [Savanna]
(9) Mtunzini, Umlalazi Nature Reserve (28°58'S, 31°48'E): TM30126. [Savanna]
(10) Harold Johnson Nature Reserve (29°12'S, 31°25'E): DM5369. [Savanna]
(11) Mount Edgecombe, Sugar Research Association Estate (29°42'S, 31°04'E): DM7143. [Savanna]
(12) Kloof, Kranskloof Nature Reserve (29°46'S, 30°49'E): TM40014, TM40015, DM5876. [Savanna]
(13) Hillcrest, Wishart Road, 26 Hathaway (29°47'S, 30°46'E): DM7016. [Savanna]
(14) Durban, Cowies Hill (29°50'S, 30°53'E): DM7201. [Savanna]
(15) Durban, Glenwood, Pigeon Valley Park (29°51'S, 30°59'E): DM5384, DM5385. [Savanna]
(16) Durban, Queensburgh, North Park Nature Reserve (29°52'S, 30°45'E): DM5403, DM5382. [Savanna]
(17) Durban, Malvern (ca. 29°53'S, 30°56'E): TM1085. [Savanna]
(18) Durban, Glenmore, 108 Bowen Avenue (ca. 29°53'S, 30°53'E): DM6893. [Savanna]
(19) Durban, Yellowwood Park, Stainbank Nature Reserve (29°54'S, 30°56'E): DM5868. [Savanna]
(20) Durban, Yellowwood Park, 18 Dove Crescent (ca. 29°54'S, 30°52'E): DM5388. [Savanna]

External
SOUTH AFRICA: KWAZULU-NATAL:
(1) Ndumu Game Reserve (26°53'S, 32°15'E): TM35207, TM35232. [Savanna]
- Kosi Lake, Department of Health Camp (26°57'30"S, 32°49'30"E): TM40456. [Savanna]
- Ngome, Ngome Forest Reserve (27°50'00"S, 31°24'45"E): TM39134, TM39840. [Grassland]
-Hluhluwe, Hluhluwe Game Reserve, Research Camp (28°04'S, 32°02'E): TM44398. [Savanna]
- St Lucia, False Bay (28°01'S, 32°21'E): TM40717. [Savanna]
(2) St. Lucia, 2 km N of St Lucia Village, Ipheva Camp Site (28°21'S, 32°25'E): DM1063, DM1064. [Savanna]
- 6 km NNE Mtubatuba, Dukuduku Forest (28°23'S, 32°21'E): TM40406, TM40417. [Savanna]
(3) Eshowe, Dlinza Forest (28°53'S, 31°27'E): DM5356, DM5397, DM5352, DM5393, DM5406, DM5360, DM5372, DM5386, DM5363, DM5374. [Savanna]
- Mtunzini, Umlalazi Nature Reserve (28°58'S, 31°48'E): TM30126. [Savanna]
(4) Harold Johnson Nature Reserve (29°12'S, 31°25'E): DM5369. [Savanna]
(5) Mount Edgecombe, Sugar Research Association Estate (29°42'S, 31°04'E): DM7143. [Savanna]
(6) Durban, Cowies Hill (29°50'S, 30°53'E): DM7201. [Savanna]
(7) Durban, Glenwood, Pigeon Valley Park (29°51'S, 30°59'E): DM5384, DM5385. [Savanna]
(8) Durban, Queensburgh, North Park Nature Reserve (29°52'S, 30°45'E): DM5403, DM5382. [Savanna]
- Durban, Sarnia Road (29°50'S, 30°53'E): DM5378. [Savanna]
(9)Durban, Yellowwood Park, Stainbank Nature Reserve (29°54'S, 30°56'E): DM5868. [Savanna]
(10) Durban, Yellowwood Park, 18 Dove Crescent (ca. 29°54'S, 30°52'E): DM5388. [Savanna]
EASTERN CAPE:
- Ngqeleni (31°46'S, 29°02'E): TM1073. [Savanna]

Pipistrellus rusticus
Cranial [Savanna]
SOUTH AFRICA: LIMPOPO PROVINCE:
(1) Messina, Messina Nature Reserve (22°23'S, 30°03'E): DM5318, DM5395, DM5399, DM5407, DM5865, DM5866, DM5379, DM5389, DM5390, DM5391, DM5394.
(2) Waterberg area, 30 km NE Vaalwater, Farm Klipfontein (24°08'S, 28°08'E): TM39813, TM39815, TM39879, TM39880, TM39883, TM39886, TM39890, TM39891, TM39894, TM40287, TM39814, TM39881, TM39884, TM40291, TM39882, TM39887.
(3) 8 km E Warmbaths, Rissik Private Nature Reserve (24°53'S, 28°27'E): TM20654.

Appendix 5.1 continued

MPUMALANGA:
(4) Nelspruit, Legogot (25°13'S, 31°15'E): BM1906.8.2.34, BM1906.8.2.37.
ZIMBABWE:
(5) Near Gwayi River, Volunteer Farms (18°49S, 27°38E): NMBZ31992.
(6) Sentinel Ranch (22°10S, 29°30E): NMBZ9901, NMBZ9893, NMBZ9891, NMBZ9896, NMBZ9892.

External [Savanna]
SOUTH AFRICA: LIMPOPO PROVINCE:
(1) Messina, Messina Nature Reserve (22°23'S, 30°03'E): DM5318, DM5395, DM5399, DM5407, DM5865, DM5866, DM5867, DM5379, DM5389, DM5390, DM5391, DM5394.
- Waterberg area, 30 km NE Vaalwater, Farm Klipfontein (24°08'S, 28°08'E): TM39879, TM39883, TM39890, TM39814, TM39881, TM39885, TM39887, TM39892.
(2) 8 km E Warmbaths, Rissik Private Nature Reserve (24°53'S, 28°27'E): TM20649, TM20651, TM20653, TM20655.

Appendix 5.2

Tooth wear class description

Specimens were assigned to one of four tooth wear classes based on the degree of wear on the molar teeth (adapted from Rautenbach 1986). The tooth wear classes are described as follows.
Tooth wear class A: Very little wear on cusps and cristae.
Tooth wear class B: Light wear on cusps and cristae, paraconal, metaconal and protoconal basins still unworn.
Tooth wear class C: Moderate wear on cusps and cristae, and paraconal, metaconal and protoconal basins starting to be worn.
Tooth wear class D: Heavy wear, with paracones and metacones worn extensively, and large areas of wear on the protocones.

Appendix 5.3

Re-identified specimens

Specimens reassigned to other species based on PCA and DFA with specimens of known species identity.

Accession number	New species assignment	Previous species assignment
NMBZ31992	*Pipistrellus rusticus*	*Hypsugo anchietae*
TM40291	*Pipistrellus rusticus*	*Hypsugo anchietae*
TM40287	*Pipistrellus rusticus*	*Hypsugo anchietae*
KM8083	*Neoromicia zuluensis*	*Neoromicia capensis*
KM8092	*Neoromicia zuluensis*	*Neoromicia capensis*
KM8094	*Neoromicia zuluensis*	*Neoromicia capensis*
TM36778	*Neoromicia* cf. *melckorum*	*Neoromicia zuluensis*
NMBZ31973	*Neoromicia capensis*	*Neoromicia zuluensis*
NMBZ31988	*Neoromicia capensis*	*Neoromicia zuluensis*

Appendix 5.4

Significantly skew or kurtotic measurements found in vespertilionid bats from southern Africa

***Eptesicus hottentotus* – South Africa, Western Cape Province**
Cranial:

Width of the fourth upper premolar (WUPM4) was significantly skewed ($P < 0.05$), but no measurements were significantly kurtotic.

***Eptesicus hottentotus* – Namibia**
Cranial:

Least inter-orbital width (LIW) was significantly skewed in females ($P < 0.05$), and width of the upper fourth premolar tooth (WUPM4) was significantly skewed in males ($P < 0.05$), but no measurements were significantly kurtotic

External:

In females, head and body length (HB) and tragus breadth (TRB) were significantly skewed (all $P < 0.05$), and head and body (HB; $P < 0.05$) and ear length (E; $P < 0.05$) and tragus breadth (TRB; $P < 0.01$) were significantly kurtotic. In measurements of males, tail length (TL) was significantly skewed, and tragus length (TRL) was significantly kurtotic (both $P < 0.05$).

Hypsugo anchietae
Cranial:

In females, least inter-orbital width (LIW) was significantly skewed and kurtotic (both $P < 0.05$), and zygomatic breadth (ZB) and condylo-incisor skull length (CIL) were significantly kurtotic (both $P < 0.05$). In males, zygomatic breadth (ZB) and least inter-orbital width (LIW) were significantly kurtotic (both $P < 0.05$), but no measurements were significantly skewed.

***Neoromicia capensis* – Namibia and South Africa, Nama-Karoo biome**
Cranial:

In females, no measurements were significantly skewed, kurtotic or non-normally distributed, but in males, length of the upper first molar (LUM1) was significantly skewed and kurtotic (both at $P < 0.05$). In specimens of tooth wear class A, no measurements were significantly skewed, but zygomatic breadth (ZB) was significantly kurtotic ($P < 0.05$). In specimens of tooth wear class B, widths of the foramen magnum (WFM) and articular surface (WAS) were both significantly skewed and kurtotic (both at $P < 0.05$), and least inter-orbital width (LIW) was significantly skewed ($P < 0.05$). In specimens of tooth wear class C, braincase breadth (BB) was significantly skewed and kurtotic (both at $P < 0.05$), and four measurements were significantly skewed; zygomatic breadth (ZB), width of the foramen magnum (WFM), width if the articular surface (WAS), and moment arm of the temporal (MAOT) (all at $P < 0.05$). In specimens of tooth wear class D, width of the foramen magnum (WFM) and moment arm of the temporal (MAOT) were significantly skewed and kurtotic (both at $P < 0.05$), and zygomatic breadth (ZB) and condylo-incisor length (CIL) were significantly kurtotic ($P < 0.05$).

***Neoromicia capensis* – South Africa, Western Cape Province**
Cranial:

In females, braincase height (BH) and least inter-orbital width (LIW) were skewed (both $P < 0.05$), and braincase breadth (BB) was kurtotic ($P < 0.05$). In males, width of the upper fourth premolar (WUPM4) was skewed and kurtotic (both at $P < 0.05$). There were too few specimens in tooth wear class A to run tests for kurtosis. However, width across the outer surfaces of the upper canine teeth (WOUC) and width between the inner surfaces of the upper first molar teeth (WIUM1) were significantly skewed (both at $P < 0.05$). In tooth wear class B, braincase breadth (BB) was significantly skewed and kurtotic (both at $P < 0.05$). In tooth wear class C, moment arm of the temporal (MAOT) was significantly skewed and kurtotic (both at $P < 0.05$). In tooth wear class D, width of the upper fourth premolar (WUPM4) was significantly kurtotic ($P < 0.05$).

***Neoromicia capensis* – South Africa, Free State Province, Grassland**
Cranial:

In females, no measurements were significantly skewed or kurtotic. In males, width of the upper fourth premolar (WUPM4) was significantly skewed and kurtotic (both at $P < 0.01$). There

Appendix 5.4 continued

were too few specimens in tooth wear class A to run kurtosis tests. However, seven measurements were significantly skewed: braincase breadth (BB), least inter-orbital width (LIW), width of the foramen magnum (WFM), width of the articular surface (WAS), width between the inner surfaces of the upper first molar teeth (WIUM1) (all at $P < 0.05$); and width of the upper fourth premolar (WUPM4), and length of the upper first molar (LUM1) (both at $P < 0.01$). There were also too few specimens in tooth wear class D to run skewedness and kurtosis tests. In specimens of tooth wear class B no measurements were skewed, but width of the upper fourth premolar (WUPM4) was significantly kurtotic ($P < 0.05$). In specimens of tooth wear class C, braincase breadth (BB) and moment arm of the temporal (MAOT) were significantly skewed and kurtotic (both at $P < 0.01$).

External:

In females, tail length (TL) was significantly skewed ($P < 0.01$) and kurtotic ($P < 0.05$), and tragus length (TRL) was significantly skewed ($P < 0.05$). In males, hind foot length (HF) was significantly skewed and kurtotic (both at $P < 0.05$), and the other hind foot length measurement (HFL) was significantly skewed ($P < 0.05$).

***Neoromicia capensis* – South Africa, Free State Province, Nama-Karoo**

Cranial:

In females, braincase breadth (BB) was significantly skewed and kurtotic (both at $P < 0.05$), but in males, no measurements were significantly skewed or kurtotic. There were too few specimens in tooth wear class A and B to run kurtosis tests. However, in tooth wear class A, four measurements were significantly skewed: width of the foramen magnum (WFM), width between the inner surfaces of the upper first molar teeth (WIUM1), width of the upper fourth premolar tooth (WUPM4), and moment arm of the temporal (MAOT) (all at $P < 0.05$). In tooth wear class B, seven measurements were significantly skewed: condylo-incisor skull length (CIL), zygomatic breadth (ZB), braincase breadth (BB), width of the foramen magnum (WFM), width of the upper fourth premolar (WUPM4), length of the upper first molar (LUM1), and moment arm of the temporal (MAOT) (all at $P < 0.05$). In tooth wear class C, braincase height (BH) was significantly skewed and kurtotic (both at $P < 0.01$). In tooth wear class D, no measurements were significantly skewed or kurtotic.

External:

In females, total (TOT), tail (T), and third metacarpal (TMETA) lengths were significantly skewed and kurtotic: T (both at $P < 0.01$); TOT (both at $P < 0.01$); TMETA (both at $P < 0.05$). In males, forearm length (FAL) was significantly skewed and kurtotic (both at $P < 0.01$), and ear length (E) was significantly skewed ($P < 0.05$). Skewedness and kurtosis were also assessed within the tooth wear classes of male specimens. However, only tooth wear classes C and D had large enough sample sizes to allow kurtosis tests, and the small sample sizes in tooth wear classes A and B probably influenced the large number of significantly skewed measurements. In males of tooth wear class A, six measurements were skewed; both measurements of hind foot (HFL, HF), forearm (FAL), ear (E), and tibia lengths (TIB) and tragus breadth (TRB) (all at $P < 0.05$). In males of tooth wear class B, eight measurements were skewed; both measurements of tail (T, TL), both hind foot (HFL, HF), both measurements of forearm (FAL, FA), and ear (E) lengths, and tragus breadth (TRB) (all at $P < 0.05$). In males of tooth wear class C, forearm (FAL: $P < 0.01$) and ear (E: $P < 0.05$) lengths were skewed, and forearm length (FAL) was also kurtotic ($P < 0.05$). In males of tooth wear class D, total (TOT: $P < 0.05$) and both hind foot (HFL: $P < 0.05$, HF: $P < 0.01$) lengths were skewed, and hind foot length (HF) was also kurtotic ($P < 0.05$).

***Neoromicia capensis* – Zimbabwe**

Cranial:

In females, braincase height (BH) was significantly skewed ($P < 0.05$), but no measurements were significantly kurtotic. In males, no measurements were significantly skewed or kurtotic. There were too few specimens in tooth wear class D to run normality, skewedness and kurtosis tests, and too few specimens in tooth wear classes A and B to run normality tests. In tooth wear class A, least inter-orbital width (LIW) and width of the foramen magnum (WFM) were significantly kurtotic ($P < 0.01$), and six measurements were significantly skewed and kurtotic: condylo-incisor length (CIL), braincase height (BH), braincase breadth (BB), width across the outer surfaces of the upper canines (WOUC), width of the fourth upper premolar (WUPM4), and

Appendix 5.4 continued

length of the first upper molar (LUM1) (all at $P < 0.05$, except the skewedness of WOUC, $P < 0.01$). In tooth wear class B, zygomatic breadth (ZB) and braincase breadth (BB) were significantly skewed and kurtotic ($P < 0.05$); condylo-incisor length (CIL) was significantly skewed ($P < 0.05$); and four other measurements were significantly kurtotic: width across the outer surfaces of the upper canine teeth (WOUC), width of the upper fourth premolar (WUPM4) (both at $P < 0.05$), width of the foramen magnum (WFM) and width of the articular surface (WAS) (both at $P < 0.01$). In tooth wear class C no measurements were significantly skewed or kurtotic.

Neoromicia* cf. *melckorum
Cranial:

In females, zygomatic breadth (ZB) was significantly skewed ($P < 0.05$), but no measurements were significantly kurtotic. In males, braincase height (BH) was significantly skewed and kurtotic ($P < 0.05$).

External:

In analyses of females, tail length (TL) was significantly kurtotic ($P < 0.05$), and four measurements were significantly skewed; total (TOT), tail (T), hind foot (HF), and forearm (FAL) lengths (all at $P < 0.05$). In males, no measurements were significantly skewed or kurtotic.

***Neoromicia africanus* – South Africa, Limpopo Province, Pafuri area**
Cranial:

In females, width across the outer surfaces of the upper canine teeth (WOUC) was significantly skewed and kurtotic (both at $P < 0.05$). In males width between the inner surfaces of the upper first molar teeth (WIUM1) was significantly skewed and kurtotic (both at $P < 0.05$), and condylo-incisor length of the skull (CIL) was significantly kurtotic ($P < 0.05$). In females of tooth wear class A, no measurements were significantly skewed or kurtotic. In females of tooth wear class B, moment arm of the temporal (MAOT) was both significantly skewed and kurtotic (both $P < 0.05$), while another five measurements were significantly kurtotic: width between the inner surfaces of the upper first molar teeth (WIUM1), braincase breadth (BB) (both at $P < 0.01$), width of the foramen magnum (WFM), zygomatic breadth (ZB) and condylo-incisor length of the skull (CIL) (all at $P < 0.05$). In females of tooth wear class C, width between the inner surfaces of the upper first molar teeth (WIUM1) was significantly kurtotic ($P < 0.05$), and three measurements were significantly skewed and kurtotic: width across the outer surfaces of the upper canine teeth (WOUC) (skewed $P < 0.05$; kurtotic $P < 0.01$), braincase height (BH) and least inter-orbital width (LIW) (all at $P < 0.05$).

***Neoromicia africanus* – South Africa and Swaziland**
Cranial:

In females, no measurements were significantly kurtotic, but condylo-incisor length of the skull (CIL) and width of the articular surface (WAS) were significantly skewed (both at $P < 0.05$). In males, no measurements were significantly kurtotic, but length of the first upper molar (LUM1) was significantly skewed ($P < 0.05$). There were too few specimens of males in tooth wear class A to run skewedness and kurtosis tests. In males of tooth wear class B, three measurements were significantly skewed and kurtotic; least inter-orbital width (LIW) (both at $P < 0.01$), width of the foramen magnum (WFM) and width of the articular surface (WAS) (both at $P < 0.05$); and another measurement, moment arm of the temporal (MAOT), was kurtotic ($P < 0.05$). In males of tooth wear class C, length of the first upper molar (LUM1) was significantly skewed ($P < 0.01$) and kurtotic ($P < 0.05$), and width of the fourth upper premolar (WUPM4) was significantly skewed ($P < 0.05$). In males of tooth wear class D, least inter-orbital width (LIW) was significantly skewed and kurtotic (both at $P < 0.05$), and three measurements were significantly kurtotic: width between the inner surfaces of the upper first molars (WIUM1), length of the upper first molar (LUM1), moment arm of the temporal (MAOT) (all at $P < 0.05$).

External:

In females, no measurements were significantly skewed or kurtotic. In males forearm length (FAL) was significantly skewed ($P < 0.01$) and kurtotic ($P < 0.05$). In tooth wear class A, forearm length (FAL) was significantly skewed ($P < 0.05$), tail length (TL) was significantly kurtotic ($P < 0.05$), and three measurements were significantly skewed and kurtotic; tail (T) and tragus lengths (TRL), and tragus breadth (TRB) (all at $P < 0.05$). In tooth wear class B, due to the small sample

Appendix 5.4 continued

sizes there were no kurtosis tests. However, three measurements were significantly skewed: total (TOT), forearm (FAL), and tragus (TRL) lengths (all at $P < 0.05$). In tooth wear class C, third metacarpal length (TMETA) was significantly skewed and kurtotic (both at $P < 0.01$), while forearm length (FAL) was significantly skewed ($P < 0.05$). In tooth wear class D, no measurements were significantly skewed, but two measurements were significantly kurtotic; tragus breadth (TRB: $P < 0.05$) and tail length (TL: $P < 0.01$).

***Neoromicia africanus* – Malawi**
External:

In females, head and body length (HB) was significantly skewed ($P < 0.01$) and kurtotic ($P < 0.05$), and tail length (T) was significantly skewed ($P < 0.05$). In males, forearm length (FA) was both significantly skewed and kurtotic ($P < 0.05$), and head and body length (HB) was significantly skewed ($P < 0.05$). In tooth wear class B of females, tibia length (TIB) was significantly skewed and kurtotic (both at $P<0.05$), and three other measurements were significantly skewed; head and body (HB), hind foot (HFL), and ear (E) lengths (all at $P < 0.05$). In tooth wear class C of females, no measurements were significantly skewed, but ear length (E) was significantly kurtotic ($P < 0.05$). In tooth wear class D of females, tragus length (TRL) and breadth (TRB) were significantly skewed and kurtotic (both at $P < 0.05$), while tail length (TL) was significantly skewed ($P < 0.05$), and forearm length (FA) was significantly kurtotic ($P < 0.05$).

***Neoromicia rueppellii* – Southern African**
External:

In females, two measurements were significantly kurtotic, tail length (T) and tragus breadth (TRB) (both at $P < 0.05$), and three measurements were significantly skewed; total (TOT) and third metacarpal (TMETA) lengths, and tragus breadth (TRB) (all at $P < 0.05$). While in males, four measurements were both significantly skewed and kurtotic; tail (T), tibia (TIB), third metacarpal (TMETA), and tragus (TRL) lengths (all at $P < 0.05$).

***Neoromicia rueppellii* – Zambia**
External:

In females, hind foot length (HFL) was significantly skewed and kurtotic (both at $P < 0.01$). In males, three measurements were significantly kurtotic; both measurements of hind foot (HFL, HF) and tragus (TRL) lengths (all at $P < 0.05$).

***Neoromicia zuluensis* – South Africa, Mpumalanga and Limpopo Provinces**
Cranial:

No measurements were significantly skewed or kurtotic in both males and females.

***Neoromicia zuluensis* – South Africa, Mpumalanga and Limpopo Provinces**
External:

In males, tibia length (TIB) was significantly skewed and kurtotic (both at $P < 0.05$), and five other measurements were significantly skewed: total (TOT), tail (T), hind foot (HFL), ear (E) and third metacarpal (TMETA) lengths (all at $P < 0.05$). No measurements were significantly skewed or kurtotic in females.

***Neoromicia zuluensis* – Namibia**
Cranial:

In females of tooth wear class B, width of the foramen magnum (WFM) and width of the articular surface (WAS) were both significantly skewed and kurtotic (all at $P < 0.01$). Given the small sample size of females of tooth wear class C, only the skewedness tests could be run and even these were probably affected by the small sample size, as six of the 14 measurements were significantly skewed: width of the articular surface (WAS), width across the outer surfaces of the upper canines (WOUC), width between the inner surfaces of the upper first molars (WIUM1), width of the upper fourth premolar (WUPM4), length of the upper first molar (LUM1), and moment arm of the temporal (MAOT) (all at $P < 0.05$). In females of tooth wear class D, no measurements were significantly skewed or kurtotic.

Pipistrellus hesperidus
Cranial:

Appendix 5.4 continued

In females of tooth wear class A, width of the upper fourth premolar (WUPM4) and length of the upper first molar (LUM1) were significantly skewed (both at $P < 0.01$) and kurtotic (both at $P < 0.05$). In females of tooth wear class B, braincase height (BH) was both significantly skewed and kurtotic (both at $P < 0.01$). In females of tooth wear class C, four measurements were significantly skewed: braincase breadth (BB), width of the articular surface (WAS), width across the outer surfaces of the upper canine teeth (WOUC), and moment arm of the temporal (MAOT) (all at $P < 0.05$). In males of tooth wear class A, width between the inner surfaces of the upper first molars (WIUM1) was significantly skewed and kurtotic ($P < 0.05$), while moment arm of the temporal (MAOT) was significantly skewed ($P < 0.05$). In males of tooth wear class B, condylo-incisor length of the skull (CIL) and width between the inner surfaces of the upper first molars (WIUM1) were significantly kurtotic (both at $P < 0.05$). In males of tooth wear class C, width of the upper fourth premolar (WUPM4) was significantly skewed and kurtotic (both at $P < 0.05$).

External:

In females, four measurements were significantly skewed and kurtotic: both measurements of tail (TL, T: all at $P < 0.05$), ear (E: skewed, $P < 0.05$; kurtotic, $P < 0.01$), and tibia (TIB: both at $P < 0.05$) lengths. In males, tragus breadth (TRB) was significantly skewed ($P < 0.05$), tail length (T) was significantly kurtotic ($P < 0.05$), and four measurements were significantly skewed and kurtotic: hind foot (HFL: both at $P < 0.05$), ear (E: both at $P < 0.05$), tragus (TRL: skewed, $P < 0.05$; kurtotic, $P < 0.01$), and tibia (TIB: both at $P < 0.05$) lengths. In females of tooth wear class A ear length (E) was significantly skewed ($P < 0.01$) and kurtotic ($P < 0.05$); head and body length (HB) was significantly skewed ($P < 0.05$); and hind foot (HF) and tragus (TRL) lengths were significantly kurtotic (both $P < 0.05$). In females of tooth wear class B, tibia (TIB) and tragus (TRL) lengths were significantly skewed and kurtotic (both at $P < 0.01$); and tail (TL) and hind foot (HFL) lengths were significantly kurtotic (both at $P < 0.05$). In males of tooth wear class A, tragus length (TRL) was significantly skewed and kurtotic ($P < 0.05$); hind foot length (HFL) was significantly kurtotic ($P < 0.05$); and tail length (T) was significantly skewed ($P < 0.05$). In males of tooth wear class B, tragus breadth (TRB) and length (TRL) were significantly skewed and kurtotic (TRB: both at $P < 0.01$; TRL: both at $P < 0.05$); and hind foot length (HFL) was significantly kurtotic ($P < 0.05$).

Pipistrellus rusticus

Cranial:

In females of tooth wear class A, width across the outer surfaces of the upper canines (WOUC) was significantly kurtotic ($P < 0.05$). In females of tooth wear class B, least inter-orbital width (LIW) and length of the upper first molar (LUM1) were significantly skewed and kurtotic (all t $P < 0.05$). In males of tooth wear class A, moment arm of the temporal was both significantly skewed and kurtotic (both at $P < 0.05$); condylo-incisor length (CIL) was significantly skewed ($P < 0.05$); and two measurements were significantly kurtotic: width between the inner surfaces of the upper first molars (WIUM1) and length of the upper first molar (LUM1) (both at $P < 0.05$). No measurements were significantly skewed or kurtotic in males of tooth wear class B. In males and females of tooth wear class C, width of the articular surface (WAS) was significantly skewed ($P < 0.01$) and kurtotic ($P < 0.05$); moment arm of the temporal (MAOT) was significantly skewed ($P < 0.05$); and zygomatic breadth (ZB) was significantly kurtotic ($P < 0.05$).

External:

In females, ear (E) and third metatarsal (TMETA) lengths were significantly skewed and kurtotic (E: both at $P < 0.05$, TMETA: both at $P < 0.01$), and forearm length was kurtotic (FAL: $P < 0.05$). No measurements were significantly skewed or kurtotic in males. In tooth wear class A, tail length (TL) was significantly skewed and kurtotic ($P < 0.05$). In tooth wear class B hind foot (HFL) and ear (E) lengths were significantly skewed (HFL: $P < 0.05$, E: $P < 0.01$) and kurtotic (both at $P < 0.01$); forearm length (FA) and tragus breadth (TRB) were significantly skewed only (both at $P < 0.05$); and tail (T); and third metatarsal (TMETA) lengths were significantly kurtotic (both at $P < 0.05$). There were insufficient specimens in tooth wear class C to test for significant skewedness and kurtosis.

Appendix 5.5

Kruskall-Wallis test results on vespertilionid bats from southern Africa

Kruskall-Wallis tests were run when the data violated the ANOVA assumptions. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively. df = degrees of freedom.

Cranial measurements

Species	Area	Factor	Measurement	Chi-square	df	Significance
Hypsugo anchietae	Southern Africa	Sex	WUPM4	0.911	1	0.340
		TW	BB	2.822	3	0.420
			WIUM1	1.884	3	0.597
			WUPM4	2.116	3	0.549
Neoromicia capensis	Namibia & South Africa	Sex	WAS	1.424	1	0.233
			LUM1	0.053	1	0.818
		TW	ZB	7.797	3	0.050
			WFM	0.592	3	0.898
			LUM1	1.915	3	0.590
			MAOT	3.452	3	0.327
Neoromicia capensis	South Africa, Western Cape	Sex	BH	1.540	1	0.215
			POW	1.619	1	0.203
			WUPM4	2.092	1	0.148
		TW	BB	3.589	3	0.309
			POW	5.189	3	0.158
			WAS	11.006	3	0.012*
			WUPM4	6.162	3	0.104
Neoromicia capensis	South Africa, Free State, Grassland	Sex	ZB	1.261	1	0.261
			WUPM4	0.003	1	0.956
		TW	MAOT	9.049	3	0.029*
Neoromicia capensis	South Africa, Free State, Nama-Karoo	Sex	BH	1.446	1	0.229
			WUPM4	6.291	1	0.012*
			LUM1	1.389	1	0.239
		TW	BH	2.777	3	0.427
			WAS	0.324	3	0.955
			WUPM4	1.793	3	0.616
Neoromicia capensis	Zimbabwe	Sex	WIUM1	0.361	1	0.548
		TW	WFM	2.543	3	0.468

Appendix 5.5 continued

Species	Area	Factor	Measurement	Chi-square	df	Significance
Neoromicia cf. *melckorum*	South Africa & Zimbabwe	Sex	WOUC	4.196	1	0.041*
		TW	CIL	8.750	3	0.033*
			ZB	6.196	3	0.102
			POW	6.188	3	0.103
			LUM1	3.071	3	0.381
Neoromicia africanus	South Africa, Limpopo, Pafuri area	Sex	POW	0.690	1	0.406
			WOUC	1.522	1	0.217
			WIUM1	0.327	1	0.567
		TW	WAS	4.119	3	0.249
			WOUC	1.867	3	0.601
			WUPM4	3.130	3	0.372
			MAOT	7.661	3	0.054
Neoromicia africanus	South Africa & Swaziland	Sex	CIL	4.726	1	0.030*
			WUPM4	1.833	1	0.176
			LUM1	3.948	1	0.047*
		TW	POW	7.529	3	0.057
			WOUC	1.047	3	0.790
			WIUM1	2.422	3	0.490
			WUPM4	2.844	3	0.416
			LUM1	1.178	3	0.758
Neoromicia rueppellii	Southern Africa	TW	CIL	0.696	2	0.706
			WIUM1	0.000	2	1.000
Neoromicia zuluensis	South Africa , Limpopo & Mpumalanga	Sex	CIL	8.044	1	0.005 **
			WAS	0.382	1	0.536
			WIUM1	2.231	1	0.135
			LUM1	3.152	1	0.076
			MAOT	9.377	1	0.002 **
		TW	WAS	10.301	3	0.016 *
			WIUM1	0.061	3	0.996
			WUPM4	2.433	3	0.487
			LUM1	4.518	3	0.211
			MAOT	2.231	3	0.526

Appendix 5.5 continued

Species	Area	Factor	Measurement	Chi-square	df	Significance
Pipistrellus hesperidus	South Africa, KwaZulu-Natal	Sex	CIL	6.191	1	0.013 *
			BH	0.099	1	0.753
			WAS	3.454	1	0.063
			WIUM1	0.820	1	0.365
			WUPM4	9.081	1	0.003 **
			MAOT	5.812	1	0.016*
		TW	WIUM1	0.467	2	0.792
			WUPM4	1.444	2	0.486
			LUM1	1.922	2	0.382
			MAOT	0.048	2	0.976
Pipistrellus rusticus	South Africa & Zimbabwe	Sex	BB	0.982	1	0.322
			WFM	0.852	1	0.356
			WAS	0.531	1	0.466
		TW	BH	3.625	2	0.163
			POW	0.393	2	0.821
			WFM	0.677	2	0.713
			WAS	1.742	2	0.418
			WIUM1	0.285	2	0.867

External:

Species	Area	Factor	Measurement	Chi-square	df	Significance
Eptesicus hottentotus	Namibia	Sex	TRB	0.017	1	0.896
		TW	TRB	1.562	2	0.458
			T	0.000	1	1.000
Hypsugo anchietae	Southern Africa	Sex	TRB	0.000	1	1.000
			T	0.810	1	0.368
Neoromicia capensis	South Africa, Free State, Grassland	Sex	HFL	0.140	1	0.708
			HF	0.015	1	0.902
			FAL	6.211	1	0.013*
			E	3.480	1	0.062
			TIB	3.125	1	0.077
			TRL	0.060	1	0.806
			TRB	0.963	1	0.326
		TW	TRL	0.627	3	0.890

Appendix 5.5 continued

Species	Area	Factor	Measurement	Chi-square	df	Significance
Neoromicia capensis	South Africa, Free State, Nama-Karoo	Sex	TOT	7.177	1	0.007**
			T	11.712	1	0.001**
			HFL	0.927	1	0.336
			FAL	11.707	1	0.001**
			FA	18.614	1	1.60E-05***
			E	0.517	1	0.472
			TIB	7.738	1	0.005**
			TRL	0.559	1	0.455
		TW	T	1.554	3	0.670
			HFL	3.618	3	0.306
			FAL	0.505	3	0.918
			E	0.797	3	0.850
Neoromicia capensis	South Africa, Eastern Cape	Sexes	T	8.557	1	0.003**
			E	0.529	1	0.467
		TW	FA	2.952	3	0.399
Neoromicia africanus	Malawi	Sex	HB	2.002	1	0.157
			T	0.018	1	0.893
			HFL	3.949	1	0.047*
			HF	1.934	1	0.164
			E	1.608	1	0.205
		TW	E	3.070	2	0.216
Neoromicia africanus	South Africa & Swaziland	Sex	TOT	1.225	1	0.268
			HB	2.441	1	0.118
			T	0.540	1	0.462
			HFL	1.194	1	0.274
			FAL	3.803	1	0.051
			FA	11.326	1	0.001**
			E	0.039	1	0.844
			TMETA	2.014	1	0.156
		TW	TOT	1.808	3	0.613
			TL	0.667	3	0.881
			HFL	1.737	3	0.629
			FA	2.937	3	0.401
			E	6.486	3	0.090
			TMETA	5.769	3	0.123

Appendix 5.5 continued

Species	Area	Factor	Measurement	Chi-square	df	Significance
Neoromicia rueppellii	Southern Africa	Sex	HFL	0.867	1	0.352
			HF	1.418	1	0.234
			TIB	0.273	1	0.602
			TRB	2.021	1	0.155
			TRL	0.889	1	0.346
		TW	TRB	4.041	2	0.133
Neoromicia rueppellii	Zambia	Sex	HFL	3.236	1	0.072
			TMETA	0.224	1	0.636
Neoromicia zuluensis	South Africa, Limpopo & Mpumalanga	Sex	HFL	2.500	1	0.114
			FA	0.106	1	0.745
			E	1.000	1	0.317
			TIB	3.608	1	0.057
Pipistrellus hesperidus	South Africa, KwaZulu-Natal	Sex	TL	0.831	1	0.776
			HFL	0.770	1	0.380
			HF	1.432	1	0.231
			E	6.582	1	0.010 *
			TRL	4.595	1	0.032 *
			TRB	1.925	1	0.165
Pipistrellus rusticus	South Africa & Zimbabwe	Sex	HFL	2.296	1	0.130
			E	1.389	1	0.239
			TMETA	1.552	1	0.213
			TRL	0.243	1	0.622
		TW	TOT	1.902	2	0.386
			TL	1.542	2	0.463
			HFL	6.880	2	0.032 *
			FAL	7.250	2	0.027 *
			E	2.872	2	0.238
			TRL	5.633	2	0.060
			TRB	1.160	2	0.560

Appendix 5.6 (A-O)

Summary statistics of cranial measurements

Summary statistics [mean, standard deviation (SD), coefficient of variation (CV), minimum and maximum] and Kolmogorov-Smirnov (K-S) tests of normality in cranial measurements of different sexes and or tooth wear classes of the different groups of different vespertilionid species analysed. n = sample size, df = degrees of freedom, P = significance. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

A1) Male and female *Eptesicus hottentotus* from two localities in the Western Cape Province of South Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (n = 3)	**Mean**	20.00	6.87	11.95	9.68	4.77	4.61	2.88	6.69	3.85	1.64	2.06	5.06
	SD	0.08	0.27	0.40	0.12	0.23	0.24	0.12	0.21	0.11	0.29	0.09	0.16
	CV	0.44	4.32	3.59	1.39	5.12	5.53	4.42	3.43	2.98	19.06	4.49	3.33
	Minimum	19.91	6.63	11.57	9.60	4.51	4.37	2.75	6.52	3.77	1.42	1.97	4.89
	Maximum	20.07	7.17	12.36	9.82	4.91	4.84	2.95	6.92	3.97	1.97	2.14	5.19
Males (n = 5)	**Mean**	19.35	6.47	11.53	9.36	4.60	4.32	2.71	6.45	3.60	1.58	2.04	4.68
	SD	0.50	0.19	0.31	0.062	0.14	0.14	0.18	0.12	0.11	0.10	0.15	0.30
	CV	2.73	3.05	2.78	0.70	3.12	3.51	6.89	1.89	3.22	6.49	7.74	6.66
	Minimum	18.54	6.20	11.08	9.26	4.46	4.14	2.55	6.31	3.41	1.46	1.90	4.38
	Maximum	19.87	6.70	11.92	9.41	4.77	4.48	3.00	6.62	3.67	1.70	2.27	5.09
Males	**K-S**	0.249	0.155	0.232	0.286	0.27	0.227	0.323	0.237	0.337	0.198	0.207	0.234
	df	5	5	5	5	5	5	5	5	5	5	5	5
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.096	0.200	0.066	0.200	0.200	0.200

A2) Tooth wear classes of *Eptesicus hottentotus* from two localities in the Western Cape Province of South Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW B (*n* = 2)	**Mean**	19.28	6.42	11.50	9.51	4.62	4.38	2.75	6.52	3.72	1.54	2.20	4.68
	SD	1.05	0.31	0.59	0.13	0.15	0.34	0.29	0.14	0.07	0.17	0.10	0.29
	CV	6.11	5.33	5.81	1.59	3.62	8.72	11.79	2.49	2.18	12.24	4.90	6.92
	Minimum	18.54	6.20	11.08	9.41	4.51	4.14	2.55	6.41	3.67	1.42	2.14	4.48
	Maximum	20.02	6.63	11.92	9.60	4.72	4.62	2.95	6.62	3.77	1.66	2.27	4.89
TW C (*n* = 3)	**Mean**	19.55	6.75	11.92	9.49	4.64	4.37	2.85	6.69	3.63	1.65	2.03	4.95
	SD	0.32	0.37	0.44	0.29	0.24	0.09	0.22	0.21	0.21	0.28	0.09	0.33
	CV	1.78	5.91	4.00	3.33	5.61	2.11	8.43	3.43	6.14	18.13	4.78	7.16
	Minimum	19.29	6.50	11.48	9.26	4.46	4.29	2.60	6.52	3.41	1.46	1.93	4.58
	Maximum	19.91	7.17	12.36	9.82	4.91	4.46	3.00	6.92	3.82	1.97	2.10	5.19
TW D (*n* = 3)	**Mean**	19.85	6.64	11.58	9.45	4.72	4.52	2.72	6.41	3.75	1.59	1.96	4.79
	SD	0.23	0.22	0.07	0.14	0.19	0.30	0.03	0.10	0.19	0.09	0.05	0.37
	CV	1.23	3.53	0.66	1.65	4.46	7.12	1.17	1.72	5.57	6.10	2.87	8.31
	Minimum	19.62	6.40	11.52	9.34	4.51	4.25	2.70	6.31	3.61	1.53	1.90	4.38
	Maximum	20.07	6.82	11.66	9.61	4.89	4.84	2.75	6.52	3.97	1.70	2.00	5.09

B1) Male and female *Eptesicus hottentotus* from five localities in Namibia.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (*n* = 13)	**Mean**	19.54	6.72	11.15	8.97	4.24	4.40	2.70	6.36	3.61	1.45	1.97	4.64
	SD	0.47	0.26	0.40	0.30	0.14	0.18	0.15	0.25	0.13	0.10	0.11	0.19
	CV	2.43	3.86	3.62	3.43	3.27	4.05	5.50	4.03	3.73	7.01	5.63	4.08
	Minimum	18.61	6.16	10.47	8.47	3.94	4.16	2.49	5.90	3.41	1.29	1.76	4.33
	Maximum	19.99	6.99	11.90	9.63	4.37	4.67	2.95	6.92	3.82	1.66	2.14	4.94
Males (*n* = 6)	**Mean**	19.12	6.55	10.80	9.03	4.23	4.32	2.63	6.24	3.55	1.42	2.02	4.56
	SD	0.31	0.23	0.41	0.27	0.18	0.10	0.20	0.25	0.11	0.13	0.12	0.43
	CV	1.69	3.73	3.94	3.12	4.42	2.29	7.83	4.11	3.09	9.41	6.34	9.90
	Minimum	18.75	6.12	10.18	8.70	4.00	4.17	2.34	5.90	3.41	1.19	1.87	4.02
	Maximum	19.62	6.79	11.32	9.30	4.43	4.45	2.85	6.52	3.72	1.53	2.17	5.09
Females	**K-S**	0.218	0.251	0.153	0.123	0.217	0.114	0.161	0.183	0.130	0.217	0.142	0.137
	df	13	13	13	13	13	13	13	13	13	13	13	13
	P	0.092	0.024 *	0.200	0.200	0.095	0.200	0.200	0.200	0.200	0.095	0.200	0.200
Males	**K-S**	0.158	0.257	0.212	0.231	0.176	0.236	0.226	0.254	0.269	0.229	0.255	0.179
	df	6	6	6	6	6	6	6	6	6	6	6	6
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.199	0.200	0.200	0.200

B2) Tooth wear classes of *Eptesicus hottentotus* from five localities in Namibia.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW B (*n* = 5)	Mean	19.12	6.33	10.71	8.73	4.15	4.36	2.51	6.23	3.55	1.44	1.99	4.46
	SD	0.45	0.19	0.40	0.12	0.15	0.16	0.13	0.29	0.12	0.07	0.10	0.36
	CV	2.48	3.21	3.89	1.46	3.75	3.89	5.54	4.91	3.43	4.83	4.84	8.54
	Minimum	18.61	6.12	10.18	8.61	4.00	4.17	2.34	5.90	3.41	1.36	1.87	4.02
	Maximum	19.58	6.57	11.21	8.93	4.33	4.55	2.70	6.62	3.67	1.53	2.10	4.84
TW C (*n* = 6)	Mean	19.40	6.78	11.10	9.00	4.27	4.38	2.73	6.50	3.63	1.46	2.06	4.67
	SD	0.54	0.17	0.33	0.15	0.13	0.14	0.11	0.22	0.12	0.09	0.10	0.250
	CV	2.92	2.64	3.07	1.71	3.09	3.33	4.01	3.49	3.54	6.13	5.28	5.55
	Minimum	18.76	6.56	10.70	8.83	4.06	4.16	2.60	6.31	3.46	1.32	1.90	4.33
	Maximum	19.99	6.99	11.53	9.20	4.40	4.53	2.85	6.92	3.82	1.56	2.17	4.94
TW D (*n* = 8)	Mean	19.60	6.79	11.24	9.14	4.27	4.39	2.74	6.25	3.58	1.42	1.93	4.68
	SD	0.34	0.13	0.43	0.34	0.15	0.18	0.15	0.20	0.14	0.14	0.11	0.23
	CV	1.77	1.93	3.94	3.79	3.70	4.27	5.78	3.23	3.99	10.42	5.88	5.08
	Minimum	19.02	6.61	10.47	8.47	3.94	4.16	2.49	5.90	3.41	1.19	1.76	4.38
	Maximum	19.96	6.95	11.90	9.63	4.43	4.67	2.95	6.52	3.82	1.66	2.10	5.09

C1) Male and female *Hypsugo anchietae* from seven localities in southern Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (*n* = 5)	**Mean**	12.51	4.71	7.25	6.50	3.55	3.14	1.44	3.95	2.45	0.92	1.32	2.93
	SD	0.31	0.10	0.18	0.08	0.13	0.13	0.12	0.19	0.04	0.12	0.02	0.08
	CV	2.88	2.60	4.81	2.02	4.17	4.18	12.21	5.94	2.95	12.78	2.03	2.63
	Minimum	12.18	4.60	7.05	6.38	3.34	3.02	1.32	3.69	2.39	0.78	1.29	2.85
	Maximum	12.82	4.86	7.44	6.59	3.65	3.32	1.63	4.17	2.49	1.09	1.36	3.05
Males (*n* = 5)	**Mean**	12.43	4.60	7.11	6.51	3.60	3.11	1.54	3.95	2.43	0.85	1.25	2.77
	SD	0.24	0.12	0.20	0.08	0.09	0.10	0.18	0.11	0.10	0.04	0.04	0.06
	CV	2.00	2.80	2.98	1.29	2.65	3.44	12.39	2.81	4.23	5.14	3.48	2.20
	Minimum	12.12	4.46	6.93	6.39	3.52	2.97	1.37	3.82	2.29	0.81	1.22	2.70
	Maximum	12.75	4.75	7.37	6.57	3.71	3.24	1.83	4.07	2.55	0.92	1.32	2.85
Females	**K-S**	0.255	0.243	0.273	0.191	0.294	0.312	0.194	0.135	0.271	0.221	0.276	0.219
	df	5	5	5	5	5	5	5	5	5	5	5	5
	P	0.200	0.200	0.200	0.200	0.184	0.127	0.200	0.200	0.200	0.200	0.200	0.200
Males	**K-S**	0.121	0.264	0.272	0.325	0.262	0.184	0.232	0.180	0.141	0.300	0.300	0.237
	df	5	5	5	5	5	5	5	5	5	5	5	5
	P	0.200	0.200	0.200	0.090	0.200	0.200	0.200	0.200	0.200	0.161	0.161	0.200

C2) Tooth wear classes of *Hypsugo anchietae* from seven localities in southern Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A (*n* = 3)	**Mean**	12.62	4.63	7.14	6.54	3.64	3.12	1.49	3.95	2.46	0.89	1.30	2.83
	SD	0.20	0.07	0.19	0.04	0.08	0.18	0.13	0.13	0.03	0.17	0.07	0.13
	CV	1.68	1.72	2.86	0.63	2.41	6.26	9.30	3.51	1.29	20.29	5.88	4.90
	Minimum	12.43	4.55	7.02	6.50	3.55	2.97	1.37	3.82	2.44	0.78	1.22	2.70
	Maximum	12.82	4.69	7.36	6.57	3.71	3.32	1.63	4.07	2.49	1.09	1.36	2.95
TW B (*n* = 4)	**Mean**	12.45	4.66	7.25	6.53	3.61	3.09	1.54	4.01	2.46	0.85	1.29	2.89
	SD	0.26	0.17	0.21	0.06	0.07	0.06	0.20	0.13	0.08	0.03	0.05	0.13
	CV	2.19	3.86	3.09	1.04	1.99	2.15	13.57	3.37	3.30	3.47	3.95	4.68
	Minimum	12.18	4.46	6.95	6.47	3.52	3.02	1.43	3.87	2.39	0.81	1.22	2.75
	Maximum	12.76	4.86	7.44	6.59	3.68	3.17	1.83	4.17	2.55	0.88	1.32	3.05
TW C (*n* = 2)	**Mean**	12.44	4.65	7.15	6.48	3.54	3.16	1.48	3.97	2.37	0.88	1.25	2.77
	SD	0.45	0.15	0.31	0.13	0.03	0.11	0.14	0.14	0.12	0.05	-	0.04
	CV	4.03	3.60	4.90	2.21	0.90	4.030	10.97	4.08	5.13	6.12	-	1.46
	Minimum	12.12	4.54	6.93	6.39	3.52	3.08	1.37	3.87	2.29	0.85	1.25	2.75
	Maximum	12.75	4.75	7.37	6.57	3.56	3.24	1.58	4.07	2.44	0.92	1.25	2.80
TW D		12.18	4.72	7.07	6.38	3.34	3.22	1.32	3.69	2.46	1.00	1.32	2.87

D1) Male and female *Neoromicia capensis* from three localities in Namibia and South Africa falling into the Nama-Karoo biome.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (*n* = 9)	**Mean**	13.56	4.67	7.68	6.68	3.46	3.53	1.58	4.44	2.60	0.94	1.35	3.31
	SD	0.35	0.10	0.23	0.11	0.11	0.08	0.09	0.17	0.08	0.09	0.06	0.22
	CV	2.63	2.11	3.11	1.72	3.27	2.40	6.06	3.90	3.25	9.39	4.24	6.85
	Minimum	12.99	4.51	7.32	6.49	3.31	3.44	1.48	4.17	2.44	0.85	1.25	3.10
	Maximum	13.91	4.78	7.98	6.85	3.63	3.66	1.78	4.73	2.70	1.08	1.42	3.77
Males (*n* = 14)	**Mean**	13.21	4.60	7.60	6.67	3.44	3.47	1.53	4.39	2.56	0.92	1.34	3.18
	SD	0.34	0.17	0.24	0.20	0.16	0.11	0.10	0.14	0.12	0.08	0.07	0.12
	CV	2.61	3.81	3.25	3.12	4.67	3.09	6.73	3.25	4.86	8.56	5.42	3.82
	Minimum	12.70	4.26	7.23	6.39	3.15	3.22	1.32	4.12	2.39	0.81	1.15	2.95
	Maximum	13.81	4.80	7.91	7.08	3.69	3.65	1.73	4.68	2.75	1.05	1.42	3.36
Females	**K-S**	0.262	0.187	0.203	0.205	0.218	0.215	0.203	0.140	0.153	0.196	0.224	0.233
	df	9	9	9	9	9	9	9	9	9	9	9	9
	P	0.076	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.171
Males	**K-S**	0.126	0.176	0.175	0.201	0.113	0.135	0.257	0.174	0.129	0.120	0.263	0.118
	df	14	14	14	14	14	14	14	14	14	14	14	14
	P	0.200	0.200	0.200	0.129	0.200	0.200	0.013 *	0.200	0.200	0.200	0.009 **	0.200

D2) Tooth wear classes of *Neoromicia capensis* from three localities in Namibia and South Africa falling into the Nama-Karoo biome.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A	Mean	13.25	4.58	7.59	6.60	3.45	3.49	1.58	4.36	2.54	0.93	1.36	3.14
	SD	0.39	0.17	0.32	0.11	0.15	0.16	0.10	0.08	0.13	0.08	0.04	0.10
	CV	3.06	3.78	4.32	1.69	4.45	4.75	6.72	1.99	5.19	8.55	2.85	3.32
	Minimum	12.70	4.28	7.28	6.42	3.27	3.22	1.43	4.28	2.39	0.85	1.32	3.05
	Maximum	13.68	4.74	7.98	6.73	3.63	3.65	1.73	4.48	2.70	1.02	1.42	3.31
TW B	Mean	13.23	4.61	7.46	6.55	3.38	3.51	1.50	4.34	2.54	0.91	1.35	3.25
	SD	0.39	0.20	0.17	0.10	0.12	0.06	0.09	0.16	0.13	0.10	0.05	0.11
	CV	3.01	4.54	2.39	1.64	3.75	1.80	6.05	3.76	5.29	10.78	3.90	3.56
	Minimum	12.71	4.26	7.23	6.39	3.15	3.44	1.32	4.12	2.39	0.81	1.25	3.10
	Maximum	13.79	4.79	7.74	6.68	3.47	3.63	1.58	4.58	2.75	1.08	1.42	3.41
TW C	Mean	13.46	4.66	7.74	6.82	3.53	3.50	1.57	4.51	2.62	0.96	1.32	3.28
	SD	0.32	0.07	0.16	0.13	0.17	0.08	0.15	0.16	0.07	0.11	0.03	0.19
	CV	2.50	1.62	2.24	1.96	5.08	2.48	10.32	3.73	2.66	11.64	2.22	6.09
	Minimum	13.14	4.59	7.51	6.64	3.31	3.43	1.43	4.33	2.55	0.81	1.29	3.10
	Maximum	13.88	4.76	7.89	6.92	3.68	3.60	1.78	4.68	2.70	1.05	1.36	3.51
TW D	Mean	13.50	4.69	7.80	6.80	3.47	3.48	1.59	4.47	2.63	0.93	1.34	3.26
	SD	0.41	0.09	0.09	0.17	0.13	0.09	0.06	0.16	0.06	0.06	0.11	0.27
	CV	3.14	2.01	1.23	2.53	3.85	2.82	3.91	3.78	2.44	6.67	8.78	8.68
	Minimum	13.06	4.53	7.63	6.62	3.35	3.38	1.53	4.28	2.55	0.85	1.15	2.95
	Maximum	13.91	4.80	7.91	7.08	3.69	3.66	1.68	4.73	2.70	1.02	1.42	3.77
TW A	K-S	0.173	0.273	0.241	0.277	0.225	0.246	0.167	0.180	0.206	0.199	0.333	0.299
	df	6	6	6	6	6	6	6	6	6	6	6	6
	P	0.200	0.181	0.200	0.165	0.200	0.200	0.200	0.200	0.200	0.200	0.036 *	0.100
TW B	K-S	0.214	0.297	0.188	0.220	0.302	0.220	0.259	0.177	0.203	0.194	0.290	0.223
	df	7	7	7	7	7	7	7	7	7	7	7	7
	P	0.200	0.061	0.200	0.200	0.053	0.200	0.172	0.200	0.200	0.200	0.077	0.200
TW D	K-S	0.278	0.268	0.333	0.222	0.178	0.340	0.223	0.217	0.209	0.185	0.273	0.333
	df	6	6	6	6	6	6	6	6	6	6	6	6
	P	0.162	0.200	0.036 *	0.200	0.200	0.029 *	0.200	0.200	0.200	0.200	0.181	0.036 *

E1) Male and female *Neoromicia capensis* from four localities in the Western Cape Province of South Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (*n* = 14)	**Mean**	14.67	5.09	8.33	7.34	3.82	3.74	1.66	4.80	2.83	1.03	1.48	3.39
	SD	0.35	0.14	0.28	0.15	0.13	0.19	0.11	0.20	0.10	0.06	0.07	0.18
	CV	2.40	2.72	3.46	2.03	3.43	5.07	6.46	4.15	3.54	5.54	4.47	5.30
	Minimum	14.24	4.74	7.89	7.06	3.67	3.37	1.49	4.53	2.70	0.88	1.39	2.99
	Maximum	15.25	5.26	8.84	7.74	4.14	4.09	1.88	5.19	2.97	1.12	1.63	3.66
Males (*n* = 7)	**Mean**	14.23	5.03	8.19	7.23	3.78	3.70	1.60	4.65	2.79	1.01	1.47	3.23
	SD	0.32	0.09	0.29	0.20	0.17	0.10	0.10	0.18	0.23	0.04	0.06	0.17
	CV	2.31	1.85	3.70	2.86	4.76	2.67	6.65	4.08	8.38	3.88	4.52	5.36
	Minimum	13.87	4.90	7.80	6.93	3.61	3.54	1.49	4.38	2.49	0.98	1.36	2.99
	Maximum	14.75	5.17	8.64	7.56	4.07	3.85	1.78	4.99	3.21	1.08	1.56	3.46
Females	**K-S**	0.177	0.287	0.115	0.167	0.210	0.160	0.184	0.167	0.191	0.252	0.144	0.137
	df	17	17	17	17	17	17	17	17	17	17	17	17
	P	0.160	0.001 **	0.200	0.200	0.044 *	0.200	0.129	0.200	0.101	0.005 **	0.200	0.200
Males	**K-S**	0.177	0.184	0.177	0.126	0.240	0.205	0.199	0.262	0.189	0.311	0.219	0.147
	df	7	7	7	7	7	7	7	7	7	7	7	7
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.160	0.200	0.039 *	0.200	0.200

E2) Tooth wear classes of *Neoromicia capensis* from four localities in the Western Cape Province of South Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A	**Mean**	14.10	4.98	8.12	7.14	3.68	3.69	1.55	4.55	2.68	0.98	1.45	3.11
	SD	0.19	0.09	0.35	0.21	0.08	0.04	0.07	0.15	0.16	-	0.10	0.14
	CV	1.45	1.86	4.64	3.19	2.38	1.06	5.00	3.50	6.61	-	7.76	4.75
	Minimum	13.89	4.90	7.80	6.93	3.61	3.66	1.49	4.38	2.49	0.98	1.36	2.99
	Maximum	14.26	5.07	8.49	7.35	3.77	3.73	1.63	4.63	2.80	0.98	1.56	3.26
TW B	**Mean**	14.63	4.99	8.17	7.31	3.84	3.62	1.56	4.71	2.82	1.05	1.48	3.20
	SD	0.41	0.16	0.21	0.23	0.18	0.17	0.06	0.14	0.10	0.05	0.05	0.12
	CV	2.89	3.27	2.64	3.25	4.86	4.89	3.92	3.00	3.70	5.41	3.30	3.82
	Minimum	14.28	4.74	7.89	7.06	3.67	3.37	1.49	4.53	2.70	0.95	1.42	2.99
	Maximum	15.25	5.17	8.42	7.74	4.14	3.82	1.63	4.94	2.95	1.08	1.53	3.31
TW C	**Mean**	14.74	5.17	8.43	7.31	3.76	3.85	1.70	4.88	2.83	1.03	1.50	3.45
	SD	0.41	0.05	0.23	0.10	0.07	0.16	0.07	0.18	0.10	0.04	0.07	0.12
	CV	2.90	1.01	2.79	1.46	1.96	4.36	3.93	3.70	3.71	4.08	5.07	3.64
	Minimum	13.87	5.09	8.16	7.10	3.65	3.54	1.61	4.68	2.70	0.98	1.39	3.19
	Maximum	15.15	5.26	8.69	7.45	3.85	4.09	1.78	5.19	2.97	1.12	1.63	3.56
TW D	**Mean**	14.44	5.08	8.31	7.38	3.89	3.71	1.69	4.76	2.86	1.00	1.46	3.44
	SD	0.25	0.11	0.35	0.14	0.15	0.13	0.12	0.23	0.19	0.06	0.05	0.15
	CV	1.82	2.24	4.35	1.94	4.01	3.70	7.34	4.95	7.02	6.35	3.41	4.59
	Minimum	14.19	4.92	7.92	7.22	3.70	3.51	1.58	4.53	2.65	0.88	1.39	3.21
	Maximum	14.87	5.24	8.84	7.56	4.07	3.85	1.88	5.09	3.21	1.08	1.53	3.66
TW B	**K-S**	0.287	0.176	0.211	0.365	0.308	0.194	0.348	0.259	0.251	0.267	0.195	0.297
	df	6	6	6	6	6	6	6	6	6	6	6	6
	P	0.133	0.200	0.200	0.012 *	0.077	0.200	0.022 *	0.200	0.200	0.200	0.200	0.105
TW C	**K-S**	0.209	0.230	0.241	0.187	0.222	0.175	0.224	0.207	0.160	0.287	0.159	0.243
	df	8	8	8	8	8	8	8	8	8	8	8	8
	P	0.200	0.200	0.189	0.200	0.200	0.200	0.200	0.200	0.200	0.051	0.200	0.182
TW D	**K-S**	0.208	0.140	0.181	0.188	0.218	0.182	0.262	0.278	0.189	0.308	0.189	0.157
	df	7	7	7	7	7	7	7	7	7	7	7	7
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.156	0.109	0.200	0.044 *	0.200	0.200

F1) Male and female *Neoromicia capensis* from three localities in the Free State Province of South Africa falling into the Grassland biome.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (*n* = 14)	**Mean**	14.18	4.88	8.11	7.12	3.66	3.61	1.69	4.72	2.75	1.01	1.45	3.43
	SD	0.24	0.13	0.33	0.14	0.16	0.16	0.12	0.13	0.11	0.07	0.08	0.15
	CV	1.71	2.63	4.13	1.93	4.36	4.53	7.03	2.80	4.12	7.36	5.38	4.54
	Minimum	13.75	4.62	7.41	6.91	3.38	3.35	1.53	4.53	2.60	0.88	1.29	3.26
	Maximum	14.51	5.09	8.53	7.42	3.93	3.99	1.83	4.99	3.00	1.12	1.56	3.77
Males (*n* = 11)	**Mean**	13.83	5.00	8.03	7.09	3.74	3.55	1.67	4.63	2.74	1.03	1.43	3.34
	SD	0.24	0.16	0.19	0.11	0.12	0.19	0.10	0.08	0.12	0.09	0.05	0.15
	CV	1.77	3.35	2.36	1.59	3.18	5.60	5.96	1.78	4.49	9.35	3.45	4.43
	Minimum	13.41	4.68	7.76	6.91	3.61	3.16	1.53	4.48	2.55	0.92	1.36	3.10
	Maximum	14.26	5.24	8.40	7.28	3.96	3.81	1.78	4.73	2.94	1.28	1.49	3.61
Females	**K-S**	0.173	0.084	0.227	0.099	0.133	0.164	0.205	0.193	0.181	0.182	0.150	0.210
	df	14	14	14	14	14	14	14	14	14	14	14	14
	P	0.200	0.200	0.049 *	0.200	0.200	0.200	0.112	0.169	0.200	0.200	0.200	0.094
Males	**K-S**	0.114	0.159	0.103	0.109	0.155	0.183	0.231	0.159	0.178	0.315	0.175	0.185
	df	11	11	11	11	11	11	11	11	11	11	11	11
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.106	0.200	0.200	0.003 **	0.200	0.200

F2) Tooth wear classes of *Neoromicia capensis* from three localities in the Free State Province of South Africa falling into the Grassland biome.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A (*n* = 4)	**Mean**	14.05	4.88	8.14	7.05	3.69	3.59	1.71	4.75	2.86	1.03	1.51	3.55
	SD	0.21	0.18	0.26	0.08	0.07	0.08	0.12	0.17	0.10	0.03	0.03	0.11
	CV	1.57	3.87	3.43	1.24	2.01	2.34	7.55	3.88	3.58	3.48	2.39	3.140
	Minimum	13.78	4.74	7.82	6.93	3.63	3.52	1.53	4.58	2.80	0.98	1.49	3.46
	Maximum	14.24	5.12	8.46	7.10	3.79	3.70	1.78	4.99	3.00	1.05	1.56	3.66
TW B (*n* = 11)	**Mean**	13.92	4.94	8.07	7.06	3.67	3.56	1.70	4.65	2.72	1.03	1.44	3.33
	SD	0.32	0.17	0.26	0.12	0.17	0.21	0.09	0.09	0.11	0.11	0.05	0.15
	CV	2.33	3.55	3.23	1.76	4.60	5.93	5.54	2.01	3.96	10.72	3.79	4.45
	Minimum	13.41	4.62	7.70	6.91	3.38	3.16	1.56	4.53	2.55	0.88	1.36	3.10
	Maximum	14.41	5.14	8.53	7.28	3.96	3.81	1.83	4.84	2.94	1.28	1.53	3.61
TW C (*n* = 8)	**Mean**	14.11	4.97	8.15	7.20	3.72	3.56	1.69	4.71	2.75	1.00	1.44	3.42
	SD	0.27	0.14	0.24	0.10	0.16	0.13	0.12	0.13	0.10	0.07	0.06	0.15
	CV	1.94	2.95	3.05	1.40	4.47	3.65	6.98	2.86	3.82	7.25	4.49	4.53
	Minimum	13.75	4.82	7.78	7.11	3.49	3.35	1.53	4.48	2.60	0.88	1.36	3.31
	Maximum	14.38	5.24	8.40	7.42	3.93	3.72	1.83	4.89	2.90	1.08	1.56	3.77
TW D (*n* = 2)	**Mean**	14.23	4.86	7.67	7.14	3.74	3.81	1.53	4.63	2.62	1.03	1.36	3.31
	SD	0.40	0.06	0.37	0.16	0.13	0.26	-	0.07	0.04	0.02	0.10	0.07
	CV	3.13	1.48	5.39	2.45	3.83	7.52	-	1.75	1.55	2.61	7.96	2.45
	Minimum	13.95	4.81	7.41	7.03	3.65	3.63	1.53	4.58	2.60	1.02	1.29	3.26
	Maximum	14.51	4.90	7.93	7.25	3.83	3.99	1.53	4.68	2.65	1.05	1.42	3.36
TW B	**K-S**	0.153	0.149	0.135	0.162	0.148	0.226	0.187	0.161	0.235	0.225	0.169	0.250
	df	11	11	11	11	11	11	11	11	11	11	11	11
	P	0.200	0.200	0.200	0.200	0.200	0.120	0.200	0.200	0.091	0.126	0.200	0.054
TW C	**K-S**	0.199	0.191	0.269	0.279	0.179	0.133	0.206	0.154	0.125	0.148	0.231	0.392
	df	8	8	8	8	8	8	8	8	8	8	8	8
	P	0.200	0.200	0.092	0.067	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.001 **

G1) Male and female *Neoromicia capensis* from two localities in the Free State Province of South Africa falling into the Nama-Karoo biome.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (*n* = 10)	**Mean**	13.98	4.92	8.14	7.02	3.64	3.51	1.73	4.72	2.82	1.04	1.41	3.44
	SD	0.27	0.23	0.22	0.13	0.12	0.13	0.09	0.18	0.15	0.08	0.06	0.13
	CV	1.97	4.74	2.74	1.95	3.40	3.83	5.60	3.92	5.60	8.19	4.64	3.99
	Minimum	13.56	4.63	7.75	6.89	3.45	3.34	1.53	4.38	2.60	0.88	1.32	3.26
	Maximum	14.37	5.29	8.55	7.33	3.83	3.68	1.83	4.94	3.10	1.15	1.53	3.66
Males (*n* =35)	**Mean**	13.69	4.81	7.89	6.99	3.63	3.52	1.66	4.57	2.69	0.96	1.39	3.27
	SD	0.23	0.12	0.23	0.19	0.14	0.12	0.10	0.15	0.12	0.08	0.06	0.13
	CV	1.72	2.58	2.95	2.76	3.75	3.54	6.09	3.34	4.46	8.44	4.62	3.91
	Minimum	13.20	4.53	7.27	6.52	3.35	3.24	1.48	4.17	2.44	0.75	1.29	3.00
	Maximum	14.15	5.14	8.29	7.40	3.90	3.76	1.88	4.99	2.95	1.12	1.56	3.56
Females	**K-S**	0.158	0.131	0.154	0.212	0.151	0.201	0.222	0.232	0.153	0.202	0.263	0.138
	df	10	10	10	10	10	10	10	10	10	10	10	10
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.179	0.135	0.200	0.200	0.048 *	0.200
Males	**K-S**	0.088	0.153	0.072	0.102	0.088	0.088	0.139	0.113	0.104	0.153	0.204	0.122
	df	35	35	35	35	35	35	35	35	35	35	35	35
	P	0.200	0.036 *	0.200	0.200	0.200	0.200	0.083	0.200	0.200	0.036 *	0.001 **	0.200

G2) Tooth wear classes of *Neoromicia capensis* from two localities in the Free State Province of South Africa falling into the Nama-Karoo biome.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A (*n* = 3)	**Mean**	13.62	4.73	7.50	6.89	3.62	3.46	1.70	4.38	2.61	0.95	1.36	3.26
	SD	0.38	0.22	0.24	0.07	0.06	0.08	0.13	0.23	0.03	0.06	0.03	0.22
	CV	3.00	5.10	3.47	1.10	1.65	2.45	8.18	5.77	1.22	6.70	2.71	7.38
	Minimum	13.27	4.53	7.27	6.82	3.56	3.41	1.58	4.17	2.60	0.88	1.32	3.10
	Maximum	14.02	4.97	7.75	6.96	3.67	3.55	1.83	4.63	2.65	0.98	1.39	3.51
TW B (*n* = 3)	**Mean**	13.95	4.87	7.95	7.03	3.63	3.57	1.66	4.60	2.63	0.93	1.39	3.29
	SD	0.17	0.10	0.21	0.09	0.13	0.13	0.08	0.08	0.08	0.14	0.06	0.03
	CV	1.31	2.12	2.80	1.34	3.94	3.85	5.07	1.83	3.20	16.02	4.58	0.97
	Minimum	13.83	4.78	7.71	6.98	3.49	3.50	1.58	4.53	2.55	0.85	1.32	3.26
	Maximum	14.14	4.97	8.08	7.13	3.75	3.72	1.73	4.68	2.70	1.08	1.42	3.31
TW C (*n* = 27)	**Mean**	13.76	4.83	7.95	7.00	3.64	3.51	1.67	4.64	2.72	0.99	1.41	3.29
	SD	0.25	0.14	0.20	0.21	0.13	0.13	0.11	0.15	0.12	0.08	0.07	0.14
	CV	1.80	2.93	2.49	3.01	3.69	3.59	6.61	3.30	4.49	7.76	4.90	4.17
	Minimum	13.36	4.60	7.64	6.52	3.35	3.24	1.48	4.38	2.44	0.81	1.29	3.00
	Maximum	14.30	5.29	8.28	7.40	3.90	3.76	1.88	4.99	2.95	1.12	1.56	3.56
TW D (*n* = 12)	**Mean**	13.73	4.89	8.03	7.02	3.62	3.54	1.68	4.58	2.77	0.99	1.38	3.37
	SD	0.31	0.19	0.28	0.14	0.15	0.13	0.09	0.18	0.18	0.11	0.06	0.16
	CV	2.33	3.86	3.54	2.02	4.24	3.84	5.65	3.96	6.52	11.05	4.05	4.92
	Minimum	13.20	4.59	7.61	6.77	3.44	3.31	1.58	4.38	2.49	0.75	1.29	3.05
	Maximum	14.37	5.21	8.55	7.21	3.89	3.68	1.83	4.94	3.10	1.15	1.49	3.66
TW C	**K-S**	0.102	0.211	0.134	0.127	0.087	0.084	0.191	0.094	0.105	0.179	0.141	0.159
	df	27	27	27	27	27	27	27	27	27	27	27	27
	P	0.200	0.003 **	0.200	0.200	0.200	0.200	0.013 *	0.200	0.200	0.026 *	0.182	0.076
TW D	**K-S**	0.216	0.156	0.133	0.190	0.200	0.197	0.223	0.221	0.158	0.199	0.168	0.116
	df	12	12	12	12	12	12	12	12	12	12	12	12
	P	0.126	0.200	0.200	0.200	0.200	0.200	0.102	0.111	0.200	0.200	0.200	0.200

H1) Male and female *Neoromicia capensis* from four localities in Zimbabwe

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (*n* = 10)	**Mean**	13.10	4.63	7.55	6.64	3.48	3.42	1.58	4.29	2.58	1.08	1.34	3.13
	SD	0.26	0.13	0.15	0.16	0.14	0.18	0.08	0.15	0.07	0.10	0.10	0.12
	CV	2.02	2.83	2.05	2.45	4.09	5.51	4.97	3.48	2.81	9.55	7.80	4.05
	Minimum	12.70	4.49	7.28	6.28	3.25	3.23	1.45	4.08	2.42	0.92	1.15	2.90
	Maximum	13.56	4.92	7.80	6.85	3.70	3.81	1.73	4.48	2.66	1.25	1.49	3.36
Males (*n* = 11)	**Mean**	13.06	4.57	7.66	6.64	3.48	3.51	1.56	4.40	2.58	0.97	1.31	3.13
	SD	0.30	0.15	0.18	0.16	0.12	0.18	0.11	0.14	0.14	0.09	0.07	0.15
	CV	2.35	3.37	2.42	2.45	3.43	5.30	6.84	3.32	5.47	9.17	5.62	4.95
	Minimum	12.51	4.30	7.44	6.37	3.30	3.19	1.43	4.22	2.44	0.85	1.22	2.95
	Maximum	13.52	4.84	8.02	6.91	3.65	3.88	1.73	4.68	2.85	1.14	1.42	3.41
Females	**K-S**	0.151	0.232	0.237	0.183	0.115	0.201	0.144	0.124	0.202	0.127	0.158	0.138
	df	10	10	10	10	10	10	10	10	10	10	10	10
	P	0.200	0.137	0.118	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200
Males	**K-S**	0.167	0.151	0.218	0.208	0.120	0.164	0.182	0.244	0.187	0.239	0.169	0.153
	df	11	11	11	11	11	11	11	11	11	11	11	11
	P	0.200	0.200	0.151	0.200	0.200	0.200	0.200	0.067	0.200	0.080	0.200	0.200

H2) Tooth wear classes of *Neoromicia capensis* from four localities in Zimbabwe.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A (*n* = 4)	**Mean**	12.95	4.52	7.65	6.71	3.46	3.50	1.55	4.31	2.54	1.09	1.36	3.06
	SD	0.28	0.15	0.13	0.14	0.17	0.35	0.13	0.15	0.04	0.12	0.04	0.09
	CV	2.25	3.45	1.78	2.19	5.26	10.47	8.81	3.67	1.82	11.43	3.22	3.00
	Minimum	12.70	4.30	7.50	6.60	3.30	3.19	1.43	4.08	2.49	0.92	1.32	2.98
	Maximum	13.34	4.62	7.81	6.91	3.62	3.88	1.73	4.38	2.60	1.18	1.42	3.18
TW B (*n* = 4)	**Mean**	12.98	4.51	7.59	6.68	3.48	3.35	1.56	4.24	2.58	1.08	1.30	3.10
	SD	0.19	0.07	0.03	0.10	0.06	0.11	0.04	0.13	0.11	0.14	0.11	0.15
	CV	1.52	1.71	0.44	1.60	1.89	3.59	2.40	3.36	4.72	13.65	8.98	5.10
	Minimum	12.83	4.42	7.54	6.59	3.41	3.24	1.52	4.08	2.42	0.95	1.22	2.90
	Maximum	13.25	4.59	7.61	6.82	3.56	3.45	1.59	4.38	2.70	1.25	1.45	3.25
TW C (*n* =11)	**Mean**	13.18	4.65	7.64	6.61	3.48	3.49	1.58	4.40	2.61	0.99	1.34	3.15
	SD	0.30	0.15	0.20	0.17	0.14	0.14	0.10	0.16	0.13	0.08	0.08	0.15
	CV	2.35	3.33	2.72	2.62	4.00	4.13	6.25	3.71	4.91	8.59	6.15	4.81
	Minimum	12.51	4.43	7.34	6.28	3.25	3.26	1.43	4.22	2.44	0.85	1.22	2.95
	Maximum	13.56	4.92	8.02	6.85	3.70	3.81	1.73	4.68	2.85	1.11	1.49	3.41
TW D (*n* = 2)	**Mean**	12.98	4.63	7.43	6.54	3.52	3.48	1.60	4.38	2.49	0.95	1.20	3.23
	SD	0.18	-	0.21	0.23	0.14	0.14	0.11	0.07	0.07	0.05	0.07	0.11
	CV	1.59	-	3.11	3.89	4.52	4.57	7.58	1.85	3.25	5.68	6.72	3.76
	Minimum	12.85	4.63	7.28	6.38	3.42	3.38	1.53	4.33	2.44	0.92	1.15	3.16
	Maximum	13.11	4.63	7.57	6.70	3.62	3.58	1.68	4.43	2.55	0.98	1.25	3.31
TW C	**K-S**	0.243	0.129	0.226	0.176	0.105	0.209	0.155	0.218	0.141	0.139	0.204	0.128
	df	11	11	11	11	11	11	11	11	11	11	11	11
	P	0.069	0.200	0.122	0.200	0.200	0.194	0.200	0.149	0.200	0.200	0.200	0.200

I1) Male and female *Neoromicia* cf. *melckorum* from two localities in Zimbabwe and South Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (n = 9)	**Mean**	14.70	4.91	8.59	7.30	3.79	3.74	1.75	4.85	2.77	1.07	1.45	3.47
	SD	0.28	0.14	0.26	0.16	0.18	0.15	0.09	0.15	0.13	0.04	0.07	0.13
	CV	1.93	2.91	3.07	2.23	4.95	4.00	5.19	3.27	4.73	3.98	5.00	3.88
	Minimum	14.28	4.75	8.03	7.03	3.53	3.48	1.63	4.68	2.60	1.02	1.39	3.21
	Maximum	15.00	5.17	8.84	7.57	4.04	3.94	1.88	5.09	2.95	1.12	1.59	3.61
Males (n = 8)	**Mean**	14.46	4.84	8.40	7.33	3.71	3.80	1.72	4.68	2.65	1.10	1.43	3.42
	SD	0.22	0.17	0.30	0.26	0.13	0.14	0.11	0.12	0.10	0.08	0.05	0.13
	CV	1.59	3.57	3.73	3.63	3.48	3.72	6.39	2.54	3.73	7.41	3.80	3.82
	Minimum	14.23	4.48	7.98	6.93	3.54	3.55	1.63	4.48	2.49	0.95	1.36	3.21
	Maximum	14.82	4.99	8.81	7.68	3.90	3.99	1.88	4.84	2.80	1.19	1.53	3.56
Females	**K-S**	0.251	0.199	0.239	0.206	0.183	0.193	0.205	0.323	0.220	0.195	0.220	0.261
	df	9	9	9	9	9	9	9	9	9	9	9	9
	P	0.107	0.200	0.148	0.200	0.200	0.200	0.200	0.007 *	0.200	0.200	0.200	0.079
Males	**K-S**	0.268	0.214	0.184	0.207	0.163	0.173	0.287	0.170	0.151	0.231	0.162	0.230
	df	8	8	8	8	8	8	8	8	8	8	8	8
	P	0.095	0.200	0.200	0.200	0.200	0.200	0.052	0.200	0.200	0.200	0.200	0.200

I2) Tooth wear classes of *Neoromicia* cf. *melckorum* from two localities in Zimbabwe and South Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A (*n* = 6)	Mean	14.38	4.77	8.28	7.16	3.71	3.76	1.68	4.69	2.66	1.07	1.46	3.43
	SD	0.10	0.17	0.34	0.22	0.15	0.14	0.08	0.11	0.11	0.08	0.04	0.12
	CV	0.71	3.64	4.24	3.15	4.21	3.81	4.89	2.52	4.45	7.97	2.82	3.62
	Minimum	14.23	4.48	7.98	6.93	3.53	3.55	1.63	4.48	2.49	0.95	1.42	3.21
	Maximum	14.46	4.99	8.72	7.54	3.90	3.89	1.83	4.79	2.80	1.15	1.53	3.56
TW B (*n* = 3)	Mean	14.86	4.87	8.72	7.32	3.60	3.78	1.80	4.90	2.833	1.09	1.46	3.53
	SD	0.09	0.11	0.15	0.14	0.05	0.27	0.11	0.16	0.13	0.06	0.12	0.03
	CV	0.65	2.40	1.90	2.08	1.59	7.60	6.38	3.62	4.90	5.86	8.73	0.90
	Minimum	14.76	4.75	8.55	7.16	3.54	3.48	1.68	4.79	2.70	1.02	1.39	3.51
	Maximum	14.93	4.95	8.84	7.43	3.64	3.99	1.88	5.09	2.95	1.12	1.59	3.56
TW C (*n* = 7)	Mean	14.70	4.96	8.62	7.43	3.87	3.79	1.77	4.81	2.72	1.08	1.42	3.45
	SD	0.28	0.12	0.16	0.15	0.14	0.11	0.08	0.16	0.12	0.04	0.06	0.15
	CV	1.94	2.55	1.89	2.13	3.62	2.91	4.68	3.34	4.46	3.48	4.15	4.39
	Minimum	14.28	4.79	8.35	7.21	3.70	3.67	1.63	4.63	2.60	1.02	1.36	3.21
	Maximum	15.00	5.17	8.81	7.68	4.04	3.94	1.88	5.09	2.95	1.12	1.53	3.61
TW D		14.25	4.84	8.29	7.38	3.67	3.68	1.63	4.58	2.65	1.19	1.42	3.26

J1) Male and female *Neoromicia africanus* from the Pafuri area in the Limpopo Province of South Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (n = 21)	**Mean**	11.05	4.14	6.37	6.17	3.42	3.15	1.22	3.43	2.33	0.70	1.07	2.46
	SD	0.24	0.15	0.23	0.15	0.13	0.15	0.10	0.17	0.09	0.09	0.04	0.09
	CV	2.20	3.74	3.73	2.43	3.77	4.66	8.47	4.94	3.84	13.34	4.00	3.50
	Minimum	10.46	3.82	5.85	5.88	3.22	2.90	1.07	2.90	2.19	0.54	1.02	2.29
	Maximum	11.43	4.46	6.81	6.44	3.68	3.39	1.43	3.72	2.49	0.88	1.15	2.65
Males (n = 8)	**Mean**	10.83	4.23	6.41	6.14	3.44	3.14	1.22	3.38	2.30	0.68	1.00	2.38
	SD	0.28	0.19	0.21	0.18	0.10	0.13	0.11	0.12	0.08	0.09	0.05	0.09
	CV	2.70	4.70	3.35	2.97	3.12	4.19	9.195	3.71	3.39	14.08	5.56	4.04
	Minimum	10.25	4.03	6.09	5.86	3.26	2.96	1.02	3.16	2.14	0.58	0.92	2.29
	Maximum	11.24	4.63	6.68	6.43	3.60	3.31	1.32	3.56	2.39	0.85	1.08	2.55
Females	**K-S**	0.089	0.092	0.135	0.134	0.199	0.132	0.179	0.189	0.143	0.181	0.175	0.152
	df	21	21	21	21	21	21	21	21	21	21	21	21
	P	0.200	0.200	0.200	0.200	0.029 *	0.200	0.078	0.048 *	0.200	0.071	0.092	0.200
Males	**K-S**	0.229	0.214	0.152	0.222	0.187	0.156	0.250	0.228	0.308	0.159	0.218	0.205
	df	8	8	8	8	8	8	8	8	8	8	8	8
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.150	0.200	0.024 *	0.200	0.200	0.200

J2) Tooth wear classes of female *Neoromicia africanus* from the Pafuri area in the Limpopo Province of South Africa.

Females		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A	**Mean**	11.02	4.13	6.38	6.14	3.42	3.17	1.22	3.42	2.36	0.71	1.07	2.45
	SD	0.24	0.16	0.25	0.15	0.16	0.13	0.11	0.12	0.11	0.09	0.04	0.08
	CV	2.26	3.94	4.06	2.50	4.85	4.32	9.46	3.47	4.55	13.57	4.19	3.22
	Minimum	10.46	3.82	5.85	5.88	3.22	2.90	1.07	3.21	2.19	0.58	1.02	2.29
	Maximum	11.28	4.32	6.78	6.34	3.68	3.34	1.43	3.61	2.49	0.88	1.15	2.55
TW B	**Mean**	11.13	4.22	6.46	6.19	3.41	3.08	1.23	3.53	2.37	0.64	1.09	2.47
	SD	0.32	0.17	0.33	0.15	0.09	0.17	0.13	0.15	0.03	0.07	0.06	0.12
	CV	3.06	4.33	5.38	2.61	2.92	5.75	10.96	4.58	1.32	11.68	5.42	5.22
	Minimum	10.76	4.06	6.11	6.02	3.31	2.91	1.07	3.36	2.34	0.54	1.02	2.39
	Maximum	11.43	4.46	6.81	6.33	3.53	3.24	1.37	3.72	2.39	0.71	1.15	2.65
TW C	**Mean**	11.06	4.10	6.28	6.21	3.41	3.17	1.23	3.39	2.27	0.74	1.06	2.46
	SD	0.21	0.14	0.10	0.16	0.08	0.16	0.08	0.25	0.03	0.09	0.04	0.09
	CV	1.95	3.48	1.59	2.61	2.49	5.33	6.91	7.66	1.28	12.95	3.43	3.77
	Minimum	10.78	3.97	6.14	6.01	3.34	2.96	1.12	2.90	2.24	0.64	1.02	2.39
	Maximum	11.39	4.36	6.40	6.44	3.56	3.39	1.32	3.61	2.29	0.85	1.12	2.60
TW A	**K-S**	0.226	0.164	0.199	0.134	0.214	0.185	0.261	0.107	0.157	0.265	0.183	0.271
	df	11	11	11	11	11	11	11	11	11	11	11	11
	P	0.121	0.200	0.200	0.200	0.169	0.200	0.036 *	0.200	0.200	0.030 *	0.200	0.023 *
TW C	**K-S**	0.170	0.309	0.229	0.164	0.302	0.203	0.208	0.374	0.319	0.212	0.293	0.277
	df	6	6	6	6	6	6	6	6	6	6	6	6
	P	0.200	0.076	0.200	0.200	0.091	0.200	0.200	0.009 **	0.056	0.200	0.117	0.168

K1) Male and female *Neoromicia africanus* from 12 localities in KwaZulu-Natal and the Eastern Cape Provinces in South Africa and Swaziland.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (*n* = 12)	**Mean**	11.30	4.51	6.61	6.03	3.44	3.18	1.17	3.67	2.42	0.80	1.07	2.48
	SD	0.24	0.11	0.17	0.14	0.09	0.09	0.09	0.16	0.09	0.09	0.04	0.06
	CV	2.16	2.44	2.56	2.35	2.53	3.01	7.48	4.57	3.69	11.49	3.62	2.58
	Minimum	10.79	4.29	6.31	5.74	3.33	3.05	1.07	3.39	2.24	0.68	1.02	2.39
	Maximum	11.55	4.73	6.88	6.22	3.57	3.32	1.37	3.97	2.55	0.95	1.12	2.55
Males (*n* = 23)	**Mean**	11.18	4.51	6.54	6.03	3.39	3.17	1.18	3.69	2.42	0.77	1.05	2.41
	SD	0.17	0.11	0.17	0.14	0.09	0.12	0.10	0.12	0.08	0.10	0.03	0.10
	CV	1.56	2.55	2.68	2.26	2.56	3.78	8.25	3.38	3.51	12.65	2.54	4.00
	Minimum	10.85	4.30	6.22	5.79	3.18	2.97	0.97	3.39	2.24	0.64	0.98	2.19
	Maximum	11.54	4.75	6.89	6.29	3.57	3.40	1.37	3.87	2.55	0.97	1.08	2.55
Females	**K-S**	0.307	0.195	0.209	0.117	0.124	0.156	0.230	0.234	0.140	0.248	0.215	0.196
	df	12	12	12	12	12	12	12	12	12	12	12	12
	P	0.003 **	0.200	0.153	0.200	0.200	0.200	0.078	0.068	0.200	0.039 *	0.131	0.200
Males	**K-S**	0.114	0.132	0.076	0.093	0.149	0.111	0.169	0.131	0.162	0.195	0.365	0.162
	df	23	23	23	23	23	23	23	23	23	23	23	23
	P	0.200	0.200	0.200	0.200	0.199	0.200	0.087	0.200	0.121	0.024 *	1.01E-08 ***	0.120

K2) Tooth wear classes of *Neoromicia africanus* from 12 localities in KwaZulu-Natal and the Eastern Cape Provinces in South Africa and Swaziland.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A	Mean	11.32	4.60	6.65	6.15	3.46	3.27	1.17	3.75	2.46	0.81	1.06	2.44
	SD	0.24	0.11	0.08	0.12	0.14	0.10	0.14	0.16	0.15	0.09	0.05	0.10
	CV	2.30	2.68	1.23	2.09	4.44	3.32	12.47	4.73	6.47	11.94	5.28	4.51
	Minimum	11.07	4.52	6.56	6.08	3.30	3.17	1.07	3.56	2.29	0.75	1.02	2.34
	Maximum	11.55	4.73	6.70	6.29	3.57	3.37	1.32	3.87	2.55	0.92	1.12	2.55
TW B	Mean	11.27	4.43	6.56	6.02	3.33	3.20	1.15	3.67	2.42	0.75	1.06	2.44
	SD	0.19	0.07	0.17	0.14	0.08	0.11	0.09	0.08	0.05	0.09	0.04	0.08
	CV	1.74	1.48	2.56	2.30	2.31	3.55	8.29	2.19	2.26	12.62	4.07	3.20
	Minimum	10.85	4.30	6.29	5.79	3.18	3.09	0.97	3.56	2.34	0.64	0.98	2.34
	Maximum	11.54	4.51	6.79	6.16	3.46	3.40	1.27	3.82	2.49	0.95	1.12	2.55
TW C	Mean	11.17	4.52	6.54	6.00	3.43	3.13	1.18	3.68	2.40	0.77	1.05	2.43
	SD	0.19	0.13	0.20	0.15	0.08	0.10	0.09	0.11	0.08	0.09	0.03	0.10
	CV	1.76	2.96	3.05	2.53	2.38	3.11	8.09	3.13	3.37	12.13	3.25	4.04
	Minimum	10.79	4.29	6.22	5.74	3.31	2.97	0.97	3.39	2.24	0.68	0.98	2.19
	Maximum	11.38	4.75	6.89	6.29	3.57	3.31	1.37	3.87	2.55	0.93	1.12	2.55
TW D	Mean	11.24	4.51	6.59	6.05	3.43	3.18	1.20	3.67	2.44	0.81	1.06	2.42
	SD	0.23	0.06	0.17	0.09	0.04	0.12	0.08	0.22	0.10	0.10	0.01	0.10
	CV	2.07	1.26	2.58	1.46	1.26	3.85	6.99	6.060	4.07	13.02	1.35	4.32
	Minimum	10.89	4.45	6.37	5.95	3.33	2.99	1.12	3.39	2.24	0.68	1.05	2.29
	Maximum	11.51	4.60	6.88	6.22	3.47	3.36	1.37	3.97	2.55	0.97	1.08	2.55

K3) Tooth wear classes of male *Neoromicia africanus* from 12 localities in KwaZulu-Natal and the Eastern Cape Provinces in South Africa and Swaziland.

Male		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A	Mean	11.20	4.54	6.62	6.19	3.44	3.27	1.22	3.69	2.42	0.83	1.03	2.39
	SD	0.18	0.02	0.09	0.14	0.19	0.14	0.14	0.18	0.18	0.12	0.02	0.07
	CV	1.85	0.53	1.44	2.57	6.25	4.87	13.26	5.49	8.38	16.24	2.61	3.39
	Minimum	11.07	4.52	6.56	6.09	3.30	3.17	1.12	3.56	2.29	0.75	1.02	2.34
	Maximum	11.33	4.55	6.68	6.29	3.57	3.37	1.32	3.82	2.55	0.92	1.05	2.44
TW B	Mean	11.24	4.40	6.52	5.99	3.30	3.18	1.17	3.69	2.43	0.71	1.05	2.41
	SD	0.25	0.07	0.19	0.16	0.07	0.13	0.12	0.09	0.07	0.05	0.04	0.08
	CV	2.33	1.54	3.09	2.75	2.13	4.26	10.71	2.43	2.86	7.91	4.15	3.36
	Minimum	10.85	4.30	6.29	5.79	3.18	3.09	0.97	3.61	2.34	0.64	0.98	2.34
	Maximum	11.54	4.47	6.79	6.16	3.34	3.40	1.27	3.82	2.49	0.78	1.08	2.49
TW C	Mean	11.19	4.55	6.54	6.02	3.41	3.14	1.18	3.70	2.39	0.74	1.04	2.42
	SD	0.15	0.14	0.21	0.14	0.06	0.11	0.11	0.10	0.09	0.08	0.03	0.11
	CV	1.40	3.06	3.31	2.41	1.88	3.63	9.39	2.75	3.77	10.86	2.25	4.56
	Minimum	10.92	4.31	6.22	5.84	3.31	2.97	0.97	3.56	2.24	0.68	0.98	2.19
	Maximum	11.38	4.75	6.89	6.29	3.54	3.31	1.37	3.87	2.55	0.92	1.05	2.55
TW D	Mean	11.10	4.51	6.50	6.04	3.42	3.16	1.17	3.65	2.45	0.86	1.06	2.41
	SD	0.15	0.05	0.10	0.07	0.05	0.13	0.03	0.20	0.06	0.11	0.01	0.12
	CV	1.45	1.11	1.60	1.19	1.64	4.38	2.92	5.80	2.42	12.98	1.18	5.09
	Minimum	10.89	4.46	6.37	5.95	3.33	2.99	1.12	3.39	2.39	0.71	1.05	2.29
	Maximum	11.28	4.58	6.61	6.12	3.47	3.36	1.21	3.87	2.49	0.97	1.07	2.55
TW B	F	0.303	0.256	0.146	0.189	0.371	0.311	0.300	0.201	0.221	0.136	0.300	0.254
	df	5	5	5	5	5	5	5	5	5	5	5	5
	P	0.149	0.200	0.200	0.200	0.023 *	0.127	0.161	0.200	0.200	0.200	0.161	0.200
TW C	F	0.137	0.135	0.116	0.200	0.204	0.111	0.152	0.191	0.136	0.274	0.432	0.155
	df	11	11	11	11	11	11	11	11	11	11	11	11
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.020 *	2.40E-06 ***	0.200
TW D	F	0.242	0.278	0.178	0.170	0.300	0.252	0.312	0.238	0.357	0.263	0.367	0.251
	df	5	5	5	5	5	5	5	5	5	5	5	5
	P	0.200	0.200	0.200	0.200	0.161	0.200	0.126	0.200	0.036 *	0.200	0.026 *	0.200

L) Male and female *Neoromicia rueppellii* from four localities in Southern Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (*n* = 2)	**Mean**	13.74	5.37	8.00	7.75	4.52	3.68	1.48	4.51	3.23	1.02	1.31	3.13
	SD	0.01	0.07	0.06	0.01	0.26	0.03	0.14	0.11	0.18	0.14	0.12	0.04
	CV	0.12	1.48	0.80	0.10	6.52	0.87	10.97	2.70	6.26	15.91	10.33	1.29
	Minimum	13.73	5.32	7.96	7.74	4.33	3.66	1.37	4.43	3.11	0.92	1.220	3.11
	Maximum	13.75	5.42	8.04	7.75	4.70	3.70	1.58	4.58	3.36	1.12	1.390	3.16
Males (*n* = 5)	**Mean**	13.37	5.38	7.82	7.51	4.34	3.59	1.53	4.19	3.03	0.96	1.25	2.95
	SD	0.29	0.10	0.24	0.13	0.18	0.17	0.07	0.18	0.12	0.09	0.05	0.16
	CV	2.31	1.85	3.18	1.85	4.42	5.04	5.04	4.41	4.16	9.94	4.37	5.84
	Minimum	13.04	5.23	7.48	7.35	4.09	3.36	1.46	4.02	2.90	0.83	1.18	2.77
	Maximum	13.81	5.47	8.11	7.69	4.56	3.83	1.63	4.48	3.21	1.05	1.32	3.12
Males	F	0.187	0.217	0.157	0.178	0.141	0.168	0.301	0.302	0.209	0.214	0.154	0.230
	df	5	5	5	5	5	5	5	5	5	5	5	5
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.158	0.153	0.200	0.200	0.200	0.200

M1) Tooth wear classes of female *Neoromicia zuluensis* from 19 localities in Mpumalanga and Limpopo Provinces of South Africa.

Female		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A	Mean	11.975	4.49	6.82	6.19	3.47	3.08	1.37	3.82	2.39	0.75	1.27	2.72
	SD	0.28	0.16	0.20	0.10	0.01	0.04	0.07	0.07	0.00	0.00	0.12	0.11
	CV	2.59	4.08	3.27	1.80	0.46	1.29	5.89	2.12	0.00	0.00	10.61	4.46
	Minimum	11.780	4.37	6.68	6.12	3.46	3.05	1.32	3.77	2.39	0.75	1.19	2.65
	Maximum	12.170	4.60	6.96	6.26	3.48	3.10	1.43	3.87	2.39	0.75	1.36	2.80
TW B	Mean	11.885	4.51	6.93	6.31	3.51	3.15	1.29	3.72	2.40	0.83	1.20	2.70
	SD	0.22	0.11	0.19	0.16	0.09	0.20	0.05	0.15	0.12	0.08	0.07	0.11
	CV	1.89	2.54	2.83	2.69	2.59	6.52	4.25	4.23	5.12	10.37	6.09	4.31
	Minimum	11.520	4.34	6.57	6.10	3.40	2.86	1.22	3.56	2.24	0.71	1.12	2.55
	Maximum	12.130	4.68	7.07	6.51	3.63	3.40	1.32	3.97	2.60	0.92	1.32	2.85
TW C	Mean	12.004	4.57	7.10	6.22	3.37	3.16	1.49	3.88	2.41	0.84	1.22	2.78
	SD	0.17	0.07	0.14	0.21	0.10	0.17	0.12	0.19	0.11	0.05	0.05	0.11
	CV	1.43	1.53	2.05	3.50	3.17	5.69	8.59	4.99	4.86	5.78	4.07	4.08
	Minimum	11.780	4.50	6.93	5.91	3.22	2.85	1.22	3.67	2.29	0.75	1.19	2.65
	Maximum	12.290	4.71	7.33	6.46	3.53	3.42	1.58	4.17	2.60	0.88	1.29	2.95
TW D	Mean	11.900	4.49	6.98	6.14	3.40	3.07	1.36	3.76	2.38	0.84	1.12	2.72
	SD	0.18	0.08	0.27	0.14	0.13	0.12	0.12	0.15	0.11	0.08	0.06	0.09
	CV	1.61	1.84	3.98	2.38	3.97	4.11	9.35	4.20	4.86	9.66	5.95	3.29
	Minimum	11.650	4.42	6.66	6.02	3.27	2.94	1.27	3.56	2.24	0.75	1.02	2.65
	Maximum	12.130	4.62	7.24	6.36	3.58	3.23	1.58	3.97	2.55	0.95	1.19	2.85
Female	K-S	0.097	0.084	0.138	0.123	0.152	0.093	0.292	0.129	0.280	0.182	0.235	0.152
	df	20	20	20	20	20	20	20	20	20	20	20	20
	P	0.200	0.200	0.200	0.200	0.200	0.200	9.31E-05 ***	0.200	2.42E-04 ***	0.080	0.005	0.200

M2) Tooth wear classes of male *Neoromicia zuluensis* from 19 localities in Mpumalanga and Limpopo Provinces of South Africa.

Male		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A	Mean	11.66	4.55	6.76	6.28	3.47	3.19	1.34	3.72	2.38	0.79	1.14	2.61
	SD	0.38	0.04	0.17	0.12	0.15	0.23	0.03	0.14	0.15	0.10	0.09	0.08
	CV	3.44	0.99	2.73	2.08	4.53	7.50	2.02	3.94	6.79	13.65	7.87	3.11
	Minimum	11.14	4.51	6.51	6.17	3.30	2.87	1.32	3.51	2.24	0.68	1.05	2.49
	Maximum	11.99	4.60	6.91	6.41	3.66	3.37	1.37	3.82	2.60	0.92	1.25	2.65
TW B	Mean	11.58	4.51	6.71	6.11	3.45	3.06	1.29	3.55	2.33	0.76	1.15	2.51
	SD	0.54	0.11	0.26	0.27	0.08	0.26	0.12	0.26	0.13	0.04	0.12	0.22
	CV	4.92	2.57	4.10	4.67	2.32	8.85	9.94	7.90	5.81	6.10	11.12	9.22
	Minimum	11.21	4.37	6.41	5.88	3.36	2.85	1.12	3.31	2.19	0.71	1.05	2.34
	Maximum	12.37	4.62	7.04	6.50	3.53	3.36	1.37	3.87	2.49	0.81	1.29	2.80
TW C	Mean	11.76	4.45	6.83	6.32	3.48	3.18	1.38	3.68	2.31	0.79	1.15	2.65
	SD	0.22	0.20	0.14	0.17	0.09	0.11	0.08	0.17	0.14	0.05	0.07	0.07
	CV	1.92	4.75	2.10	2.86	2.83	3.60	5.73	4.76	6.23	6.81	6.55	2.86
	Minimum	11.39	4.17	6.66	6.08	3.38	3.04	1.27	3.41	2.09	0.75	1.09	2.60
	Maximum	11.93	4.64	7.02	6.55	3.59	3.34	1.48	3.82	2.39	0.88	1.25	2.75
TW D	Mean	11.63	4.52	6.87	6.24	3.42	3.03	1.34	3.70	2.38	0.80	1.13	2.65
	SD	0.20	0.15	0.16	0.01	0.17	0.23	0.08	0.03	0.03	0.11	0.05	0.00
	CV	1.85	3.60	2.47	0.10	5.39	8.29	6.28	0.86	1.34	14.71	4.96	0.00
	Minimum	11.41	4.38	6.70	6.23	3.32	2.77	1.27	3.67	2.34	0.68	1.09	2.65
	Maximum	11.79	4.68	7.01	6.24	3.62	3.22	1.43	3.72	2.39	0.88	1.19	2.65
Males	K-S	0.122	0.157	0.107	0.096	0.116	0.176	0.174	0.202	0.209	0.161	0.158	0.230
	df	16	16	16	16	16	16	16	16	16	16	16	16
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.079	0.059	0.200	0.200	0.024 *

M3) Male and female *Neoromicia zuluensis* from 19 localities in Mpumalanga and Limpopo Provinces of South Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (*n* = 20)	**Mean**	11.94	4.52	6.99	6.22	3.43	3.13	1.39	3.79	2.40	0.83	1.19	2.73
	SD	0.19	0.09	0.20	0.17	0.11	0.16	0.13	0.16	0.10	0.07	0.08	0.10
	CV	1.58	2.10	2.92	2.81	3.30	5.06	9.25	4.38	4.31	8.24	6.57	3.78
	Minimum	11.52	4.34	6.57	5.91	3.22	2.85	1.22	3.56	2.24	0.71	1.02	2.55
	Maximum	12.29	4.71	7.33	6.51	3.63	3.42	1.58	4.17	2.60	0.95	1.36	2.95
Males (*n* = 16)	**Mean**	11.67	4.50	6.79	6.24	3.46	3.13	1.34	3.66	2.34	0.79	1.15	2.60
	SD	0.33	0.14	0.18	0.18	0.11	0.20	0.08	0.17	0.12	0.07	0.08	0.13
	CV	2.87	3.05	2.65	2.93	3.24	6.39	6.26	4.78	5.16	9.08	6.96	4.86
	Minimum	11.14	4.17	6.41	5.88	3.30	2.77	1.12	3.31	2.09	0.68	1.05	2.34
	Maximum	12.37	4.68	7.04	6.55	3.66	3.37	1.48	3.87	2.60	0.92	1.29	2.80

M4) Tooth wear classes of *Neoromicia zuluensis* from 19 localities in Mpumalanga and Limpopo Provinces of South Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A	Mean	11.77	4.53	6.78	6.25	3.47	3.15	1.35	3.75	2.38	0.77	1.19	2.65
	SD	0.36	0.09	0.16	0.12	0.12	0.18	0.04	0.12	0.12	0.08	0.11	0.10
	CV	3.15	1.99	2.52	1.92	3.44	6.09	3.29	3.43	5.15	10.96	9.41	3.80
	Minimum	11.14	4.37	6.51	6.12	3.30	2.87	1.32	3.51	2.24	0.68	1.05	2.49
	Maximum	12.17	4.60	6.96	6.41	3.66	3.37	1.43	3.87	2.60	0.92	1.36	2.80
TW B	Mean	11.76	4.51	6.84	6.23	3.48	3.11	1.29	3.65	2.37	0.80	1.18	2.62
	SD	0.38	0.10	0.23	0.22	0.09	0.21	0.08	0.21	0.12	0.07	0.09	0.18
	CV	3.33	2.35	3.52	3.64	2.51	6.99	6.35	5.84	5.21	9.43	7.83	7.04
	Minimum	11.21	4.34	6.41	5.88	3.36	2.85	1.12	3.31	2.19	0.71	1.05	2.34
	Maximum	12.37	4.68	7.07	6.51	3.63	3.40	1.37	3.97	2.60	0.92	1.32	2.85
TW C	Mean	11.90	4.52	6.99	6.26	3.42	3.17	1.45	3.79	2.37	0.82	1.19	2.72
	SD	0.22	0.15	0.19	0.19	0.11	0.15	0.12	0.20	0.13	0.05	0.07	0.12
	CV	1.87	3.30	2.77	3.16	3.29	4.67	8.17	5.37	5.66	6.45	5.65	4.27
	Minimum	11.39	4.17	6.66	5.91	3.22	2.85	1.22	3.41	2.09	0.75	1.09	2.60
	Maximum	12.29	4.71	7.33	6.55	3.59	3.42	1.58	4.17	2.60	0.88	1.29	2.95
TW D	Mean	11.80	4.50	6.94	6.17	3.41	3.06	1.36	3.74	2.38	0.83	1.12	2.69
	SD	0.22	0.10	0.23	0.12	0.13	0.16	0.10	0.12	0.09	0.09	0.06	0.07
	CV	1.94	2.33	3.35	1.96	4.04	5.25	7.73	3.27	3.68	10.59	5.11	2.84
	Minimum	11.41	4.38	6.66	6.02	3.27	2.77	1.27	3.56	2.24	0.68	1.02	2.65
	Maximum	12.13	4.68	7.24	6.36	3.62	3.23	1.58	3.97	2.55	0.95	1.19	2.85

N1) Tooth wear classes of female *Pipistrellus hesperidus* from 20 localities in the KwaZulu-Natal Province of South Africa.

Female		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A	Mean	12.47	4.78	7.38	6.75	3.77	3.42	1.38	4.24	2.80	1.00	1.32	2.90
	SD	0.24	0.04	0.24	0.09	0.14	0.08	0.17	0.19	0.17	0.07	0.04	0.05
	CV	2.02	0.86	3.42	1.34	3.91	2.39	12.92	4.67	6.19	6.96	3.53	1.84
	Minimum	12.19	4.72	7.04	6.64	3.63	3.32	1.17	4.02	2.55	0.88	1.29	2.85
	Maximum	12.83	4.82	7.71	6.86	4.00	3.50	1.58	4.48	3.00	1.05	1.39	2.95
TW B	Mean	12.81	5.07	7.66	6.80	3.82	3.42	1.57	4.41	2.83	0.93	1.31	3.00
	SD	0.40	0.66	0.18	0.19	0.15	0.15	0.09	0.13	0.12	0.05	0.05	0.12
	CV	3.20	13.52	2.41	2.81	4.13	4.50	5.60	3.11	4.53	6.01	4.27	4.23
	Minimum	12.21	4.58	7.40	6.55	3.57	3.15	1.43	4.28	2.60	0.88	1.22	2.75
	Maximum	13.24	6.68	7.89	7.08	4.00	3.68	1.68	4.63	3.00	1.02	1.39	3.16
TW C	Mean	12.83	4.87	7.70	6.72	3.82	3.54	1.60	4.41	2.90	0.88	1.32	2.99
	SD	0.34	0.18	0.32	0.20	0.16	0.06	0.03	0.06	0.10	0.03	0.03	0.25
	CV	2.87	4.02	4.49	3.26	4.56	1.84	2.00	1.44	3.80	4.17	2.78	9.11
	Minimum	12.53	4.70	7.43	6.49	3.67	3.48	1.58	4.38	2.80	0.85	1.29	2.70
	Maximum	13.20	5.06	8.05	6.85	3.99	3.60	1.63	4.48	3.00	0.92	1.36	3.16
TW A	K-S	0.202	0.280	0.218	0.174	0.227	0.230	0.199	0.206	0.300	0.421	0.330	0.241
	df	5	5	5	5	5	5	5	5	5	5	5	5
	sig	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.161	0.004 **	0.079	0.200
TW B	K-S	0.190	0.422	0.222	0.181	0.175	0.244	0.185	0.219	0.189	0.247	0.218	0.234
	df	8	8	8	8	8	8	8	8	8	8	8	8
	sig	0.200	1.38E-04 ***	0.200	0.200	0.200	0.179	0.200	0.200	0.200	0.162	0.200	0.200
TW C	K-S	0.157	0.340	0.126	0.107	0.154	0.154	0.238	0.183	0.207	0.222	0.176	0.150
	df	16	16	16	16	16	16	16	16	16	16	16	16
	sig	0.200	2.54E-05 ***	0.200	0.200	0.200	0.200	0.016 *	0.155	0.065	0.034 *	0.199	0.200

N2) Tooth wear classes of male *Pipistrellus hesperidus* from 20 localities in the KwaZulu-Natal Province of South Africa.

Male		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A	Mean	12.54	4.88	7.51	6.66	3.80	3.51	1.53	4.35	2.84	0.87	1.31	2.91
	SD	0.32	0.11	0.18	0.21	0.08	0.19	0.19	0.14	0.12	0.06	0.06	0.10
	CV	2.65	2.26	2.53	3.20	2.04	5.51	12.92	3.42	4.47	7.61	4.61	3.69
	Minimum	12.14	4.73	7.21	6.28	3.68	3.30	1.32	4.07	2.60	0.78	1.22	2.85
	Maximum	13.02	5.04	7.80	6.88	3.91	3.87	1.83	4.53	2.95	0.95	1.39	3.11
TW B	Mean	12.37	4.83	7.48	6.69	3.78	3.44	1.43	4.27	2.81	0.88	1.28	2.85
	SD	0.24	0.125	0.20	0.165	0.10	0.15	0.09	0.11	0.10	0.09	0.07	0.11
	CV	1.98	2.43	2.70	2.40	2.70	4.34	6.13	2.55	3.68	9.90	5.22	4.00
	Minimum	11.98	4.64	7.17	6.36	3.61	3.08	1.27	4.07	2.55	0.78	1.19	2.70
	Maximum	12.97	5.08	7.90	6.97	3.90	3.63	1.53	4.48	2.95	1.05	1.42	3.11
TW C	Mean	12.43	4.85	7.48	6.71	3.78	3.39	1.45	4.31	2.77	0.88	1.25	2.89
	SD	0.21	0.11	0.12	0.13	0.16	0.13	0.18	0.20	0.12	0.08	0.07	0.11
	CV	1.79	2.44	1.72	2.04	4.25	3.93	12.71	4.74	4.64	9.76	5.36	4.05
	Minimum	12.18	4.68	7.33	6.53	3.54	3.23	1.27	4.12	2.60	0.81	1.15	2.75
	Maximum	12.81	5.00	7.65	6.85	3.98	3.59	1.78	4.63	2.95	1.05	1.36	3.11
TW A	K-S	0.168	0.208	0.177	0.250	0.131	0.205	0.217	0.297	0.238	0.172	0.170	0.427
	df	7	7	7	7	7	7	7	7	7	7	7	7
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.062	0.200	0.200	0.200	3.29E-04 ***
TW B	K-S	0.178	0.146	0.112	0.104	0.156	0.151	0.185	0.207	0.238	0.324	0.255	0.214
	df	13	13	13	13	13	13	13	13	13	13	13	13
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.132	0.042 *	0.001 **	0.020 *	0.107
TW C	K-S	0.163	0.227	0.184	0.231	0.225	0.197	0.199	0.229	0.149	0.230	0.158	0.341
	df	7	7	7	7	7	7	7	7	7	7	7	7
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.014 *
Males	K-S	0.122	0.104	0.096	0.159	0.098	0.096	0.171	0.115	0.200	0.244	0.163	0.266
	df	28	28	28	28	28	28	28	28	28	28	28	28
	P	0.200	0.200	0.200	0.067	0.200	0.200	0.036 *	0.200	0.006 **	1.76E-04 ***	0.056	2.17E-05 ***

N3) Male and female *Pipistrellus hesperidus* from 20 localities in the KwaZulu-Natal Province of South Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Female (*n* = 16)	**Mean**	12.71	4.94	7.58	6.77	3.81	3.44	1.51	4.36	2.83	0.94	1.31	2.97
	SD	0.36	0.48	0.25	0.16	0.14	0.12	0.14	0.16	0.13	0.07	0.05	0.14
	CV	2.89	9.83	3.38	2.35	3.79	3.61	9.37	3.70	4.70	7.21	3.52	4.61
	Minimum	12.19	4.58	7.04	6.49	3.57	3.15	1.17	4.02	2.55	0.85	1.22	2.70
	Maximum	13.24	6.68	8.05	7.08	4.00	3.68	1.68	4.63	3.00	1.05	1.39	3.16
Male (*n* = 27)	**Mean**	12.43	4.85	7.48	6.69	3.78	3.44	1.46	4.30	2.81	0.88	1.28	2.88
	SD	0.26	0.11	0.17	0.16	0.11	0.15	0.15	0.14	0.11	0.08	0.06	0.11
	CV	2.05	2.73	2.34	2.39	3.12	4.84	9.83	3.58	4.87	8.80	5.00	3.75
	Minimum	11.98	4.64	7.17	6.28	3.54	3.08	1.27	4.07	2.55	0.78	1.15	2.70
	Maximum	13.02	5.08	7.90	6.97	3.98	3.87	1.83	4.63	2.95	1.05	1.42	3.11

O1) Tooth wear classes of female *Pipistrellus rusticus* from six localities in Zimbabwe and South Africa.

Female		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A	Mean	11.63	4.37	6.96	6.20	3.56	3.22	1.34	4.07	2.71	0.91	1.23	2.74
	SD	0.28	0.08	0.29	0.11	0.13	0.20	0.10	0.17	0.09	0.07	0.05	0.20
	CV	2.51	1.77	4.27	1.87	3.85	6.41	7.59	4.38	3.37	8.10	4.03	7.50
	Minimum	11.23	4.28	6.49	6.02	3.40	2.95	1.22	3.67	2.55	0.81	1.15	2.29
	Maximum	12.23	4.51	7.33	6.34	3.80	3.58	1.53	4.28	2.85	1.02	1.29	2.95
TW B	Mean	11.40	4.29	7.11	6.20	3.45	3.22	1.34	3.97	2.70	0.80	1.20	2.76
	SD	0.32	0.11	0.26	0.07	0.10	0.11	0.09	0.22	0.12	0.08	0.05	0.13
	CV	2.93	2.71	3.76	1.09	2.94	3.45	7.20	5.79	4.69	9.95	4.66	4.93
	Minimum	10.75	4.07	6.70	6.14	3.33	3.05	1.17	3.56	2.49	0.71	1.15	2.55
	Maximum	11.68	4.45	7.49	6.32	3.67	3.35	1.48	4.33	2.90	0.92	1.32	2.95
Male													
TW C	Mean	11.63	4.45	7.05	6.20	3.54	3.23	1.47	3.88	2.69	0.89	1.21	2.67
	SD	0.23	0.14	0.39	0.18	0.18	0.12	0.27	0.16	0.16	0.09	0.03	0.17
	CV	2.06	3.35	5.83	3.12	5.27	4.03	19.20	4.19	6.32	11.02	2.44	6.66
	Minimum	11.40	4.31	6.61	5.97	3.35	3.05	1.27	3.69	2.53	0.78	1.18	2.55
	Maximum	11.96	4.64	7.47	6.46	3.80	3.39	1.94	4.07	2.90	1.00	1.25	2.95
Female													
TW A	K-S	0.162	0.137	0.168	0.163	0.173	0.267	0.281	0.196	0.345	0.230	0.168	0.220
	df	10	10	10	10	10	10	10	10	10	10	10	10
	P	0.200	0.200	0.200	0.200	0.200	0.042 *	0.024 *	0.200	0.001 **	0.143	0.200	0.188
TW B	K-S	0.232	0.296	0.136	0.204	0.299	0.226	0.196	0.160	0.266	0.212	0.253	0.144
	df	8	8	8	8	8	8	8	8	8	8	8	8
	P	0.200	0.038 *	0.200	0.200	0.033 *	0.200	0.200	0.200	0.099	0.200	0.142	0.200
Male													
TW C	K-S	0.210	0.289	0.251	0.214	0.215	0.179	0.364	0.160	0.222	0.273	0.246	0.281
	df	5	5	5	5	5	5	5	5	5	5	5	5
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.029 *	0.200	0.200	0.200	0.200	0.200

O2) Tooth wear classes of male *Pipistrellus rusticus* from six localities in Zimbabwe and South Africa.

Male		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A (*n* = 5)	Mean	11.27	4.19	6.83	6.13	3.44	3.10	1.29	3.86	2.62	0.88	1.19	2.70
	SD	0.21	0.10	0.08	0.23	0.16	0.17	0.07	0.17	0.13	0.10	0.08	0.15
	CV	1.97	2.49	1.24	3.93	4.85	5.86	5.70	4.64	5.33	11.62	6.60	5.95
	Minimum	10.92	4.07	6.75	5.85	3.23	2.90	1.22	3.67	2.49	0.78	1.12	2.44
	Maximum	11.42	4.30	6.95	6.37	3.62	3.32	1.38	4.07	2.77	1.00	1.28	2.85
TW B (*n* = 7)	Mean	11.42	4.37	6.88	6.15	3.52	3.24	1.39	3.88	2.67	0.85	1.18	2.73
	SD	0.36	0.10	0.34	0.21	0.12	0.12	0.19	0.14	0.19	0.07	0.04	0.18
	CV	3.31	2.46	5.12	3.48	3.60	3.96	14.32	3.65	7.29	9.03	3.32	6.96
	Minimum	10.93	4.24	6.40	5.86	3.34	3.12	1.17	3.72	2.39	0.78	1.12	2.39
	Maximum	11.89	4.53	7.32	6.46	3.70	3.44	1.73	4.07	2.95	0.98	1.22	2.95
TW A	K-S	0.272	0.207	0.179	0.199	0.175	0.177	0.217	0.203	0.233	0.247	0.235	0.282
	df	5	5	5	5	5	5	5	5	5	5	5	5
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200
TW B	K-S	0.171	0.206	0.162	0.159	0.121	0.244	0.205	0.176	0.153	0.240	0.173	0.262
	df	7	7	7	7	7	7	7	7	7	7	7	7
	P	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.160

O3) Male and female *Pipistrellus rusticus* from six localities in Zimbabwe and South Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Females (*n* = 22)	**Mean**	11.55	4.36	7.04	6.21	3.52	3.23	1.37	4.00	2.71	0.87	1.22	2.74
	SD	0.30	0.12	0.30	0.10	0.14	0.15	0.15	0.19	0.11	0.09	0.05	0.17
	CV	2.65	2.75	4.35	1.68	3.94	4.72	11.40	4.90	4.13	10.78	3.99	6.17
	Minimum	10.75	4.07	6.49	6.02	3.33	2.95	1.17	3.56	2.49	0.71	1.15	2.29
	Maximum	12.23	4.64	7.49	6.46	3.80	3.58	1.94	4.33	2.90	1.02	1.32	2.95
Males (*n* = 13)	**Mean**	11.38	4.29	6.86	6.13	3.48	3.17	1.34	3.87	2.64	0.86	1.18	2.70
	SD	0.31	0.13	0.25	0.20	0.13	0.15	0.15	0.14	0.16	0.08	0.05	0.16
	CV	2.75	3.06	3.66	3.38	3.92	4.95	11.44	3.74	6.10	9.24	4.42	6.20
	Minimum	10.92	4.07	6.40	5.85	3.23	2.90	1.17	3.67	2.39	0.78	1.12	2.39
	Maximum	11.89	4.53	7.32	6.46	3.70	3.44	1.73	4.07	2.95	1.00	1.28	2.95

O4) Tooth wear classes of *Pipistrellus rusticus* from six localities in Zimbabwe and South Africa.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
TW A (*n* = 15)	**Mean**	11.51	4.31	6.92	6.18	3.52	3.18	1.32	4.00	2.68	0.90	1.22	2.72
	SD	0.31	0.12	0.24	0.16	0.15	0.20	0.09	0.19	0.11	0.08	0.06	0.18
	CV	2.74	2.83	3.59	2.57	4.30	6.25	7.12	4.94	4.16	8.90	4.96	6.77
	Minimum	10.92	4.07	6.49	5.85	3.23	2.90	1.22	3.67	2.49	0.78	1.12	2.29
	Maximum	12.23	4.51	7.33	6.37	3.80	3.58	1.53	4.28	2.85	1.02	1.29	2.95
TW B (*n* = 15)	**Mean**	11.41	4.33	7.00	6.18	3.48	3.23	1.36	3.93	2.69	0.82	1.19	2.74
	SD	0.33	0.11	0.31	0.15	0.11	0.11	0.15	0.19	0.15	0.08	0.05	0.15
	CV	2.95	2.62	4.53	2.39	3.26	3.52	10.80	4.83	5.74	9.69	4.07	5.66
	Minimum	10.75	4.07	6.40	5.86	3.33	3.05	1.17	3.56	2.39	0.71	1.12	2.39
	Maximum	11.89	4.53	7.49	6.46	3.70	3.44	1.73	4.33	2.95	0.98	1.32	2.95
TW C (*n* = 5)	**Mean**	11.63	4.45	7.05	6.20	3.54	3.23	1.47	3.88	2.69	0.89	1.21	2.67
	SD	0.23	0.14	0.39	0.18	0.18	0.12	0.27	0.16	0.16	0.09	0.03	0.17
	CV	2.06	3.35	5.83	3.12	5.27	4.03	19.21	4.19	6.32	11.02	2.44	6.66
	Minimum	11.40	4.31	6.61	5.97	3.35	3.05	1.27	3.69	2.53	0.78	1.18	2.55
	Maximum	11.96	4.64	7.47	6.46	3.80	3.39	1.94	4.07	2.90	1.00	1.25	2.95

Appendix 5.7 (A-M)

Summary statistics of external measurements

Summary statistics [mean, standard deviation (SD), coefficient of variation (CV), minimum and maximum] and Kolmogorov-Smirnov (K-S) tests of normality in external measurements of different sexes and or tooth wear classes of the different groups of different vespertilionid species analysed. n = sample size, df = degrees of freedom, P = significance. *, ** and *** denote significance at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

A) Male and female *Eptesicus hottentotus* from six localities in Namibia.

		TOT	HB	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Females	*n*	2	5	7	7	7	10	2	11	7	10	11	9	11
	Mean	128.5	72.2	54.1	48.00	9.9	9.19	49.5	50.22	18.5	19.87	49.58	8.90	2.31
	SD	5.0	3.4	6.1	3.51	0.7	0.55	6.4	1.94	1.4	1.07	2.36	0.74	0.42
	CV	4.3	4.9	11.7	7.58	7.3	6.09	14.5	3.95	8.1	5.54	4.87	8.57	18.61
	Minimum	125.0	70.0	46.0	43.64	9.0	8.27	45.0	46.33	17.0	18.55	44.73	7.66	1.91
	Maximum	132.0	78.0	65.0	53.67	11.0	10.14	54.0	52.63	20.0	21.32	53.05	9.97	3.47
Males	*n*	1	1	2	3	2	4	1	4	2	3	4	4	4
	Mean	131.0	65.0	51.0	43.09	9.5	9.13	49.0	47.60	18.5	18.47	46.22	8.82	2.23
	SD	-	-	4.2	7.89	0.7	0.19	-	0.86	2.1	1.12	1.89	0.96	0.22
	CV	-	-	9.4	19.84	8.4	2.25	-	1.91	12.9	6.58	4.34	11.55	10.44
	Minimum	131.0	65.0	48.0	38.27	9.0	8.86	49.0	46.63	17.0	17.31	43.59	7.84	1.94
	Maximum	131.0	65.0	54.0	52.20	10.0	9.32	49.0	48.68	20.0	19.55	47.72	9.88	2.47
TW D	*n*	3	4	7	6	7	9	3	10	7	8	10	8	10
	Mean	129.3	71.0	52.9	47.28	9.9	9.26	49.3	49.44	18.5	19.79	49.14	9.11	2.28
	SD	3.8	5.4	3.3	4.86	0.7	0.56	4.5	1.94	1.4	1.05	2.47	0.79	0.45
	CV	3.2	8.0	6.4	10.71	7.3	6.18	9.9	4.03	8.1	5.47	5.15	8.94	20.19
	Minimum	125.0	65.0	48.0	38.81	9.0	8.27	45.0	46.33	17.0	18.55	44.73	7.84	1.91
	Maximum	132.0	78.0	57.0	52.20	11.0	10.14	54.0	52.63	20.0	21.32	53.05	9.97	3.47
Females	**K-S**	-	0.324	0.177	0.141	0.296	0.143	-	0.227	0.279	0.195	0.159	0.145	0.320
	df	-	5	7	7	7	10	-	11	7	10	11	9	11
	P	-	0.094	0.200	0.200	0.063	0.200	-	0.119	0.106	0.200	0.200	0.200	0.002
TW D	**K-S**	-	-	0.207	0.254	0.296	0.207	-	0.159	0.279	0.176	0.146	0.212	0.292
	df	-	-	7	6	7	9	-	10	7	8	10	8	10
	P	-	-	0.200	0.200	0.063	0.200	-	0.200	0.106	0.200	0.200	0.200	0.016 *

B) Male and female *Hypsugo anchietae* from five localities in southern Africa.

		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Females	*n*	4	4	4	4	6	4	5	4	4	6	6	6
	Mean	83.0	36.0	35.52	6.1	6.15	31.4	30.71	11.5	11.30	31.02	5.37	1.77
	SD	3.7	3.2	2.301	0.3	0.44	0.8	1.27	1.0	0.81	0.66	0.36	0.54
	CV	4.8	9.3	6.88	4.3	7.46	2.7	4.36	9.3	7.60	2.22	6.89	32.03
	Minimum	78.0	32.0	33.82	6.0	5.56	30.3	28.50	11.0	10.63	29.97	4.92	1.24
	Maximum	87.0	39.0	38.77	6.5	6.80	32.0	31.56	13.0	12.29	31.80	5.77	2.63
Males	*n*	3	3	2	3	2	3	3	3	2	3	3	3
	Mean	77.3	34.3	35.18	6.3	5.93	30.5	29.42	11.0	10.80	29.13	5.11	1.58
	SD	3.8	0.6	2.07	0.67	0.33	1.5	1.72	1.0	0.28	1.57	0.34	0.23
	CV	5.3	1.8	6.60	9.9	6.31	5.3	6.35	9.8	2.87	5.84	7.23	15.89
	Minimum	73.0	34.0	33.72	6.0	5.69	29.0	28.42	10.0	10.60	27.34	4.79	1.36
	Maximum	80.0	35.0	36.64	7.0	6.16	32.0	31.41	12.0	10.99	30.29	5.47	1.82
F	**K-S**	-	-	-	-	0.186	-	-	-	-	0.141	0.195	0.336
	df	-	-	-	-	6	-	-	-	-	6	6	6
	P	-	-	-	-	0.200	-	-	-	-	0.200	0.200	0.033 *

C1) Male and female *Neoromicia capensis* from Brandfort in the Free State Province of South Africa falling into the Grassland biome.

		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Females	*n*	10	10	9	10	10	7	10	10	9	10	10	10
	Mean	90.5	33.7	30.55	8.3	6.84	35.3	35.48	11.5	11.82	32.80	5.87	1.57
	SD	4.0	2.5	1.39	0.5	0.39	1.0	0.77	1.6	0.62	0.94	0.73	0.07
	CV	4.5	7.6	4.68	6.0	5.84	2.8	2.23	14.1	5.41	2.93	12.79	4.30
	Minimum	86.0	31.0	27.27	8.0	6.30	34.0	33.96	10.0	10.60	31.26	4.27	1.47
	Maximum	98.0	39.0	31.68	9.0	7.45	36.0	36.31	14.0	12.74	34.55	6.52	1.65
Males	*n*	9	9	5	9	9	9	9	9	9	9	9	9
	Mean	85.1	30.1	28.87	8.2	6.78	33.4	33.87	10.3	11.37	30.90	5.85	1.53
	SD	4.4	3.6	2.67	0.4	0.83	1.3	1.45	0.5	0.66	1.55	0.80	0.15
	CV	5.3	12.1	9.69	5.5	12.51	4.1	4.41	5.0	5.95	5.16	14.07	10.25
	Minimum	79.0	23.0	24.87	8.0	4.86	32.0	32.05	10.0	10.43	29.11	4.46	1.35
	Maximum	93.0	35.0	31.59	9.0	7.76	36.0	36.55	11.0	12.72	33.47	6.59	1.76
Females	**K-S**	0.153	0.252	0.241	0.433	0.237	0.345	0.141	0.324	0.335	0.111	0.216	0.149
	df	10	10	9	10	10	7	10	10	9	10	10	10
	P	0.200	0.071	0.140	7.56E-06 ***	0.117	0.012 *	0.200	0.004 **	0.004**	0.200	0.200	0.200
Males	**K-S**	0.156	0.265	0.179	0.471	0.284	0.227	0.222	0.414	0.213	0.199	0.358	0.164
	df	9	9	5	9	9	9	9	9	9	9	9	9
	P	0.200	0.067	0.200	2.11E-06 ***	0.035 *	0.198	0.200	7.32E-05 ***	0.200	0.200	0.001 **	0.200

C2) Tooth wear classes of *Neoromicia capensis* from Brandfort in the Free State Province of South Africa falling into the Grassland biome.

		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
TW A		93.0	30.0		8.0	7.76	33.0	34.13	11.0	11.48	29.86	6.01	1.43
TW B	*n*	9	9	6	9	9	9	9	9	9	9	9	9
	Mean	86.4	31.1	29.86	8.2	6.56	34.0	34.38	10.44	11.39	31.22	5.65	1.55
	SD	3.7	3.9	2.63	0.4	0.69	1.4	1.57	0.53	0.77	1.52	0.95	0.12
	CV	4.4	13.0	9.06	5.5	10.79	4.3	4.70	5.19	6.91	4.99	17.27	7.58
	Minimum	80.0	23.0	24.87	8.0	4.86	32.0	32.05	10.0	10.43	29.11	4.27	1.35
	Maximum	92.0	35.0	31.68	9.0	7.14	36.0	36.55	11.0	12.72	33.47	6.59	1.75
TW C	*n*	7	7	6	7	7	6	7	7	6	7	7	7
	Mean	87.3	32.9	29.65	8.3	7.11	34.8	35.25	10.7	11.94	32.52	6.03	1.56
	SD	5.3	3.2	1.72	0.5	0.32	1.6	1.32	1.1	0.49	1.05	0.53	0.13
	CV	6.2	10.2	6.27	6.1	4.65	4.7	3.88	10.8	4.79	3.34	9.06	8.75
	Minimum	79.0	30.0	27.27	8.0	6.57	32.0	32.45	10.0	11.41	30.48	4.95	1.36
	Maximum	96.0	39.0	31.44	9.0	7.51	36.0	36.20	13.0	12.74	33.55	6.47	1.76
TW D	*n*	2	2	2	2	2	0	2	2	2	2	2	2
	Mean	94.5	34.0	31.13	8.5	6.45	-	34.66	14.0	11.55	33.79	6.12	1.60
	SD	5.0	2.8	0.45	0.7	0.21	-	0.98	-	0.68	1.08	0.57	0.07
	CV	5.9	9.4	1.61	9.4	3.70	-	3.191	-	6.61	3.58	10.54	4.97
	Minimum	91.0	32.0	30.81	8.0	6.30	-	33.96	14.0	11.07	33.03	5.71	1.55
	Maximum	98.0	36.0	31.44	9.0	6.60	-	35.35	14.0	12.03	34.55	6.52	1.65

D1) Male and female *Neoromicia capensis* from Jagersfontein in the Free State Province of South Africa falling into the Nama-Karoo biome.

		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Females	*n*	14	14	11	14	14	14	14	14	14	14	13	13
	Mean	88.3	35.4	33.59	8.3	7.28	35.4	35.62	10.6	11.90	31.81	6.00	1.53
	SD	5.3	3.2	1.89	0.5	0.39	1.1	1.26	1.5	0.56	1.43	0.78	0.19
	CV	6.1	9.1	5.72	5.8	5.50	3.1	3.59	13.8	4.76	4.58	13.23	12.56
	Minimum	73.0	26.0	30.71	8.0	6.54	33.0	33.13	9.0	10.95	27.86	4.48	1.25
	Maximum	94.0	38.0	36.81	9.0	8.16	37.0	38.00	14.0	13.04	33.83	7.02	1.99
Males	*n*	42	42	41	42	42	42	42	42	40	42	40	41
	Mean	85.4	33.3	31.00	8.1	7.10	34.0	33.66	10.4	11.40	30.06	6.20	1.53
	SD	3.9	2.1	2.34	0.6	0.41	1.4	1.24	1.60	0.53	1.06	0.42	0.17
	CV	4.6	6.3	7.59	6.8	5.79	4.1	3.71	15.2	4.65	3.55	6.74	11.42
	Minimum	77.0	28.0	25.87	7.0	6.37	29.0	30.64	9.0	10.16	27.72	5.34	1.20
	Maximum	91.0	37.0	36.56	9.0	8.03	37.0	36.05	14.0	12.29	32.27	7.04	1.95
Females	**K-S**	0.198	0.286	0.142	0.443	0.187	0.295	0.110	0.188	0.184	0.209	0.161	0.200
	df	14	14	11	14	14	14	14	14	14	14	13	13
	P	0.144	0.003**	0.200	2.74E-08 ***	0.200	0.002 **	0.200	0.193	0.200	0.098	0.200	0.163
Males	**K-S**	0.163	0.209	0.082	0.371	0.077	0.252	0.157	0.222	0.166	0.072	0.106	0.096
	df	42	42	41	42	42	42	42	42	40	42	40	41
	P	0.007 **	7.75E-05 ***	0.200	2.80E-16 ***	0.200	3.72E-07 ***	0.011 *	1.77E-05 ***	0.007 **	0.200	0.200	0.200

D2) Tooth wear classes of male *Neoromicia capensis* from Jagersfontein in the Free State Province of South Africa falling into the Nama-Karoo biome.

		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
TW A	*n*	3	3	2	3	3	3	3	3	3	3	2	3
	Mean	83.7	32.7	30.45	7.3	6.71	33.3	32.34	10.0	11.29	28.72	5.77	1.48
	SD	2.12	1.5	0.11	0.6	0.53	0.6	1.09	1.7	0.38	1.05	0.29	0.20
	CV	2.7	5.1	0.40	8.5	8.50	1.9	3.64	18.8	3.63	3.97	5.45	14.34
	Minimum	82.0	31.0	30.37	7.0	6.37	33.0	31.44	9.0	11.02	27.72	5.56	1.37
	Maximum	86.0	34.0	30.53	8.0	7.32	34.0	33.55	12.0	11.72	29.82	5.97	1.71
TW B	*n*	3	3	3	3	3	3	3	3	3	3	3	3
	Mean	86.0	33.3	32.02	8.7	7.08	34.3	34.11	9.67	11.49	30.63	6.32	1.52
	SD	3.6	1.2	1.11	0.6	0.52	0.6	0.67	1.16	0.31	0.26	0.08	0.13
	CV	4.5	3.8	3.74	7.2	7.94	1.8	2.13	12.9	2.89	0.92	1.29	9.19
	Minimum	82.0	32.0	30.75	8.0	6.71	34.0	33.35	9.0	11.15	30.38	6.24	1.37
	Maximum	89.0	34.0	32.78	9.0	7.67	35.0	34.61	11.0	11.74	30.90	6.39	1.61
TW C	*n*	21	21	21	21	21	21	21	21	19	21	21	21
	Mean	85.4	33.5	31.16	8.1	7.19	33.7	33.64	10.5	11.28	29.96	6.14	1.53
	SD	3.8	1.5	2.41	0.5	0.41	1.6	1.34	1.6	0.60	1.06	0.42	0.16
	CV	4.6	4.7	7.83	6.3	5.81	4.7	4.03	15.8	5.40	3.56	6.88	10.39
	Minimum	77.0	31.0	27.06	7.0	6.51	29.0	30.64	9.0	10.16	27.95	5.35	1.20
	Maximum	91.0	36.0	36.13	9.0	8.03	36.0	35.85	14.0	12.08	32.27	6.76	1.80
TW D	*n*	12	12	12	12	12	12	12	12	12	12	12	12
	Mean	86.4	33.5	31.04	8.3	7.09	34.4	34.02	10.7	11.57	30.35	6.31	1.53
	SD	3.9	2.8	2.77	0.5	0.33	1.4	0.95	1.8	0.47	1.08	0.46	0.20
	CV	4.6	8.6	9.11	5.6	4.82	4.1	2.86	17.5	4.14	3.63	7.38	13.17
	Minimum	77.0	28.0	25.87	8.0	6.81	32.0	32.62	9.0	10.64	28.23	5.34	1.27
	Maximum	91.0	37.0	36.56	9.0	7.94	37.0	36.05	14.0	12.29	32.13	7.04	1.91
TW C	K-S	0.183	0.260	0.152	0.395	0.137	0.287	0.159	0.198	0.150	0.122	0.120	0.118
	df	21	21	21	21	21	21	21	21	19	21	21	21
	P	0.066	0.001 **	0.200	1.85E-09 ***	0.200	8.34E-05 ***	0.180	0.031 *	0.200	0.200	0.200	0.200
TW D	K-S	0.192	0.237	0.158	0.460	0.220	0.285	0.211	0.236	0.218	0.095	0.172	0.150
	df	12	12	12	12	12	12	12	12	12	12	12	12
	P	0.200	0.061	0.200	8.26E-08 ***	0.112	0.008 **	0.145	0.064	0.119	0.200	0.200	0.200

E) Male and female *Neoromicia capensis* from King Williams Town in the Eastern Cape Province of South Africa.

		TOT	HB	T	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Females	*n*	-	11	12	12	12	2	11	12	4	12	12	12
	Mean	-	52.1	36.3	6.9	6.56	35.3	34.10	11.3	11.86	31.53	5.13	1.78
	SD	-	3.5	1.7	1.2	0.43	2.5	1.33	1.3	1.15	1.52	0.93	0.26
	CV	-	6.8	4.8	16.9	6.76	7.9	3.99	11.5	10.34	4.91	18.54	15.19
	Minimum	-	45.0	34.0	5.0	6.15	33.5	31.55	10.0	10.89	29.08	3.77	1.40
	Maximum	-	56.0	39.0	9.0	7.50	37.0	36.35	14.0	13.52	34.23	6.62	2.23
Males	*n*	3	6	9	9	9	3	8	9	1	9	9	9
	Mean	84.0	46.4	32.1	7.4	6.31	32.0	31.43	11.4	10.98	28.89	4.82	1.62
	SD	2.7	3.6	3.2	1.2	0.57	1.0	1.19	0.9	-	1.00	0.55	0.21
	CV	3.4	8.2	10.1	16.2	9.31	3.4	3.91	8.2	-	3.57	11.77	13.24
	Minimum	82.0	42.0	27.0	5.0	5.47	31.0	29.43	10.0	10.98	27.43	4.22	1.37
	Maximum	87.0	53.0	36.0	9.0	7.31	33.0	33.21	13.0	10.98	30.64	5.80	2.00
Females	**K-S**	-	0.183	0.191	0.196	0.211	-	0.213	0.245	-	0.158	0.176	0.152
	df	-	11	12	12	12	-	11	12	-	12	12	12
	P	-	0.200	0.200	0.200	0.148	-	0.177	0.046 *	-	0.200	0.200	0.200
Males	**K-S**	-	0.270	0.172	0.238	0.197	-	0.202	0.239	-	0.117	0.186	0.171
	df	-	6	9	9	9	-	8	9	-	9	9	9
	P	-	0.197	0.200	0.151	0.200	-	0.200	0.148	-	0.200	0.200	0.200

F) Male and female *Neoromicia* cf. *melckorum* from two localities in Zimbabwe and South Africa.

		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Females	***n***	3	3	5	3	5	3	8	3	5	5	5	5
	Mean	99.0	40.3	34.89	7.3	6.4	37.3	37.21	11.0	12.86	35.30	6.59	1.85
	SD	2.7	3.3	2.11	0.6	0.3	1.2	0.84	1.0	0.43	0.43	0.40	0.16
	CV	2.9	8.6	6.35	8.5	5.6	3.4	2.46	9.9	3.53	1.27	6.38	9.10
	Minimum	96.0	38.0	32.50	7.0	6.1	36.0	36.10	10.0	12.45	34.67	6.26	1.68
	Maximum	101.0	44.0	36.95	8.0	6.9	38.0	38.70	12.0	13.45	35.69	7.17	2.06
Males	***n***	-	-	7	-	7	-	7	-	7	7	7	7
	Mean	-	-	34.62	-	6.22	-	35.12	-	12.62	34.43	6.57	1.84
	SD	-	-	3.10	-	0.40	-	0.95	-	0.39	0.69	0.17	0.12
	CV	-	-	9.25	-	6.72	-	2.80	-	3.19	2.07	2.70	6.48
	Minimum	-	-	29.65	-	5.74	-	33.68	-	12.21	33.24	6.27	1.68
	Maximum	-	-	37.53	-	6.81	-	36.26	-	13.25	35.41	6.80	1.98
Females	**K-S**	-	-	0.249	-	0.214	-	0.231	-	0.208	0.263	0.263	0.205
	df	-	-	5	-	5	-	8	-	5	5	5	5
	P	-	-	0.200	-	0.200	-	0.200	-	0.200	0.200	0.200	0.200
Males	**K-S**	-	-	0.261	-	0.160	-	0.223	-	0.227	0.167	0.244	0.179
	df	-	-	7	-	7	-	7	-	7	7	7	7
	P	-	-	0.162	-	0.200	-	0.200	-	0.200	0.200	0.200	0.200

G1) Male and female *Neoromicia africanus* from 15 localities in KwaZulu-Natal and the Eastern Cape Provinces in South Africa and Swaziland.

		TOT	HB	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Females	*n*	8	6	14	9	14	15	9	17	15	14	16	16	16
	Mean	77.5	42.9	35.5	29.94	6.4	5.50	30.9	30.96	10.3	11.67	29.26	4.58	1.45
	SD	4.5	1.6	3.2	1.90	0.6	0.52	0.6	0.90	1.4	0.63	1.67	0.63	0.37
	CV	6.0	3.9	9.1	6.51	10.0	9.54	2.1	2.95	13.7	5.48	5.79	13.96	25.85
	Minimum	70.0	41.0	30.0	27.27	5.0	4.77	30.0	29.17	8.5	10.30	26.62	3.69	0.91
	Maximum	82.0	45.0	42.0	33.45	7.0	6.57	32.0	32.34	13.0	12.63	33.32	6.10	2.22
Males	*n*	16	3	19	18	18	23	18	23	21	21	22	22	23
	Mean	76.1	46.7	34.3	30.81	6.0	5.56	31.0	29.59	10.24	11.18	28.48	4.40	1.20
	SD	4.3	4.7	3.5	2.00	0.8	0.56	2.3	1.36	1.07	0.57	0.83	0.52	0.31
	CV	5.8	10.3	10.2	6.57	14.3	10.26	7.6	4.63	10.6	5.18	2.95	12.02	25.77
	Minimum	68.0	43.0	29.0	27.71	4.0	4.63	29.4	27.34	8.0	10.13	26.11	3.45	0.73
	Maximum	83.0	52.0	40.0	35.31	7.0	6.56	37.5	33.05	12.0	12.33	29.78	5.42	1.92
Females	**K-S**	0.381	0.173	0.228	0.184	0.230	0.105	0.328	0.128	0.219	0.155	0.148	0.157	0.157
	df	8	6	14	9	14	15	9	17	15	14	16	16	16
	P	0.001 **	0.200	0.047 *	0.159	0.121	0.200	0.006 **	0.200	0.050	0.200	0.200	0.200	0.200
Males	**K-S**	0.153	-	0.161	0.159	0.265	0.106	0.363	0.194	0.191	0.149	0.131	0.139	0.158
	df	16	-	19	18	18	23	18	23	21	21	22	22	23
	P	0.200	-	0.200	0.200	0.002 **	0.200	8.27E-07 ***	0.025 *	0.045 *	0.200	0.200	0.200	0.140

G2) Tooth wear classes of *Neoromicia africanus* from 15 localities in KwaZulu-Natal and the Eastern Cape Provinces in South Africa and Swaziland.

		TOT	HB	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
TW A	*n*	2	2	4	4	3	4	3	4	4	4	3	4	4
	Mean	76.0	47.5	36.3	31.19	6.5	5.32	31.8	30.67	11.0	11.27	27.54	4.35	1.32
	SD	9.9	6.4	5.0	1.90	0.5	0.74	2.0	1.84	0.7	0.38	1.28	0.53	0.39
	CV	14.7	15.1	14.6	6.47	8.3	14.75	6.7	6.38	6.8	3.60	5.05	12.92	31.44
	Minimum	69.0	43.0	29.0	29.09	6.0	4.63	30.3	28.58	10.5	10.86	26.11	3.58	0.99
	Maximum	83.0	52.0	40.0	33.16	7.0	6.33	34.0	33.05	12.0	11.74	28.59	4.73	1.88
TW B	*n*	3	-	3	3	3	3	3	3	3	3	3	3	3
	Mean	73.7	-	31.7	30.13	6.0	5.97	32.3	28.85	10.8	11.31	28.45	4.37	0.94
	SD	4.9	-	1.5	0.16	1.0	0.53	4.5	1.56	1.3	1.00	0.77	0.44	0.08
	CV	7.3	-	5.2	0.58	18.1	9.63	15.2	5.86	12.6	9.59	2.92	11.00	8.83
	Minimum	68.0	-	30.0	29.96	5.0	5.45	29.4	27.37	9.5	10.28	27.84	3.87	0.87
	Maximum	77.0	-	33.0	30.28	7.0	6.51	37.5	30.48	12.0	12.28	29.31	4.71	1.02
TW C	*n*	12	4	16	13	16	18	12	19	16	18	19	19	19
	Mean	77.3	42.4	35.0	30.41	6.2	5.43	30.30	30.21	10.2	11.31	28.86	4.62	1.36
	SD	4.0	1.5	3.4	1.66	0.6	0.43	0.71	1.45	1.0	0.55	1.32	0.62	0.41
	CV	5.2	3.9	10.0	5.55	9.9	8.08	2.39	4.87	9.4	4.89	4.64	13.60	30.67
	Minimum	70.0	41.0	30.0	27.27	5.0	4.71	29.5	27.34	8.5	10.13	27.35	3.67	0.73
	Maximum	82.0	44.5	42.0	33.45	7.0	6.22	32.0	32.34	11.5	12.41	33.32	6.10	2.22
TW D	*n*	7	-	7	4	7	6	6	7	7	7	6	7	7
	Mean	76.6	-	35.9	32.10	5.8	5.59	30.4	29.99	9.4	11.31	29.41	4.47	1.22
	SD	3.7	-	2.0	3.18	1.1	0.69	0.6	1.14	1.0	0.77	0.96	0.57	0.27
	CV	5.0	-	5.6	10.51	19.1	12.87	2.1	3.94	10.7	7.06	3.40	13.29	22.56
	Minimum	70.0	-	33.0	29.10	4.0	4.92	29.8	28.19	8.0	10.29	27.92	3.68	0.91
	Maximum	80.0	-	39.0	35.31	7.0	6.57	31.3	31.68	11.0	12.23	30.66	5.36	1.47
TW C	K-S	0.151		0.194	0.104	0.272	0.130	0.247	0.158	0.242	0.126	0.223	0.157	0.160
	df	12		16	13	16	18	12	19	16	18	19	19	19
	P	0.200		0.109	0.200	0.003 **	0.200	0.041 *	0.200	0.013 *	0.200	0.014 *	0.200	0.200
TW D	K-S	0.316		0.243	-	0.154	0.263	0.262	0.174	0.241	0.190	0.177	0.154	0.276
	df	7		7	-	7	6	6	7	7	7	6	7	7
	P	0.033 *		0.200	-	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.200	0.114

H1) Male and female *Neoromicia africanus* from three localities in Malawi.

		HB	T	TL	HFL	HF	FA	E	TIB	TMETA	TRL	TRB
Females	*n*	22	21	24	22	25	27	22	22	27	20	21
	Mean	42.7	37.1	32.35	6.5	5.72	31.93	11.2	11.61	30.52	4.63	1.38
	SD	2.0	1.6	2.24	0.4	0.40	0.86	0.3	0.60	0.91	0.41	0.17
	CV	4.8	4.2	6.99	6.0	7.09	2.72	3.0	5.23	2.99	9.03	12.39
	Minimum	40.0	33.0	27.35	6.0	4.76	30.43	10.5	10.47	28.87	4.00	0.98
	Maximum	49.0	39.0	37.46	7.0	6.51	33.40	12.0	12.81	32.20	5.35	1.71
Males	*n*	3	3	6	3	7	7	3	7	7	6	7
	Mean	41.3	37.3	31.23	6.0	5.28	30.18	11.0	11.53	29.38	4.24	1.44
	SD	0.6	1.5	1.26	-	0.62	1.45	-	0.66	0.89	0.61	0.13
	CV	1.5	4.4	4.36	-	12.63	5.19	-	6.20	3.28	15.56	9.98
	Minimum	41.0	36.0	29.15	6.0	4.42	27.23	11.0	10.58	27.81	3.39	1.18
	Maximum	42.0	39.0	33.05	6.0	5.93	31.44	11.0	12.22	30.40	5.03	1.58
Females	**K-S**	0.256	0.245	0.145	0.201	0.107	0.115	0.289	0.128	0.127	0.131	0.130
	df	22	21	24	22	25	27	22	22	27	20	21
	P	0.001 **	0.002 **	0.200	0.022 *	0.200	0.200	4.36E-05 ***	0.200	0.200	0.200	0.200
Males	**K-S**	-	-	0.260	-	0.256	0.266	-	0.176	0.187	0.194	0.244
	df	-	-	6	-	7	7	-	7	7	6	7
	P	-	-	0.200	-	0.185	0.145	-	0.200	0.200	0.200	0.200

H2) Tooth wear classes of female *Neoromicia africanus* from three localities in Malawi.

Female		HB	T	TL	HFL	HF	FA	E	TIB	TMETA	TRL	TRB
TW B	*n*	3	3	5	3	5	5	3	5	5	5	4
	Mean	42.0	36.7	31.92	6.3	5.70	32.00	11.3	11.02	30.15	4.56	1.33
	SD	1.7	1.5	3.29	0.3	0.15	1.15	0.3	0.25	0.80	0.30	0.08
	CV	4.5	4.5	10.83	4.9	2.67	3.78	2.8	2.36	2.77	6.97	6.33
	Minimum	40.0	35.0	27.35	6.0	5.46	30.43	11.0	10.84	28.87	4.14	1.23
	Maximum	43.0	38.0	35.98	6.5	5.85	33.32	11.5	11.44	31.05	4.85	1.40
TW C	*n*	6	6	7	6	8	8	6	6	8	5	6
	Mean	42.7	36.2	31.88	6.4	5.69	32.00	11.0	11.98	30.35	4.48	1.54
	SD	1.0	1.9	1.37	0.4	0.48	0.78	0.4	0.18	0.79	0.55	0.14
	CV	2.5	5.6	4.45	6.6	8.70	2.51	3.0	1.53	2.67	12.82	9.50
	Minimum	41.0	33.0	29.99	6.0	4.76	31.06	10.5	11.72	29.20	4.00	1.37
	Maximum	44.0	38.0	34.24	7.0	6.25	33.40	11.5	12.20	31.66	5.35	1.71
TW D	*n*	5	4	4	5	5	5	5	4	5	4	5
	Mean	41.2	37.8	32.54	6.4	5.73	31.31	11.4	11.43	30.23	4.81	1.35
	SD	0.8	1.3	2.28	0.4	0.28	0.57	0.4	0.74	1.22	0.32	0.21
	CV	2.1	3.5	7.44	6.9	5.14	1.91	3.9	6.90	4.24	7.12	16.53
	Minimum	40.0	36.0	30.50	6.0	5.42	30.69	11.0	10.47	28.88	4.35	0.98
	Maximum	42.0	39.0	35.73	7.0	6.16	31.92	12.0	12.28	32.20	5.09	1.49
TW B	K-S	-	-	0.231	-	0.283	0.152	-	0.277	0.314	0.287	-
	df	-	-	5	-	5	5	-	5	5	5	-
	P	-	-	0.200	-	0.200	0.200	-	0.200	0.120	0.200	-
TW C	K-S	0.293	0.172	0.179	0.180	0.259	0.220	0.333	0.170	0.151	0.202	0.231
	df	6	6	7	6	8	8	6	6	8	5	5
	P	0.117	0.200	0.200	0.200	0.123	0.200	0.036 *	0.200	0.200	0.200	0.200
TW D	K-S	0.231	-	-	0.231	0.255	0.253	0.201	-	0.293	-	0.334
	df	5	-	-	5	5	5	5	-	5	-	5
	P	0.200	-	-	0.200	0.200	0.200	0.200	-	0.186	-	0.072

I) Male and female *Neoromicia rueppellii* from six localities in Southern Africa.

		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Females	*n*	5	5	3	5	4	-	6	5	2	6	6	6
	Mean	92.8	36.2	33.8	8.0	6.7	-	35.4	11.6	13.3	32.8	4.8	1.8
	SD	3.0	3.8	4.2	1.0	0.4	-	1.0	1.3	1.9	2.0	0.5	0.3
	CV	3.3	10.9	13.4	13.1	6.8	-	2.9	12.1	15.8	6.3	11.0	19.4
	Minimum	88.0	32.0	29.2	7.0	6.40	-	34.4	10.0	12.0	29.2	4.2	1.6
	Maximum	95.0	40.0	37.2	9.0	7.3	-	37.0	13.0	14.7	34.7	5.4	2.5
Male	*n*	8	8	6	8	8	2	11	7	7	10	8	8
	Mean	90.4	38.6	29.2	8.6	7.3	34.0	34.4	12.1	13.1	32.7	5.2	1.6
	SD	7.7	3.5	3.4	1.4	0.8	-	1.2	1.6	1.0	1.4	0.7	0.3
	CV	8.8	9.5	12.3	16.8	11.3	-	3.6	13.4	38.9	4.5	41.0	17.1
	Minimum	76.0	31.0	23.2	6.0	6.2	34.0	32.8	10.0	11.5	29.2	3.9	1.3
	Maximum	100.0	42.0	33.2	11.0	8.3	34.0	36.3	14.0	14.0	34.0	5.8	2.0
Females	**K-S**	0.258	0.243	-	0.241	-	-	0.264	0.273	-	0.242	0.297	0.327
	df	5	5	-	5	-	-	6	5	-	6	6	6
	P	0.200	0.200	-	0.200	-	-	0.200	0.200	-	0.200	0.200	0.043 *
Males	**K-S**	0.231	0.274	0.263	0.357	0.201	-	0.168	0.195	0.367	0.205	0.298	0.166
	df	8	7	6	7	8	-	11	7	8	10	8	8
	P	0.200	0.120	0.200	0.007 **	0.200	-	0.200	0.200	0.002 **	0.200	0.035*	0.200

J) Male and female *Neoromicia rueppellii* from Balovale in Zambia.

		HB	T	TL	HFL	HF	FA	E	TIB	TMETA	TRL	TRB
Females	*n*	8	8	8	8	8	8	8	8	8	5	8
	Mean	47.4	33.1	29.51	8.9	7.19	32.11	12.56	10.52	26.99	4.73	1.18
	SD	1.9	2.0	2.00	0.2	0.73	1.47	0.48	0.88	1.84	0.33	0.14
	CV	4.0	6.3	6.98	2.0	10.45	4.74	3.92	8.59	7.05	7.10	11.84
	Minimum	45.0	29.0	26.59	8.5	5.77	30.05	12.00	9.20	23.36	4.35	0.96
	Maximum	50.0	35.0	32.26	9.0	8.17	34.29	13.25	11.86	29.36	5.11	1.36
Males	*n*	9	9	7	9	9	9	9	9	8	5	8
	Mean	47.4	31.2	28.61	8.7	7.52	31.25	12.3	10.35	26.95	4.73	1.15
	SD	1.0	2.2	3.04	0.3	0.60	1.52	0.4	0.90	1.78	0.34	0.17
	CV	2.2	7.1	11.02	3.1	8.21	4.99	3.0	8.91	6.79	7.63	15.08
	Minimum	46.0	28.0	24.64	8.5	6.68	29.23	12.0	9.09	24.16	4.17	0.86
	Maximum	49.0	34.0	33.40	9.0	8.86	33.57	13.0	11.34	29.63	5.11	1.38
Females	**K-S**	0.257	0.292	0.165	0.513	0.195	0.188	0.195	0.120	0.190	0.255	0.140
	df	8	8	8	8	8	8	8	8	8	5	8
	P	0.127	0.044 *	0.200	5.42E-07 ***	0.200	0.200	0.200	0.200	0.200	0.200	0.200
Males	**K-S**	0.264	0.196	0.178	0.356	0.186	0.131	0.272	0.165	0.328	0.305	0.201
	df	9	9	7	9	9	9	9	9	8	5	8
	P	0.071	0.200	0.200	0.002 **	0.200	0.200	0.054	0.200	0.011 *	0.146	0.200

K) Male and female *Neoromicia zuluensis* from 11 localities in Mpumalanga and Limpopo Provinces of South Africa.

		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Females	*n*	3	3	4	3	6	3	6	3	5	6	6	6
	Mean	80.0	35.7	32.23	7.0	5.44	30.2	29.47	11.0	10.96	29.34	5.08	1.25
	SD	2.0	4.5	2.37	-	0.36	0.8	1.53	-	0.54	1.30	0.57	0.15
	CV	2.7	13.7	7.80	-	6.80	2.7	5.41	-	5.13	4.62	11.70	12.52
	Minimum	78.0	31.0	29.68	7.0	5.02	29.5	27.45	11.0	10.28	27.59	4.32	1.12
	Maximum	82.0	40.0	35.23	7.0	5.99	31.0	31.26	11.0	11.54	30.89	5.91	1.49
Males	*n*	3	3	3	3	10	2	10	3	10	10	9	10
	Mean	79.0	34.0	28.70	5.7	5.37	31.5	29.78	10.5	11.46	28.97	4.74	1.23
	SD	2.7	1.7	1.31	1.2	0.32	0.7	0.80	0.9	0.78	1.21	0.41	0.12
	CV	3.6	5.5	4.95	22.1	6.06	2.5	2.76	8.9	6.95	4.29	8.87	10.22
	Minimum	77.0	32.0	27.41	5.0	4.93	31.0	28.58	9.5	9.57	26.18	4.26	1.06
	Maximum	82.0	35.0	30.03	7.0	5.76	32.0	30.72	11.0	12.22	30.10	5.32	1.41
Females	**K-S**	-	-	-	-	0.211	-	0.250	-	0.237	0.199	0.149	0.289
	df	-	-	-	-	6	-	6	-	5	6	6	6
	P	-	-	-	-	0.200	-	0.200	-	0.200	0.200	0.200	0.128
Males	**K-S**	-	-	-	-	0.159	-	0.261	-	0.221	0.224	0.158	0.165
	df	-	-	-	-	10	-	10	-	10	10	9	10
	P	-	-	-	-	0.200	-	0.052	-	0.180	0.170	0.200	0.200

L1) Male and female *Pipistrellus hesperidus* from 17 localities in the KwaZulu-Natal Province of South Africa.

		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Females	***n***	11	12	9	11	14	11	14	12	13	12	14	14
	Mean	85.4	35.1	31.76	7.6	6.41	33.0	31.61	11.5	10.66	31.65	4.91	1.74
	SD	2.9	2.0	3.82	0.5	0.73	1.0	0.94	0.9	0.78	1.29	0.37	0.28
	CV	3.4	5.8	12.30	7.1	11.66	3.2	3.05	8.0	7.49	4.18	7.62	16.19
	Minimum	81.0	30.0	27.51	7.0	5.20	31.0	29.68	9.0	8.55	28.86	4.05	1.39
	Maximum	91.0	38.0	40.56	8.0	7.31	34.7	32.87	12.0	11.67	33.20	5.35	2.23
Males	***n***	15	18	12	16	18	17	19	17	17	18	17	18
	Mean	81.2	32.3	30.17	7.4	6.21	32.39	30.87	10.8	10.56	30.75	5.14	1.66
	SD	4.3	3.4	3.42	1.3	0.48	0.76	1.17	0.8	0.90	0.88	0.39	0.50
	CV	5.3	10.6	11.54	17.3	7.89	2.37	3.86	7.8	8.69	2.92	7.74	30.78
	Minimum	70.0	25.0	23.25	6.0	5.41	30.60	29.07	8.5	9.57	29.04	3.99	1.14
	Maximum	87.0	42.0	34.17	11.0	6.99	34.05	33.00	12.0	13.19	32.13	5.69	2.84
Females	**K-S**	0.187	0.233	0.309	0.353	0.167	0.127	0.129	0.376	0.209	0.200	0.212	0.226
	df	11	12	9	11	14	11	14	12	13	12	14	14
	P	0.200	0.071	0.013 *	4.04E-04 ***	0.200	0.200	0.200	4.30E-05 ***	0.125	0.200	0.087	0.052
Males	**K-S**	0.192	0.196	0.155	0.260	0.091	0.187	0.133	0.349	0.152	0.135	0.217	0.297
	df	15	18	12	16	18	17	19	17	17	18	17	18
	P	0.142	0.065	0.200	0.005 **	0.200	0.115	0.200	5.91E-06 ***	0.200	0.200	0.032 *	1.89E-04 ***

L2) Tooth wear classes of female *Pipistrellus hesperidus* from 17 localities in the KwaZulu-Natal and Eastern Cape Provinces of South Africa.

Female		TOT	HB	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
TW A	*n*	3	3	4	1	3	5	3	5	4	4	3	5	5
	Mean	84.0	45.0	34.3	27.81	8.0	5.90	33.0	31.82	11.3	10.88	30.56	4.96	1.96
	SD	3.6	-	3.3	-	-	0.66	1.0	0.73	1.5	0.40	1.63	0.20	0.22
	CV	4.7	-	10.3	-	-	11.81	3.3	2.40	14.2	3.88	5.79	4.23	12.02
	Minimum	81.0	45.0	30.0	27.81	8.0	5.22	32.0	30.86	9.0	10.45	28.86	4.72	1.63
	Maximum	88.0	45.0	38.0	27.81	8.0	7.00	34.0	32.80	12.0	11.37	32.12	5.14	2.23
TW B	*n*	6	-	6	6	6	6	6	6	6	6	6	6	6
	Mean	86.5	-	35.5	32.43	7.5	7.01	32.9	31.43	11.5	10.29	31.91	5.00	1.52
	SD	2.7	-	1.1	4.41	0.6	0.23	1.3	1.17	0.6	0.88	1.09	0.48	0.09
	CV	3.3		3.1	14.15	7.6	3.35	4.0	3.88	5.0	8.93	3.55	10.02	6.07
	Minimum	84.0	-	34.0	27.51	7.0	6.70	31.0	29.68	11.0	8.55	30.32	4.05	1.39
	Maximum	91.0	-	37.0	40.56	8.0	7.31	34.7	32.87	12.0	11.03	33.20	5.35	1.61
TW A	K-S	-	-	-	-	-	-	-	-	0.314	0.141	0.274	0.223	-
	df	-	-	-	-	-	-	-	-	5	5	5	5	-
	P	-	-	-	-	-	-	-	-	0.119	0.200	0.200	0.200	-
TW B	K-S	0.208	0.183	0.139	-	0.229	0.367	0.319	0.211	0.170	0.135	0.368	0.280	0.327
	df	6	6	6	-	6	6	6	6	6	6	6	6	6
	P	0.200	0.200	0.056	-	0.200	0.011 *	0.056	0.200	0.200	0.200	0.011 *	0.156	0.044 *

L3) Tooth wear classes of male *Pipistrellus hesperidus* from 17 localities in the KwaZulu-Natal and Eastern Cape Provinces of South Africa.

Male		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
TW A	*n*	6	6	5	6	6	6	6	6	6	6	6	6
	Mean	80.3	30.8	29.42	7.0	6.43	32.81	30.63	11.0	10.26	30.98	5.06	1.40
	SD	6.1	3.2	2.94	0.6	0.28	0.71	1.07	0.6	0.57	0.80	0.23	0.15
	CV	7.9	10.8	10.49	9.4	4.56	2.26	3.63	6.0	5.74	2.69	4.65	10.75
	Minimum	70.0	25.0	25.04	6.0	6.17	32.00	29.62	10.0	9.57	30.01	4.63	1.21
	Maximum	87.0	34.0	33.05	8.0	6.90	34.05	32.18	12.0	10.96	32.06	5.27	1.63
TW B	*n*	7	7	5	7	6	7	7	7	6	6	7	7
	Mean	81.7	32.1	29.81	7.9	6.42	31.9	30.30	10.9	10.30	30.53	5.10	1.59
	SD	3.1	2.3	4.26	1.6	0.49	0.7	1.12	0.7	0.50	0.41	0.55	0.57
	CV	3.9	7.3	15.00	20.7	8.01	2.2	3.84	6.6	5.08	1.41	11.13	37.20
	Minimum	77.0	29.0	23.25	6.0	5.83	30.6	29.07	10.0	9.58	29.91	3.99	1.14
	Maximum	86.0	35.0	33.66	11.0	6.99	32.8	32.30	12.0	10.92	30.93	5.57	2.84
TW A	K-S	0.247	0.230	0.225	0.333	0.258	0.227	0.249	0.333	0.177	0.172	0.286	0.280
	df	6	6	5	6	6	6	6	6	6	6	6	6
	P	0.200	0.200	0.200	0.036 *	0.200	0.200	0.200	0.036 *	0.200	0.200	0.135	0.154
TW B	K-S	0.199	0.222	0.258	0.321	0.196	0.280	0.169	0.296	0.201	0.292	0.291	0.366
	df	7	7	5	7	6	7	7	7	6	6	7	7
	P	0.200	0.200	0.200	0.028 *	0.200	0.103	0.200	0.063	0.200	0.121	0.075	0.005 **

L4) Tooth wear classes of female *Pipistrellus hesperidus* from 17 localities in the KwaZulu-Natal and Eastern Cape Provinces of South Africa.

Female		TOT	HB	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
TW A	*n*	9	1	10	6	9	11	9	11	10	10	9	11	11
	Mean	81.6	45.0	32.2	29.16	7.3	6.19	32.87	31.17	11.1	10.51	30.84	5.01	1.66
	SD	5.5	-	3.5	2.71	0.7	0.54	0.76	1.08	1.0	0.58	1.06	0.21	0.34
	CV	6.9		11.2	9.68	9.9	8.90	2.38	3.55	9.2	5.62	3.52	4.28	21.00
	Minimum	70.0	-	25.0	25.04	6.0	5.22	32.00	29.62	9.0	9.57	28.86	4.63	1.21
	Maximum	88.0	-	38.0	33.05	8.0	7.00	34.05	32.80	12.0	11.37	32.12	5.27	2.23
TW B	*n*	13	0	13	11	13	12	13	13	13	12	12	13	13
	Mean	83.9	-	33.7	31.24	7.7	6.71	32.4	30.82	11.2	10.29	31.22	5.06	1.56
	SD	3.8	-	2.5	4.34	1.2	0.48	1.12	1.24	0.7	0.68	1.07	0.50	0.41
	CV	4.6		7.5	4.57	15.7	4.56	3.4	4.11	6.3	15.69	7.27	10.08	26.80
	Minimum	77.0	-	29.0	23.25	6.0	5.83	30.6	29.07	10.0	8.55	29.91	3.99	1.14
	Maximum	91.0	-	37.0	40.56	11.0	7.31	34.7	32.87	12.0	11.03	33.20	5.57	2.84
TW C	*n*	3	0	3	3	3	3	3	3	3	3	3	3	3
	Mean	83.7	-	34.7	32.52	7.0	6.46	33.2	31.63	11.7	11.00	32.23	4.75	1.64
	SD	1.2	-	1.5	1.65	-	0.11	0.2	1.06	0.6	1.03	1.02	0.44	0.21
	CV	1.5		4.7	5.50	-	1.87	0.7	3.61	5.4	10.10	3.42	10.04	13.95
	Minimum	83.0	-	33.0	30.87	7.0	6.38	33.0	30.50	11.0	9.82	31.06	4.37	1.46
	Maximum	85.0	-	36.0	34.17	7.0	6.59	33.4	32.59	12.0	11.67	32.92	5.23	1.87

M1) Male and female *Pipistrellus rusticus* from three localities in the Limpopo Province of South Africa.

		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
Females	*n*	8	8	10	8	11	8	11	8	11	11	11	11
	Mean	75.0	30.2	25.92	6.9	5.47	28.9	27.71	10.2	8.80	27.09	4.18	1.52
	SD	5.1	1.9	2.77	0.6	0.64	1.0	1.78	0.4	0.99	1.63	0.43	0.36
	CV	7.0	6.5	10.95	9.6	11.99	3.7	6.57	3.6	11.54	6.17	10.47	24.38
	Minimum	70.0	28.0	23.00	6.0	4.33	27.5	25.60	10.0	7.29	23.17	3.59	1.15
	Maximum	85.0	33.0	30.54	8.0	6.19	31.0	31.02	11.0	10.20	28.91	5.01	2.12
Males	*n*	8	8	11	8	13	8	13	8	13	13	13	13
	Mean	73.8	28.9	24.97	6.2	5.23	28.7	28.10	10.5	9.53	26.56	4.18	1.58
	SD	4.9	2.0	2.86	1.0	0.41	0.9	1.47	0.8	0.93	0.70	0.54	0.46
	CV	6.9	7.0	11.73	16.7	7.88	3.0	5.34	7.4	9.90	2.70	13.20	29.62
	Minimum	65.0	25.0	18.93	5.0	4.54	28.0	26.07	10.0	8.04	24.95	3.19	0.66
	Maximum	80.0	31.0	29.60	7.0	5.85	30.0	30.15	12.0	10.89	27.82	4.81	2.34
Females	**K-S**	0.162	0.225	0.185	0.327	0.192	0.223	0.220	0.513	0.212	0.161	0.146	0.218
	df	8	8	10	8	11	8	11	8	11	11	11	11
	P	0.200	0.200	0.200	0.012 *	0.200	0.200	0.143	5.42E-07 ***	0.178	0.200	0.200	0.148
Males	**K-S**	0.181	0.275	0.161	0.311	0.173	0.269	0.144	0.371	0.148	0.236	0.206	0.190
	df	8	8	11	8	13	8	13	8	13	13	13	13
	P	0.200	0.075	0.200	0.022 *	0.200	0.091	0.200	0.002 *	0.200	0.045 *	0.047 *	0.200

M2) Tooth wear classes of *Pipistrellus rusticus* from three localities in the Limpopo Province of South Africa.

		TOT	T	TL	HFL	HF	FAL	FA	E	TIB	TMETA	TRL	TRB
TW A	*n*	2	2	7	2	7	2	7	2	7	7	7	7
	Mean	77.5	29.0	25.96	6.0	5.05	30.0	28.97	10.5	9.67	26.90	4.54	1.67
	SD	10.6	2.8	2.26	-	0.53	1.5	1.26	0.7	0.49	1.18	0.26	0.54
	CV	15.4	11.0	9.03	-	10.81	5.6	4.50	7.6	5.27	4.52	5.99	33.53
	Minimum	70.0	27.0	24.36	6.0	4.33	28.9	27.42	10.0	9.00	24.95	4.23	0.66
	Maximum	85.0	31.0	30.54	6.0	5.85	31.0	31.02	11.0	10.20	28.19	5.01	2.12
TW B	*n*	10	10	9	10	11	10	11	10	11	11	11	11
	Mean	73.0	29.2	24.60	6.9	5.53	28.3	26.72	10.1	8.51	26.55	4.07	1.49
	SD	3.9	1.9	1.80	0.7	0.54	0.5	1.01	0.3	0.77	1.42	0.52	0.39
	CV	5.4	6.6	7.54	11.0	9.92	1.6	3.87	3.2	9.27	5.46	13.18	26.91
	Minimum	65.0	25.0	22.78	5.0	4.54	27.5	25.60	10.0	7.29	23.17	3.26	1.15
	Maximum	78.0	32.0	27.86	8.0	6.19	29.1	28.79	11.0	10.05	28.83	4.81	2.34
TW C	*n*	2	2	2	2	2	2	2	2	2	2	2	2
	Mean	77.5	32.0	24.31	5.5	5.38	29.63	28.85	11.0	10.16	27.75	4.03	1.37
	SD	0.7	1.4	7.60	0.7	0.61	0.53	1.84	1.4	0.92	1.65	0.11	0.08
	CV	1.0	5.0	35.18	14.5	12.72	2.01	7.17	14.5	10.18	6.68	2.97	6.41
	Minimum	77.0	31.0	18.93	5.0	4.95	29.25	27.55	10.0	9.51	26.58	3.95	1.31
	Maximum	78.0	33.0	29.68	6.0	5.81	30.00	30.15	12.0	10.81	28.91	4.10	1.42
TW A	**K-S**	-	-	0.299	-	0.154	-	0.244	-	0.224	0.221	0.183	0.279
	df	-	-	7	-	7	-	7	-	7	7	7	7
	P	-	-	0.058	-	0.200	-	0.200	-	0.200	0.200	0.200	0.107
TW B	**K-S**	0.118	0.257	0.226	0.454	0.180	0.161	0.220	0.524	0.210	0.2-4	0.179	0.255
	df	10	10	9	10	11	10	11	10	11	11	11	11
	P	0.200	0.059	0.200	1.76E-06 ***	0.200	0.200	0.143	7.96E-09 ***	0.191	0.200	0.200	0.044 *

APPENDIX 5.8

Eigenvalues for principal components one (PC I) and two (PC II) of all principal component analyses of vespertilionid species from southern Africa.

Cranial measurements

Species and area		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Eptesicus hottentotus	PC I	0.742	0.543	0.688	0.600	0.561	0.545	0.633	0.782	0.742	0.316	0.356	0.541
Namibia	PC II	0.402	0.135	0.295	0.398	-0.126	0.408	-0.426	-0.437	0.117	0.394	-0.766	-0.539
Neoromicia capensis	PC I	0.897	0.717	0.804	0.595	0.495	0.429	0.144	0.803	0.618	0.079	0.278	0.592
Namibia & South Africa	PC II	0.288	-0.024	-0.377	-0.596	-0.600	0.108	0.203	0.271	-0.260	0.508	0.758	0.557
Neoromicia capensis	PC I	0.749	0.708	0.849	0.698	0.608	0.436	0.728	0.834	0.798	0.152	0.446	0.752
South Africa, W. Cape	PC II	0.178	-0.351	-0.133	0.265	0.551	-0.577	-0.349	0.002	0.404	0.637	-0.015	-0.266
Neoromicia capensis	PC I	0.477	0.303	0.710	0.495	0.284	0.584	0.585	0.623	0.749	-0.112	0.549	0.174
South Africa, Free State, Grassland	PC II	0.476	0.525	-0.512	0.273	0.387	0.418	-0.480	-0.510	-0.162	-0.079	0.222	0.443
Neoromicia capensis	PC I	0.781	0.685	0.840	0.527	0.494	0.245	0.414	0.814	0.618	0.499	0.583	0.651
South Africa, Free State, Nama-Karoo	PC II	0.391	0.289	-0.005	0.468	0.043	0.409	-0.137	-0.329	-0.423	-0.634	-0.185	0.219
Neoromicia capensis	PC I	0.794	0.387	0.445	0.110	-0.469	0.357	0.792	0.661	0.522	0.000	0.444	0.726
Zimbabwe	PC II	0.302	0.602	0.613	0.747	0.518	0.542	-0.016	-0.382	-0.308	0.066	-0.309	-0.297
Neoromicia cf. *melckorum*	PC I	0.623	0.719	0.890	0.787	0.397	0.057	0.774	0.516	0.521	-0.111	-0.303	0.395
South Africa & Zimbabwe	PC II	0.000	-0.424	0.059	-0.429	-0.424	-0.296	0.154	0.546	0.713	0.103	0.798	0.654
Neoromicia africanus	PC I	0.785	0.636	0.678	0.821	0.366	0.642	0.097	0.528	0.657	0.170	0.353	0.390
South Africa, Limpopo, Pafuri area	PC II	0.267	-0.024	0.206	0.051	-0.602	-0.276	0.780	-0.252	-0.046	-0.516	0.234	0.291
Neoromicia africanus	PC I	0.661	0.473	0.434	0.715	0.495	0.606	-0.253	0.719	0.762	0.291	0.129	0.709
South Africa & Swaziland	PC II	0.314	0.306	0.652	0.226	0.198	-0.047	0.764	-0.349	-0.328	-0.008	0.262	-0.287
Neoromicia zuluensis	PC I	0.791	0.436	0.651	0.591	0.155	0.303	0.516	0.864	0.655	-0.013	0.682	0.743
South Africa, Limpopo & Mpumalanga	PC II	0.170	0.373	-0.340	0.547	0.648	0.448	-0.468	-0.215	-0.037	-0.541	-0.220	-0.055
Pipistrellus hesperidus	PC I	0.829	-0.057	0.706	0.663	0.475	0.305	0.613	0.819	0.711	0.051	0.589	0.652
South Africa, KwaZulu-Natal	PC II	0.077	0.257	-0.328	0.062	0.148	-0.529	-0.374	0.118	0.141	0.921	0.398	-0.027
Pipistrellus rusticus	PC I	0.772	0.754	0.710	0.653	0.466	0.491	0.095	0.848	0.856	0.185	0.652	0.587
South Africa & Zimbabwe	PC II	0.178	0.348	-0.482	-0.244	-0.015	0.279	0.379	-0.100	-0.070	0.872	0.099	-0.247

External measurements

Species and area		HF	TIB	FA	TMETA	TRL	TRB			
Eptesicus hottentotus	PC I	0.584	0.847	0.848	0.982	0.107	-0.371			
Namibia	PC II	0.520	-0.490	0.015	-0.069	-0.862	-0.698			
Neoromicia capensis		TOT	T	HFL	E	TIB	FA	TMETA	TRL	TRB
South Africa, Free State, Grassland	PC I	0.746	0.883	0.034	0.400	0.813	0.856	0.865	-0.480	0.284
	PC II	0.374	0.161	0.685	0.661	-0.283	-0.014	0.016	0.694	-0.521
Neoromicia capensis		TOT	T	HFL	FAL	E	TIB	TMETA	TRL	TRB
South Africa, Free State, Nama-Karoo	PC I	0.718	0.601	0.395	0.798	0.208	0.783	0.752	-0.285	0.092
	PC II	0.115	0.408	-0.553	-0.158	-0.816	0.011	0.120	-0.171	0.419
Neoromicia capensis		T	HFL	E	FA	TMETA	TRL	TRB		
South Africa, E. Cape	PC I	0.499	-0.703	-0.561	0.847	0.856	0.457	0.716		
	PC II	0.582	0.387	-0.366	0.327	0.214	-0.748	-0.476		
Neoromicia cf. *melckorum*		HF	TIB	FA	TMETA	TRL	TRB	TL		
South Africa & Zimbabwe	PC I	0.099	0.607	0.913	0.743	0.300	0.470	0.472		
	PC II	0.564	-0.703	-0.163	0.062	0.881	0.024	0.421		
Neoromicia africanus		T	HFL	E	TIB	FA	TMETA	TRL	TRB	
South Africa & Swaziland	PC I	0.455	0.442	0.477	0.646	0.579	-0.430	0.689	0.812	
	PC II	0.033	-0.343	-0.739	0.293	0.736	0.601	-0.083	0.233	
Neoromicia africanus		HB	E	HF	TIB	FA	TMETA	TRL	TRB	TL
Malawi	PC I	0.706	-0.006	0.652	0.685	0.718	0.837	0.723	0.126	0.471
	PC II	0.335	0.362	-0.070	-0.424	0.459	0.371	-0.486	-0.817	-0.179

External measurements

Neoromicia rueppellii	Meas	TOT	T	HFL	E	FA	TMETA	TRL	TRB	
Southern Africa	**PC I**	0.723	0.702	0.879	-0.926	0.127	-0.029	-0.100	-0.641	
	PC II	0.057	0.241	-0.198	-0.112	-0.880	-0.514	-0.839	0.199	

Neoromicia rueppellii	Meas	HB	T	HFL	E	TIB	FA	TMETA	TRB	
Zambia	**PC I**	0.439	0.817	-0.056	0.759	0.935	0.921	0.866	0.174	
	PC II	0.415	-0.235	-0.764	-0.012	-0.048	-0.074	-0.074	0.879	

Neoromicia zuluensis	Meas	HF	TIB	FA	TMETA	TRL	TRB			
South Africa, Limpopo & Mpumalanga	**PC I**	0.544	-0.829	-0.944	-0.566	-0.313	-0.499			
	PC II	0.413	0.397	0.147	0.623	-0.776	-0.706			

Pipistrellus hesperidus	Meas	TOT	T	HFL	FAL	E	TIB	TMETA	TRL	TRB
South Africa, KwaZulu-Natal	**PC I**	0.783	0.800	0.448	0.697	0.777	0.464	0.763	-0.388	0.303
	PC II	0.448	0.288	0.441	-0.354	0.018	-0.779	0.025	0.079	-0.570

Pipistrellus rusticus	Meas	TOT	T	HFL	FAL	E	TIB	TMETA	TRL	TRB
South Africa & Zimbabwe	**PC I**	0.834	0.475	-0.842	0.741	0.869	0.863	0.332	0.468	0.585
	PC II	0.439	0.760	0.408	0.101	-0.259	-0.315	0.657	0.299	-0.546

APPENDIX 5.9

Discriminant function (DF) coefficients for all discriminant function analyses of vespertilionid bats from southern Africa.

Cranial measurements

Species & area	DF	CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Eptesicus hottentotus	I	1.672	0.845	-1.605	2.813	1.051	0.735	4.386	-5.007	-1.094	0.544	-1.848	3.276
Namibia	II	-1.808	1.344	0.667	-0.149	0.232	-0.220	-0.788	1.297	0.431	0.155	0.378	-0.624
Neoromicia capensis	I	0.572	-0.598	-0.118	1.519	-0.232	-0.787	0.882	0.637	-0.049	0.201	-0.066	-0.303
Namibia & South Africa	II	-0.431	-0.027	0.712	-0.229	0.714	-0.318	0.400	0.089	-0.822	-0.061	1.248	-0.872
Neoromicia capensis	I	0.618	0.100	-0.243	0.130	-1.176	0.565	0.823	-0.915	0.393	0.792	-0.361	1.009
South Africa, W. Cape	II	1.082	0.118	-0.050	-0.248	-0.756	-0.165	-0.310	0.188	-0.130	0.352	0.425	-0.284
Neoromicia capensis	I	-1.341	-1.203	1.218	-2.032	1.379	0.802	0.333	-0.916	1.222	0.225	-0.661	2.459
South Africa, Free State, Grassland	II	0.443	0.666	0.280	0.656	-0.556	-1.439	-0.232	0.162	0.814	-0.452	0.431	0.161
Neoromicia capensis	I	-0.407	-0.245	-1.234	0.443	0.308	0.175	0.652	-1.159	0.771	0.542	-0.116	1.302
South Africa, Free State, Nama-Karoo	II	-0.942	0.549	0.951	0.203	-0.403	0.041	-0.135	-0.426	0.223	0.180	-0.225	0.451
Neoromicia capensis	I	1.184	-0.017	0.565	-2.989	2.477	1.363	0.529	0.789	-1.593	-0.555	1.592	0.231
Zimbabwe	II	-0.770	-0.116	0.827	-0.099	0.218	0.465	-0.314	1.354	-1.044	0.660	0.933	-0.367
Neoromicia cf. *melckorum*	I	-1.357	3.701	-0.106	2.494	-1.043	-0.597	-2.303	-5.400	1.576	-1.132	6.400	-1.693
South Africa & Zimbabwe	II	0.573	0.094	-1.334	0.033	1.625	-0.840	0.617	0.942	-1.646	0.813	-0.429	1.186

Cranial measurements

Species & area	DF	CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Neoromicia africanus	I	-0.976	0.540	0.610	0.070	-0.043	-0.799	-0.097	0.272	0.342	-0.128	0.403	-0.104
South Africa, Limpopo, Pafuri area	II	-0.014	-0.477	0.011	-0.772	0.369	0.377	-0.025	-0.338	0.901	-0.010	0.408	0.123
Neoromicia africanus	I	-0.758	0.843	-0.045	-0.436	0.851	-0.444	0.408	0.587	-0.428	-0.145	-0.109	0.354
South Africa & Swaziland	II	0.164	0.109	0.147	0.273	0.328	0.399	0.034	-0.121	0.486	0.096	0.213	-0.740
Neoromicia zuluensis	I	0.290	-0.191	-0.592	0.242	0.344	0.164	-0.058	-1.940	0.993	0.085	1.400	-0.260
South Africa, Limpopo & Mpumalanga	II	0.183	0.084	-0.472	0.458	-0.066	0.277	0.666	-0.026	-0.482	0.220	0.753	-0.358
Pipistrellus hesperidus	I	-0.096	-0.498	-0.204	-0.265	-0.324	0.843	-0.023	-0.081	-0.046	0.683	0.752	-0.301
South Africa, KwaZulu-Natal	II	-0.584	0.600	0.391	0.766	-0.010	-0.250	-0.365	-0.718	0.494	-0.045	0.423	0.101
Pipistrellus rusticus	I	0.635	-1.483	-0.207	-0.428	0.546	-0.011	-0.238	1.394	-0.358	0.444	0.040	-0.281
South Africa & Zimbabwe	II	0.674	0.210	0.455	-0.182	0.389	-0.416	0.139	-0.621	-0.595	0.573	0.603	-0.225

External measurements

Species & area	DF	TOT	T	HFL	FAL	E	TIB	TMETA	TRL	TRB
Neoromicia capensis	I	-0.328	0.069	0.350	0.221	-0.252	-0.241	0.752	0.815	0.457
South Africa, Free State, Nama-Karoo	II	0.495	-0.088	-1.000	-0.575	0.699	0.065	0.224	0.249	0.305
		T	HFL	E	TIB	FA	TMETA	TRL	TRB	
Neoromicia africanus	I	1.069	0.192	-1.084	0.288	-0.713	0.666	0.322	0.129	
South Africa & Swaziland	II	-0.024	-0.776	0.606	1.263	-1.413	1.300	-0.109	0.299	
		HB	E	HF	TIB	FA	TMETA	TRL		
Neoromicia africanus	I	-0.393	-2.953	3.410	3.607	4.800	-0.821	-4.647		
Malawi	II	0.332	0.458	-1.270	0.162	1.448	-2.472	1.372		
		TOT	T	HFL	FAL	E	TIB	TMETA	TRL	TRB
Pipistrellus hesperidus	I	0.518	0.210	0.157	-1.298	-0.666	0.441	1.150	-0.114	-0.151
South Africa, KwaZulu-Natal	II	-0.271	-0.162	-0.434	-0.085	0.088	-0.008	0.872	-0.433	0.732

CHAPTER 6

INTRA-SPECIFIC VARIATION OF TRADITIONAL CRANIAL MORPHOMETRIC MEASUREMENTS IN VESPERTILIONID BATS FROM SOUTHERN AFRICA

6.1. INTRODUCTION

The aim of this chapter was to examine geographic patterns of intra-specific variation identified by traditional morphometric methods applied to 12 cranial measurements in ten species of vesper bats of the genera *Eptesicus, Hypsugo, Neoromicia* and *Pipistrellus* over their distributional range in southern Africa. An understanding of the pattern of variation of a species across its geographic range and the possible causes for variation is useful in the delimitation of subspecies and species. Variation in relation to climatic and environmental conditions often has little taxonomic value which if not appreciated can lead to erroneous decisions in relation to subspecies and species boundaries.

The analysis of shape morphometrics (Chapter 3) identified significant geographic variation in cranial shape correlated with latitude and longitude in *N. capensis,* and significant geographic variation in cranial centroid size correlated with latitude and longitude in *N. capensis*, *E. hottentotus* and *P. hesperidus*. Size and shape increased across their distribution to localities in the south-west. As indicated in the discussion of Chapter 3, intra-specific variation in relation to geographic patterns of latitude and longitude has also been documented in a number of other vespertilionid species from other parts of the world (Findlay and Jones, 1967; Findlay and Traut, 1970; Burnett, 1983; Kitchener and Caputi, 1985; Bogdanowicz, 1990; Barlow *et al.*, 1997).

While it has been recognised that *N. capensis* shows considerable variation across its distribution (Rosevear, 1962; Rautenbach and Schlitter, 1985; Skinner and Smithers, 1990; Taylor, 2000), this variation has never been clearly quantified. This study represented, with the exception of the study on *E. hottentotus* by Schlitter and Aggundey (1986), the first analysis of geographic variation for these species in southern Africa and attempted to encompass the widest geographic coverage of each species range within southern Africa. Even though, as indicated in Chapter 1 in the background to each of the 10 species in question, the known distributions of each of the species in southern Africa varies considerably (Meester *et al.*, 1986; Taylor, 2000; Skinner and Smithers, 1990), from species like *N. rendalli* and *N. rueppellii* which are known from very few localities to the ubiquitous *N. capensis*.

6.2 MATERIAL AND METHODS

The 12 cranial, dental and mandible measurements selected in Chapter 4 were used for the analyses of intra- and inter-specific variation. Following the results of the analyses of variation within limited geographic localities of nine of the species in relation to sex and/or tooth wear class in Chapter 5, specimens of some populations were separated for further analyses of intra- and inter-specific variation. These were males and females of *N. capensis* from Jagersfontein in the Free State Province, which indicated sufficient sexual dimorphism and the tooth wear classes of *E. hottentotus* from Namibia, which showed sufficient variation. Although variation due to sexual dimorphism and tooth wear class variation was observed in other localities of these and other species, their degree of variation was thought to be insufficient to merit separate analyses.

The statistical analyses were run using the statistical packages of SPSS 9.0.1 (SPSS Inc., 1999) and NTSYS-pc, version 2.01h (Rohlf, 1997).

6.2.1 Intra-specific variation

As indicated in Chapter 5, there were problems of accurate identification of the species in question and thus museum specimens could have been mis-identified. Therefore, discriminant function (DFA) and principal component (PCA) analyses of each species were performed combining specimens identified using morphological character identification keys with specimens of "known" identity based on chromosome (for *N.* cf. *melckorum,* specimens in the Transvaal Museum collection identified as having the chromosome diploid number 2n = 40 were used; TM41860,TM41861, TM37906, TM37924, TM37937, TM37944, TM37945) and/or, bacula information (see Kearney *et al.*, 2002 in Appendix I). Specimens of *N. zuluensis* thought to be those karyotyped by Rautenbach *et al.* (1993) and measured in this analysis were indicated in the PCA scatterplots and UPGMA phenograms. However, since their identity was not certain because the specimen numbers were not recorded in Rautenbach *et al.* (1993) and the match was made based on locality description and period of collection, these specimens were not used in the DFA. Given the small number of known identity specimens and hence the potentially limited power of species distinction, the discriminant function probabilities of group membership were also taken into account.

Where the sample size per species was unmanageable for a single PCA, specimens were split into more manageable sized groups based firstly, on geographic proximity and secondly, on similar vegetation biomes. Identification of the vegetation biome for a locality was based on the biome information of Rutherford and Westfall (1994) supplied as a GIS shape file data "SA Biomes (Rutherford)" at the South African National Biodiversity Institute (SANBI) website http://www.plantzafrica.com/vegetation/vegmain.htm. For areas not covered by the Rutherford and Westfall (1994) biome categorisation (Zimbabwe and Mozambique), the biome information of Olsen and Dinerstein (2002) supplied as a GIS shape file data at the World Wildlife Foundation (WWF) Global 200 Ecoregions website http://worldwildlife.org/science/data/terreco.cfm was used. Distinctions between specimens in the PCAs suggestive of different species were followed with UPGMA cluster analyses.

Operational Taxonomic Units (OTUs) were identified for each species, either of single localities where these were represented by three or more individuals (to comply with minimum sample size requirements of the statistical programs), or by pooling closely spaced localities with less than three individuals to maintain as wide a geographic coverage of the species known range as possible. Localities were pooled by grouping adjacent localities, while attempting to keep inter-locality geographic distance to a minimum (see Chapter 5, page 138) and pooling localities of like vegetation biomes (as described above). Where OTU numbers were fewer than the number of measurements, PCA and cluster analyses were also run at individual specimen level.

Univariate analyses included the computation of summary statistics (arithmetic mean, standard deviation, coefficient of variation, and minimum and maximum values), and Model III (for unequal cell numbers) one-way analyses of variance (ANOVA) of different OTUs. Multivariate analyses included PCAs of among measurement correlation matrices based on standardised data, and unweighted pair-group arithmetic average cluster analyses (UPGMA) of average taxonomic distance matrices based on standardised data. Principal component one and two scores of OTUs and the values for each measurement were correlated with the latitudes and longitudes of each OTU. Appendix 6.1 gives the locality details of the specimens used in this analysis.

6.3 RESULTS

6.3.1 Species by species analysis

6.3.1.1 *Eptesicus hottentotus*

An initial PCA of 43 specimens identified one outlier, ZM41419 a female of tooth wear class C from the Cederberg in the Western Cape Province, which plotted on the larger value side of the first principal component. This specimen was retained in the analysis as there were no obvious measurement errors, and the individual was the only female of tooth wear C from this locality. The specimens were allocated to eight OTUs (Table 6.1), which included the separation of the significantly different tooth wear classes of specimens from Namibia. As there was only one specimen of tooth wear class C from the more southerly Namibian localities (TM37551), this specimen was removed from further analyses. OTUs representative of each of the three subspecies recognised in southern Africa were included in the analyses (Table 6.1).

The PCA scatterplot based on eight OTUs (Fig. 6.1A) showed a similar pattern to that based on individuals (Fig. 6.1B). The PCA scatterplot of 42 individuals showed some separation between the individuals along both principal component one and two in relation to geographic distribution (Fig. 6.1B). The Western Cape specimens representing the subspecies *E. h. hottentotus,* were distributed on the higher values side of the first principal component axis, whereas those from Zimbabwe and the Limpopo Province and representing the subspecies *E. h. bensoni,* were on the lower value side of the first principal component axis and were separated along the second principal component axis. The specimens from Namibia, Lesotho (representing the subspecies *E. h. pallidior*) and the KwaZulu-Natal Province (representing the subspecies *E. h. bensoni*) were found in the middle and overlapping with the groups scattered around the extreme values of the first principal component axis. The first principal component axis explained 71.87% and 52.58% of the variance in the analyses of OTUs and individuals, respectively. In both analyses, all first principal component eigenvector scores were positive. However, the measurements that loaded highest were different (Table 6.2), since width between the inner surfaces of the upper first molars and moment arm of the temporal loaded highest in the analyses of OTUs, whereas condylo-incisor length and width across the outer surfaces of the upper

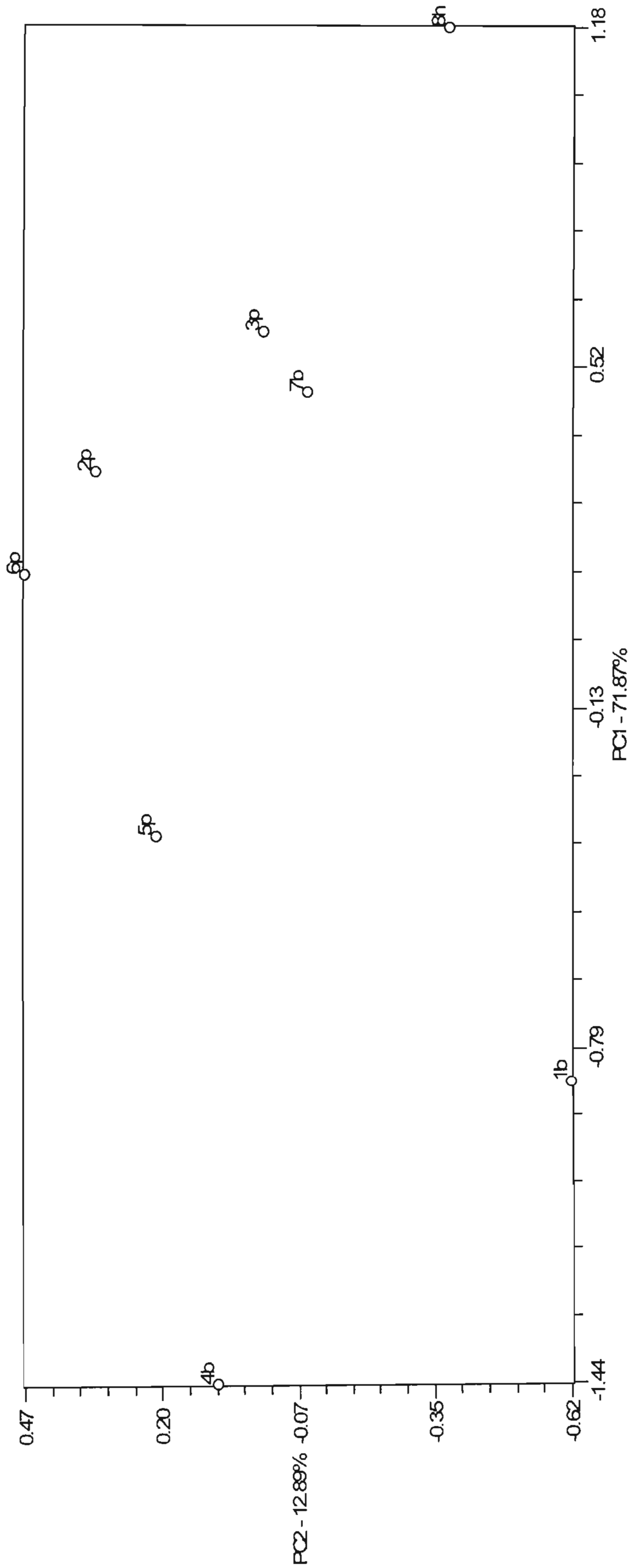


Figure 6.1 A) Scatterplot of the first two principal component axes based on eight OTUs of *Eptesicus hottentotus* from southern Africa. OTU numbers and subspecies codes correspond to those in Table 6.1.

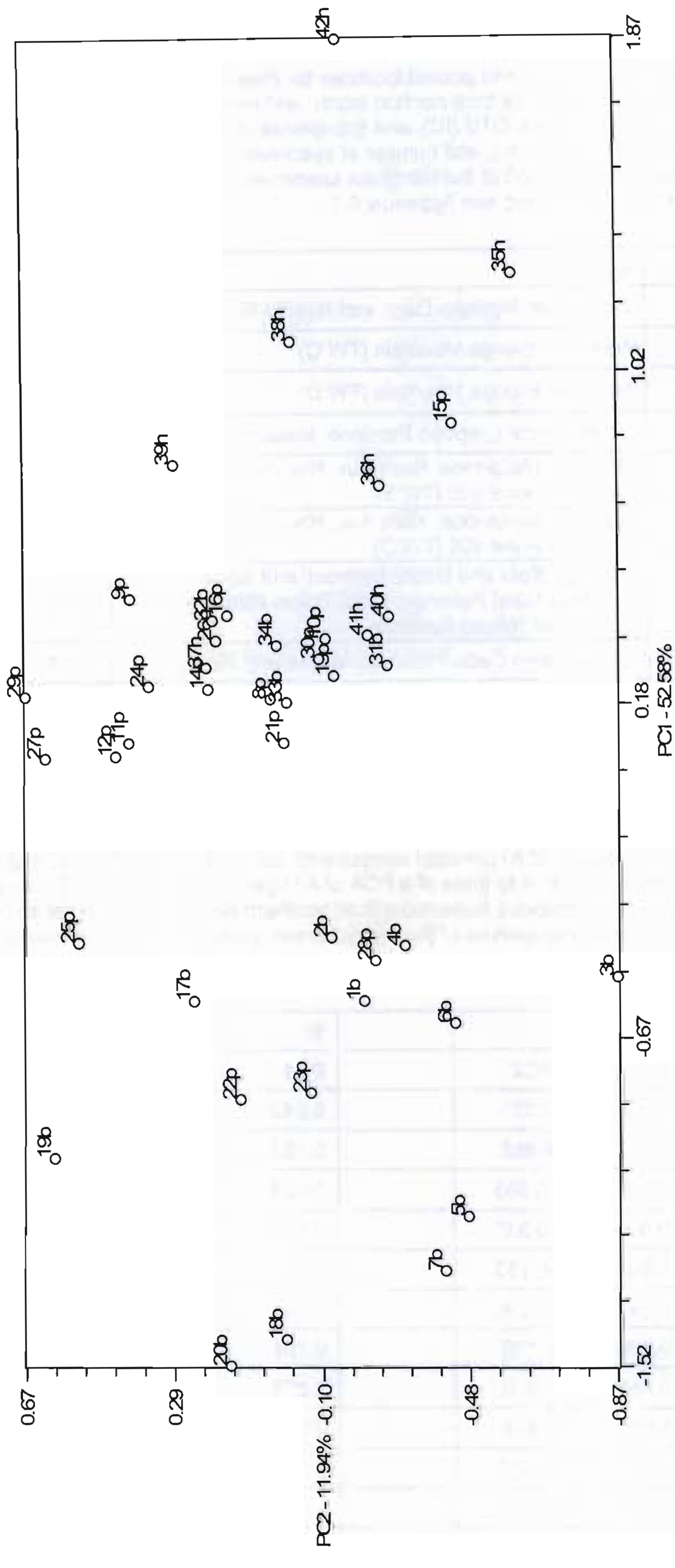


Figure 6.1 B) Scatterplot of the first two principal component axes based on 42 specimens of *Eptesicus hottentotus* from southern Africa. Individual numbers and subspecies codes correspond to those in Table 6.1.

Table 6.1 Eight OTUs of single and pooled localities for *Eptesicus hottentotus* in southern Africa arranged in relation to occurrence from north to south, and east to west, with associated numbering of individuals in each OTU (IC), and subspecies (*E. h. bensoni* = *E.h.b.*; *E. h. pallidior* = *E.h.p.*; *E. h. hottentotus* = *E.h.h.*), and number of specimens included in each OTU (*n*). Different tooth wear classes (TW) of the Namibian specimens were also separated. For details on the localities and specimens used see Appendix 6.1.

OTU	IC	Locality	Subspecies	n
1	1-7	Zimbabwe: Nyshato Dam, and Nyadiri River	*E.h.b.*	7
2	8-12	Namibia: Eronga Mountain (TW C)	*E.h.p.*	5
3	13-16	Namibia: Eronga Mountain (TW D)	*E.h.p.*	4
4	17-20	South Africa: Limpopo Province; Messina and Pafuri	*E.h.b.*	4
5	21-25	Namibia: Maltahohe, Klein Aus, Rheinvels Farm, and Bethanie Huns 106 (TW B)	*E.h.p.*	5
6	26-30	Namibia: Maltahohe, Klein Aus, Rheinvels Farm, and Bethanie Huns 106 (TW D)	*E.h.p.*	5
7	31-34	Lesotho: Kofa and Mount Moorosi; and South Africa: KwaZulu-Natal Province; Ithala Game Reserve and Kranskloof Nature Reserve	*E.h.b.*	4
8	35-42	SA: Western Cape Province; Algeria and Kliphuis	*E.h.h.*	8

Table 6.2 Eigenvector scores of A) principal components one and two of a PCA of eight OTUs and B) principal components one to three of a PCA of 42 specimens based on 12 cranial measurements (Meas) of *Eptesicus hottentotus* from southern Africa. See material and methods section of Chapter 5 for an explanation of the measurement codes. Highest and lowest scores are indicated in bold type.

	A)			B)		
Meas	**PC1**	**PC2**		**PC1**	**PC2**	**PC3**
CIL	0.923	0.285		**0.842**	0.010	0.352
BH	0.763	**0.468**		0.685	0.046	**0.502**
ZB	0.908	-0.365		0.829	-0.242	-0.011
BB	0.906	-0.337		0.806	-0.348	-0.210
POW	0.604	**-0.753**		0.541	-0.464	**-0.552**
WFM	0.747	-0.296		0.446	**-0.606**	0.335
WAS	0.890	0.185		0.794	0.266	0.155
WOUC	0.885	0.330		**0.873**	0.366	-0.036
WIUM1	**0.970**	0.125		0.820	-0.019	0.013
WUPM4	0.917	-0.247		0.649	-0.104	-0.394
LUM1	0.628	0.320		0.499	**0.613**	-0.385
MAOT	**0.934**	0.151		0.753	0.277	0.044

canines loaded highest in the analyses of individuals. The second principal component axis explained 12.89% and 13.32% of the variance in the analyses of OTUs and individuals, respectively. In both analyses, the eigenvector scores were of mixed sign. However, the measurements that loaded highest and lowest were different (Table 6.2), since braincase height and post-orbital width loaded highest and lowest in the analysis of OTUs, whereas length of the upper first molar and greatest width of the foramen magnum loaded highest and lowest in the analysis of individuals.

Given the size component of the first principal component axis, a scatterplot of the second and third principal component axes was plotted (Fig. 6.2), which identified two outliers on either extreme of the third principal component axis. These were TM32566, a female of tooth wear class D from Rheinvels Farm in Namibia (*E. h. pallidior*) and TM35150, a male of tooth wear class B from Algeria Forest campsite in the Western Cape Province (*E. h. hottentotus*). The third principal component axis also suggested a separation of *E. h. pallidior* specimens from those of *E. h. bensoni* and *E. h. hottentotus,* while specimens of *E. h. bensoni* and *E. h. hottentotus* overlapped. The third principal component explained 9.73% of the variation, and the measurements with the highest and lowest eigenvector scores were braincase height and post-orbital width. The distance phenogram based on eight OTUs resolved little, other than the distinction of the Zimbabwe and Limpopo OTUs (Fig. 6.3A), whereas the distance phenogram based on 42 specimens of *E. hottentotus* revealed a similar pattern of variation between the specimens as that observed in the PCA of the first two principal components (Fig. 6.3B).

An assessment of the currently described subspecies in relation to the variation of the different OTUs along the first principal component axis was carried out in the form of a scatterplot of the first two principal components (Fig. 6.1A). This plot indicated that, apart from OTU 6 of specimens from Lesotho and KwaZulu-Natal (*E. h. bensoni)* being more similar in size to the OTUs representative of *E. h. pallidior*, the distribution of the OTUs along the first principal component axis separated the OTUs into the currently described subspecies. The UPGMA phenogram (Fig. 6.3A), however, separated the OTUs of the *E. h. bensoni* subspecies from all others, but the OTU of *E. h. hottentotus* clustered together with the OTUs of *E. h. pallidior*. Analyses at the individual level on a scatterplot of the first two principal component axes (Fig. 6.1B) showed overlaps between individuals of the different subspecies on the first principal component axis. However, there was more overlap between specimens of the subspecies *E. h. bensoni* and *E. h. pallidior*, while *E. h. hottentotus* remained more distinct. Removing the size component (the first principal component axis), an assessment of the second and third principal component axes (Fig. 6.2) indicated even less clarity between the subspecies, since there was overlap of specimens of all three subspecies. The greatest overlap was between *E. h. bensoni* and *E. h. hottentotus*, while *E. h. pallidior* was more distinct from these subspecies.

Table 6.3 presents the basic statistics and the results of the one-way ANOVAs between OTUs for each measurement, which showed all but one measurement, width of the foramen magnum, were significantly different between the different OTUs. The maximally non-significant subsets identified by the Tukey post-hoc tests (Appendix 6.2 A), were different for each measurement but, there was a similar pattern with the Zimbabwe and Limpopo Province specimens (OTUs 1 and 4) being smaller than the Western Cape specimens (OTU 8). However, although OTUs at the latitudinal and longitudinal extremes of the analysed range appeared to show some geographic pattern in their variation, the localities in between did not.

Although 11 of the 12 measurements were significantly different between the OTUs, these differences were significantly negatively correlated with latitude in two measurements only and with longitude in five measurements, whereas neither the first nor the second principal component scores were significantly correlated with either latitude or longitude (Table 6.4). The significant latitudinal correlations identified greater size in width of the upper fourth premolar and length of the upper first molar of northern specimens. Similarly, the significant longitudinal correlations showed that in eastern specimens size increased in condylo-incisor skull length, width across the outer surfaces of the upper canines, width between the inner surfaces of the upper first molars, length between the condylar and the coronoid processes of the mandible and was greatest in width of the articular surface. Hence, while there was geographic variation in size of the 12 cranial measurements in *E. hottentotus* in southern Africa, some of which was latitudinally and longitudinally clinal, there were no significant overall latitudinal and longitudinal clinal variation in the 12 cranial measurements.

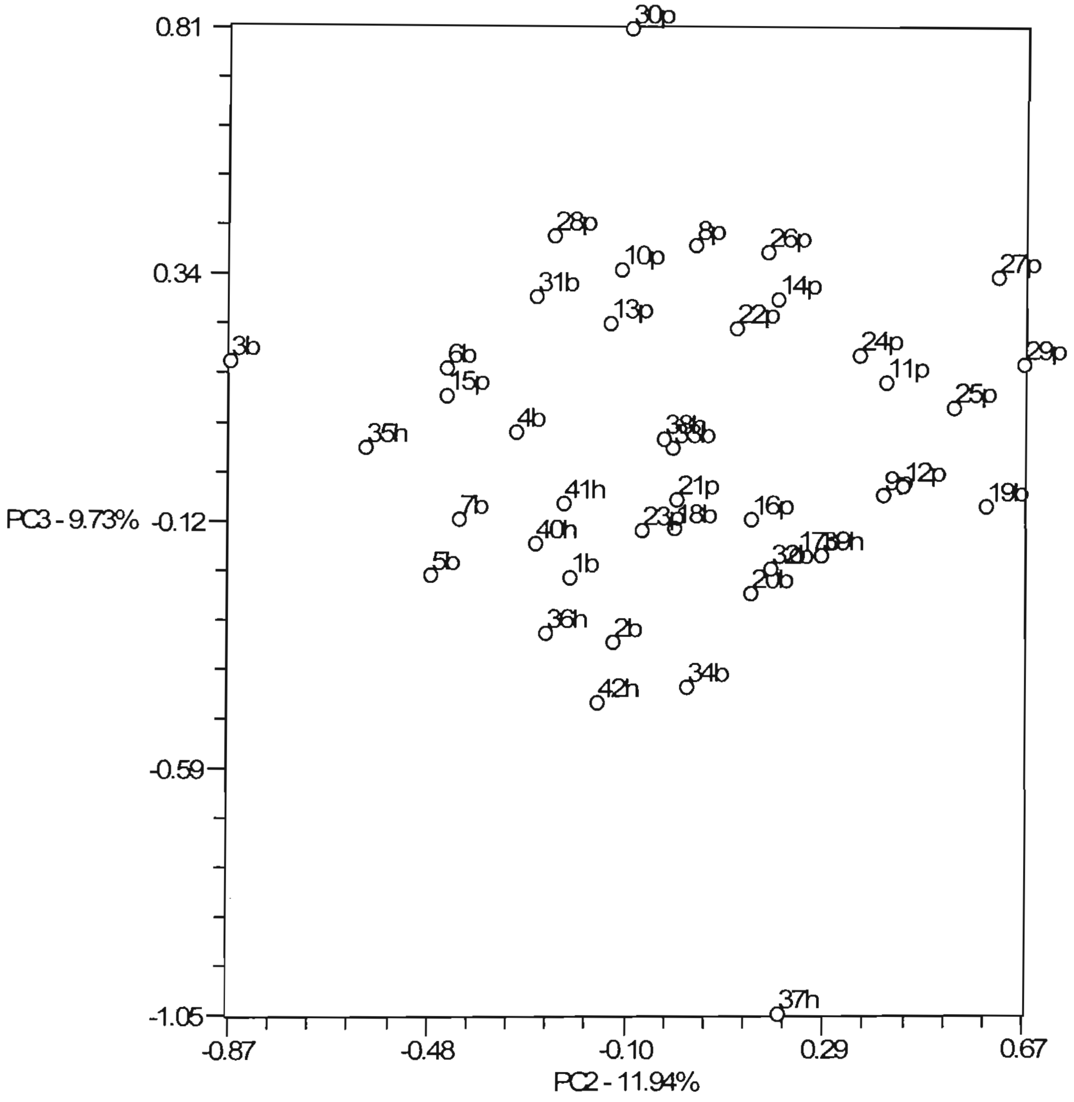


Figure 6.2 Scatterplot of the second and third principal component axes based on 42 specimens of *Eptesicus hottentotus* from southern Africa. Individual numbers and subspecies codes correspond to those in Table 6.1.

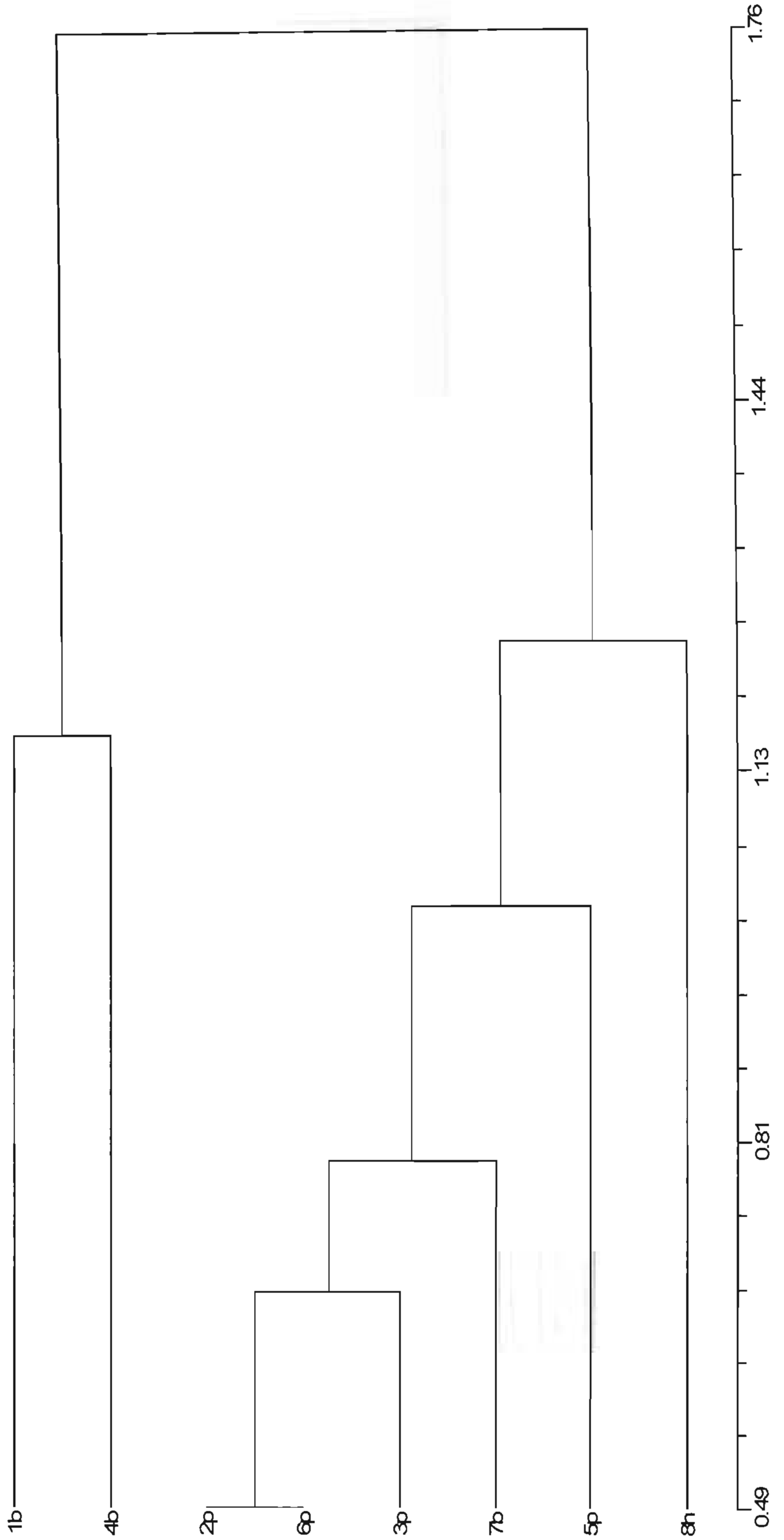


Figure 6.3 A) Distance phenogram of cluster analysis of average taxonomic distance, using UPGMA, based on eight OTUs of *Eptesicus hottentotus* from southern Africa. OTU and individual numbers and subspecies codes correspond to those in Table 6.1. Cophenetic correlation coefficient = 0.811.

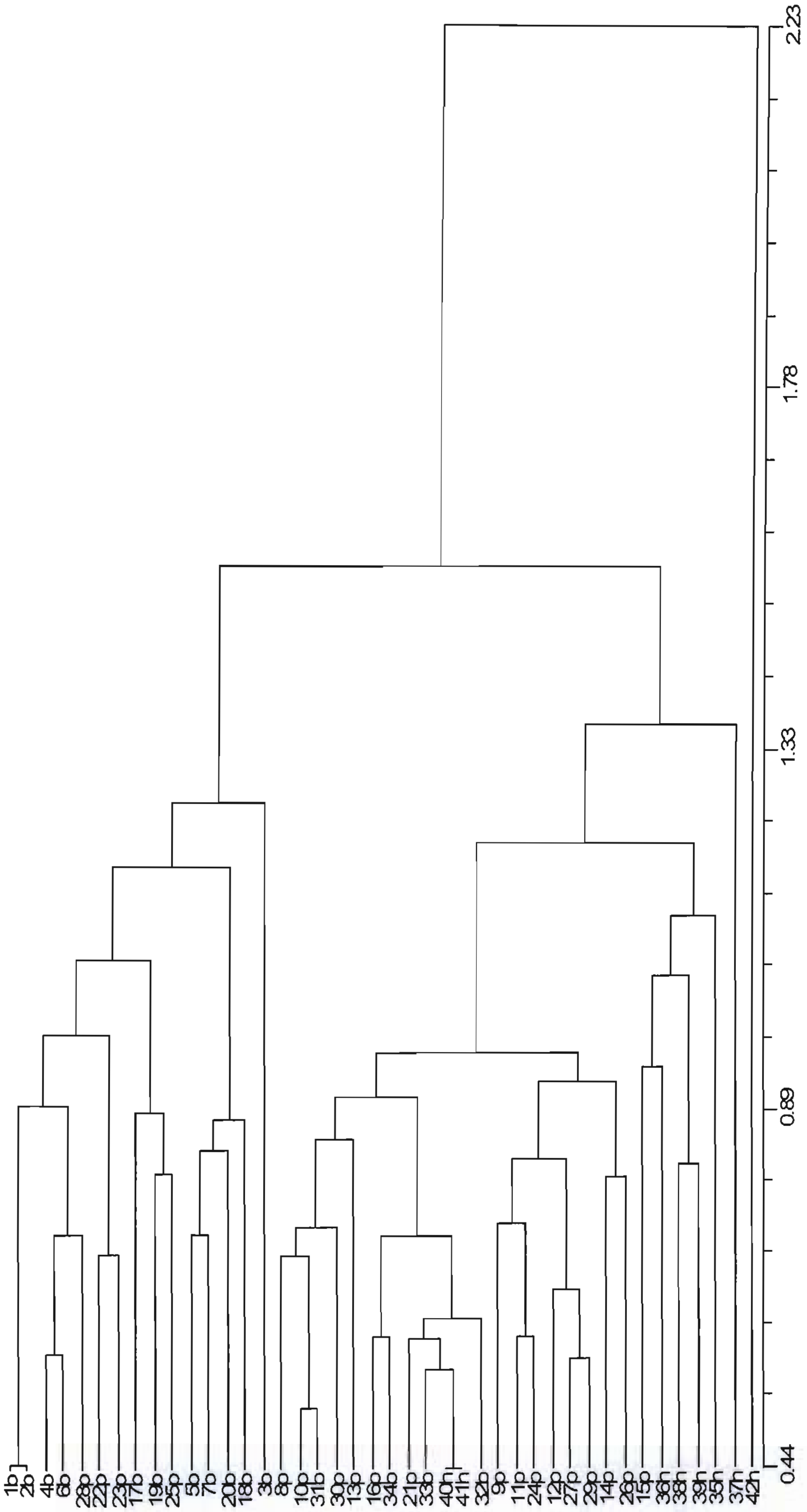


Figure 6.3 B) Distance phenogram of cluster analysis of average taxonomic distance, using UPGMA, based on 42 individuals of *Eptesicus hottentotus* from southern Africa. OTU and individual numbers and subspecies codes correspond to those in Table 6.1. Cophenetic correlation coefficient = 0.737.

Table 6.3 Basic statistics and ANOVA results to test for OTU variation in eight OTUs of *Eptesicus hottentotus* from southern Africa. SD = standard deviation; CV = coefficient of variation; Min = minimum value; Max = maximum value; n = sample size; SS = sum of squares; df = degrees of freedom; P = significance of F values; ** denotes significance at $P < 0.01$; *** denotes significance at $P < 0.001$. See Table 6.1 for a description of the OTU codes, and methods and material of Chapter 5 for an explanation of the measurement codes.

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
1	**Mean**	18.14	6.28	11.06	8.89	4.40	4.38	2.49	5.66	3.37	1.37	1.82	4.32
(n = 7)	**SD**	0.37	0.19	0.43	0.14	0.10	0.13	0.13	0.18	0.19	0.15	0.06	0.15
	CV	2.10	3.08	4.03	1.59	2.37	2.95	5.32	3.20	5.76	11.35	3.64	3.55
	Min	17.51	6.02	10.30	8.71	4.28	4.28	2.29	5.40	3.11	1.19	1.73	4.07
	Max	18.65	6.47	11.56	9.14	4.55	4.62	2.65	5.90	3.61	1.59	1.93	4.48
2	**Mean**	19.28	6.76	11.18	9.03	4.26	4.35	2.71	6.41	3.59	1.44	2.04	4.61
(n = 5)	**SD**	0.52	0.18	0.29	0.14	0.14	0.13	0.10	0.07	0.09	0.08	0.11	0.24
	CV	2.80	2.76	2.75	1.61	3.41	3.22	3.80	1.18	2.70	5.70	5.57	5.35
	Min	18.76	6.56	10.85	8.89	4.06	4.16	2.60	6.31	3.46	1.32	1.90	4.33
	Max	19.93	6.99	11.53	9.20	4.40	4.50	2.85	6.52	3.72	1.53	2.17	4.94
3	**Mean**	19.66	6.69	11.39	9.36	4.37	4.38	2.72	6.34	3.64	1.46	1.94	4.76
(n = 4)	**SD**	0.28	0.09	0.36	0.18	0.05	0.18	0.16	0.15	0.12	0.20	0.12	0.28
	CV	1.53	1.35	3.39	2.08	1.20	4.40	6.17	2.56	3.54	14.55	6.32	6.26
	Min	19.29	6.61	11.05	9.22	4.31	4.27	2.49	6.21	3.56	1.19	1.83	4.48
	Max	19.96	6.81	11.90	9.63	4.43	4.65	2.85	6.52	3.82	1.66	2.10	5.09
4	**Mean**	17.72	6.25	10.50	8.61	4.18	4.07	2.33	5.88	3.30	1.29	1.94	4.37
(n = 4)	**SD**	0.57	0.27	0.33	0.14	0.17	0.19	0.11	0.34	0.21	0.07	0.05	0.16
	CV	3.40	4.51	3.35	1.66	4.26	4.83	5.15	6.08	6.75	5.59	2.78	3.97
	Min	16.99	5.94	10.09	8.42	3.98	3.89	2.24	5.50	3.05	1.25	1.87	4.12
	Max	18.33	6.58	10.78	8.71	4.38	4.33	2.49	6.21	3.56	1.39	1.97	4.48

Table 6.3 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
5	**Mean**	19.12	6.33	10.71	8.73	4.15	4.36	2.51	6.23	3.55	1.44	1.99	4.46
(*n* = 5)	**SD**	0.45	0.19	0.40	0.12	0.15	0.16	0.13	0.29	0.12	0.07	0.09	0.36
	CV	2.48	3.21	3.89	1.46	3.75	3.89	5.54	4.91	3.43	4.83	4.84	8.54
	Min	18.61	6.12	10.18	8.61	4.00	4.17	2.34	5.90	3.41	1.36	1.87	4.02
	Max	19.58	6.57	11.21	8.93	4.33	4.55	2.70	6.62	3.67	1.53	2.10	4.84
6	**Mean**	19.50	6.83	11.05	8.91	4.15	4.34	2.77	6.21	3.55	1.40	1.95	4.65
(*n* = 5)	**SD**	0.37	0.14	0.40	0.28	0.15	0.22	0.16	0.22	0.14	0.07	0.12	0.18
	CV	2.01	2.20	3.81	3.29	3.77	5.24	5.89	3.65	4.17	4.90	6.65	4.11
	Min	19.02	6.60	10.47	8.47	3.94	4.13	2.55	5.90	3.41	1.29	1.76	4.38
	Max	19.92	6.95	11.44	9.22	4.31	4.67	2.95	6.41	3.72	1.46	2.07	4.84
7	**Mean**	19.29	6.56	11.35	9.20	4.38	4.51	2.58	6.36	3.60	1.48	2.09	4.59
(*n* = 4)	**SD**	0.30	0.17	0.21	0.19	0.08	0.17	0.06	0.18	0.11	0.11	0.07	0.08
	CV	1.67	2.78	1.95	2.19	1.86	3.88	2.63	2.94	3.33	7.52	3.55	1.77
	Min	19.02	6.41	11.04	9.03	4.30	4.40	2.49	6.21	3.51	1.39	2.03	4.53
	Max	19.68	6.80	11.50	9.47	4.48	4.75	2.65	6.62	3.77	1.63	2.17	4.68
8	**Mean**	19.60	6.62	11.69	9.48	4.66	4.43	2.77	6.54	3.70	1.60	2.05	4.82
(*n* = 8)	**SD**	0.51	0.29	0.38	0.18	0.18	0.22	0.17	0.19	0.16	0.17	0.12	0.31
	CV	2.68	4.52	3.36	1.99	4.01	5.18	6.48	2.94	4.55	11.18	6.19	6.58
	Min	18.54	6.20	11.08	9.26	4.46	4.14	2.55	6.31	3.41	1.42	1.90	4.38
	Max	20.07	7.17	12.36	9.82	4.91	4.84	3.00	6.92	3.97	1.97	2.27	5.19

Table 6.3 continued

		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
ANOVA	**SS**	18.245	1.832	5.467	3.513	1.374	0.464	0.893	3.816	0.698	0.353	0.297	1.367
	df	7	7	7	7	7	7	7	7	7	7	7	7
	F	13.572	6.021	5.779	16.158	10.215	2.074	6.761	12.551	4.351	2.997	4.324	3.308
	P	3.20E-08***	1.30E-04***	1.83E-04***	3.79E-09***	8.06E-07***	0.074	4.76E-05***	8.02E-08***	0.002**	0.015**	0.002**	0.009**

Table 6.4 Pearson correlation coefficients for correlations between latitude and longitude and principal component scores and eight OTUs of 12 cranial measurements of *Eptesicus hottentotus* in southern Africa. * denotes significance at $P < 0.05$; ** denotes significance at $P < 0.01$.

	PC1	PC2	CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Latitude														
Pearson Correlation	-0.658	-0.135	-0.458	-0.268	-0.586	-0.618	-0.613	-0.392	-0.346	-0.706	-0.597	-0.756	-0.799	-0.625
Significance (2-tailed)	0.076	0.750	0.254	0.520	0.127	0.102	0.106	0.337	0.402	0.050	0.118	0.03*	0.017**	0.097
Longitude														
Pearson Correlation	-0.658	0.431	-0.764	-0.681	-0.415	-0.475	-0.086	-0.227	-0.732	-0.749	-0.747	-0.518	-0.357	-0.735
Significance (2-tailed)	0.076	0.287	0.027*	0.063	0.307	0.234	0.840	0.588	0.039*	0.032*	0.033*	0.188	0.386	0.038*

6.3.1.2 *Hypsugo anchietae*

This species is relatively poorly represented in collections and is difficult to identify with the current identification key (Kearney and Taylor, 1997). Following the initial PCA and DFA analyses, four specimens were re-assigned to other species (NMBZ32658, NMBZ31992, TM40291, TM40287). Although the PCA suggested that DM5364 from Harold Johnson Nature Reserve in KwaZulu-Natal Province was an outlier, this specimen was retained in the analysis as its identity was not contradicted by a DFA with known identity specimens, and scrutiny of the individual measurements did not reveal any obvious mistakes but, rather, suggested an overall larger size in this female of tooth wear class D relative to the other specimens most of which were males. Although the 12 remaining specimens were too few to provide a robust assessment of intra-specific geographic variation, the analyses were implemented to provide the first, albeit tentative, information about geographic variation within southern Africa for *H. anchietae*. The 12 specimens from seven different localities were split into five different OTUs (Table 6.5).

A PCA scatterplot (Fig. 6.4.) of the 12 individuals showed some separation along principal component one in relation to latitudinal distribution, whereas the pattern of individual distribution along the second principal component did not relate to geographic variation. The first principal component accounted for 37.69% of the variation. Although not very high in magnitude, eigenvector loadings were, with one exception, positive. The measurements loading highest and lowest were, width across the outer surfaces of the upper canines and width of the upper fourth premolar (Table 6.6). The second principal component accounted for 21.09 % of the variation, the eigenvector loadings were of mixed signs and the measurements loading highest and lowest were length of the upper first molar, post-orbital width and width of the articular surface. The distance phenogram based on 12 specimens of *H. anchietae* revealed a similar pattern of variation between the specimens compared with that observed in the PCA (Fig. 6.5).

Table 6.7 lists the basic statistics and the results of one-way ANOVAs between OTUs for each measurement, which showed significant variation between the different OTUs in only one measurement, post-orbital width. A post-hoc Tukey test of the non-significant subsets was not possible since the Zimbabwe locality was represented by a single specimen. However, the measurements of post-orbital width for each of the localities indicated that post-orbital width was smaller in the Zimbabwe specimen than in the other localities; an analysis run without the Zimbabwe specimen did not show significant variation in post-orbital width among the other localities.

Only one measurement, length of the upper first molar showed a significant positive correlation between OTUs and latitude whereby length of the upper first molar decreased from north to south. Condylo-incisor skull length showed a significant positive correlation with longitude since condylo-incisor skull length increased from west to east (Table 6.8). The first principal component scores of the OTUs were significantly negatively correlated with latitude, indicating an overall north to south clinal pattern of variation of increasing size in the 12 cranial measurements of *H. anchietae*, whereas there was no significant correlation between principal component scores of the OTUs and longitude (Table. 6.8).

6.3.1.3 *Neoromicia capensis*

Initial PCA, DFA and cluster analyses of 414 specimens identified in the various collections as *N. capensis* and *N. melckorum,* split into 15 manageable groups, identified 41 outliers or potentially misidentified specimens of which 33 were removed from further analyses (TM34864, TM34951, KM29004, KM29439, TM8976, TM8974, TM35310, TM35314, MM7064, MM7067, NM7806, SR Site 75/4/96, TM32547, TM35599, TM35587, TM32548, NMB5886, TM27772, TM37298, NMB7693, NMB7633, NMB7639, NMB7699, TM7847), five were re-assigned to *N.* cf. *melckorum* (TM34263, TM34240, TM34185, TM37833, TM34186), and three were re-assigned to *N. zuluensis* (KM8083, KM8092, KM8094). The inclusion of the type specimen of *Neoromicia capensis nkatiensis* (Roberts, 1932) from northern Botswana, which is currently recognised as a synonym of *N. capensis* (Meester *et al.*, 1986), in an analysis with specimens from Botswana and Zimbabwe confirmed the synonymy of this specimen with *N. capensis.*

In three PCAs of specimens from the Succulent Karoo and the northern and southern Fynbos areas, specimens were clustered into two groups, but this was not taken as indicative of another species, although the DFA suggested the larger specimens were *N.* cf. *melckorum*. This interpretation was due to the following:

1. A PCA scatterplot (Fig. 6.6) of individual specimens from the northern area of the Fynbos biome showed that known identity specimens of *N. capensis* occurred in both clusters; and

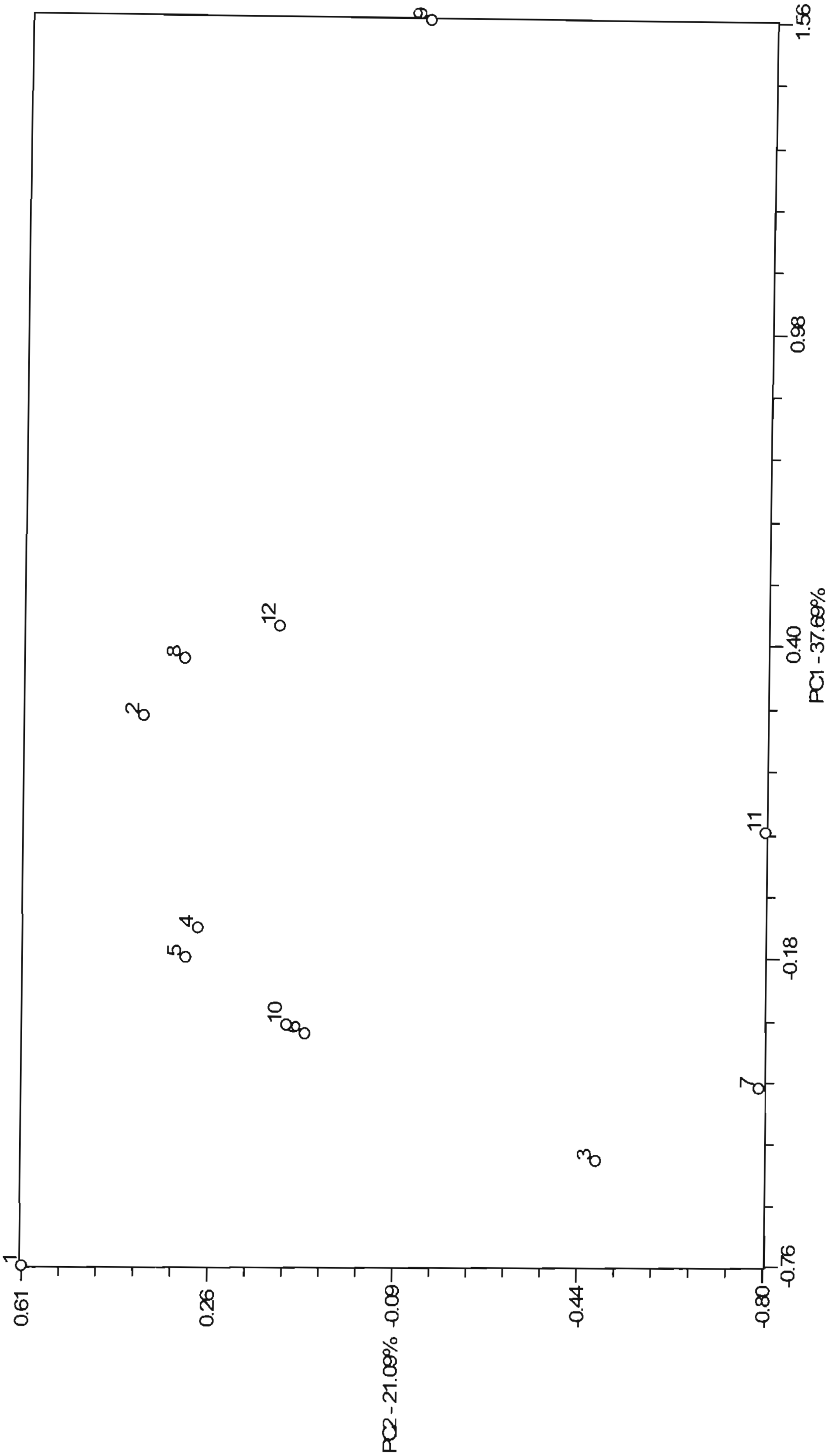


Figure 6.4 Scatterplot of the first two principal component axes based on 12 specimens of *Hypsugo anchietae* from southern Africa. Individual numbers correspond to those in Table 6.5.

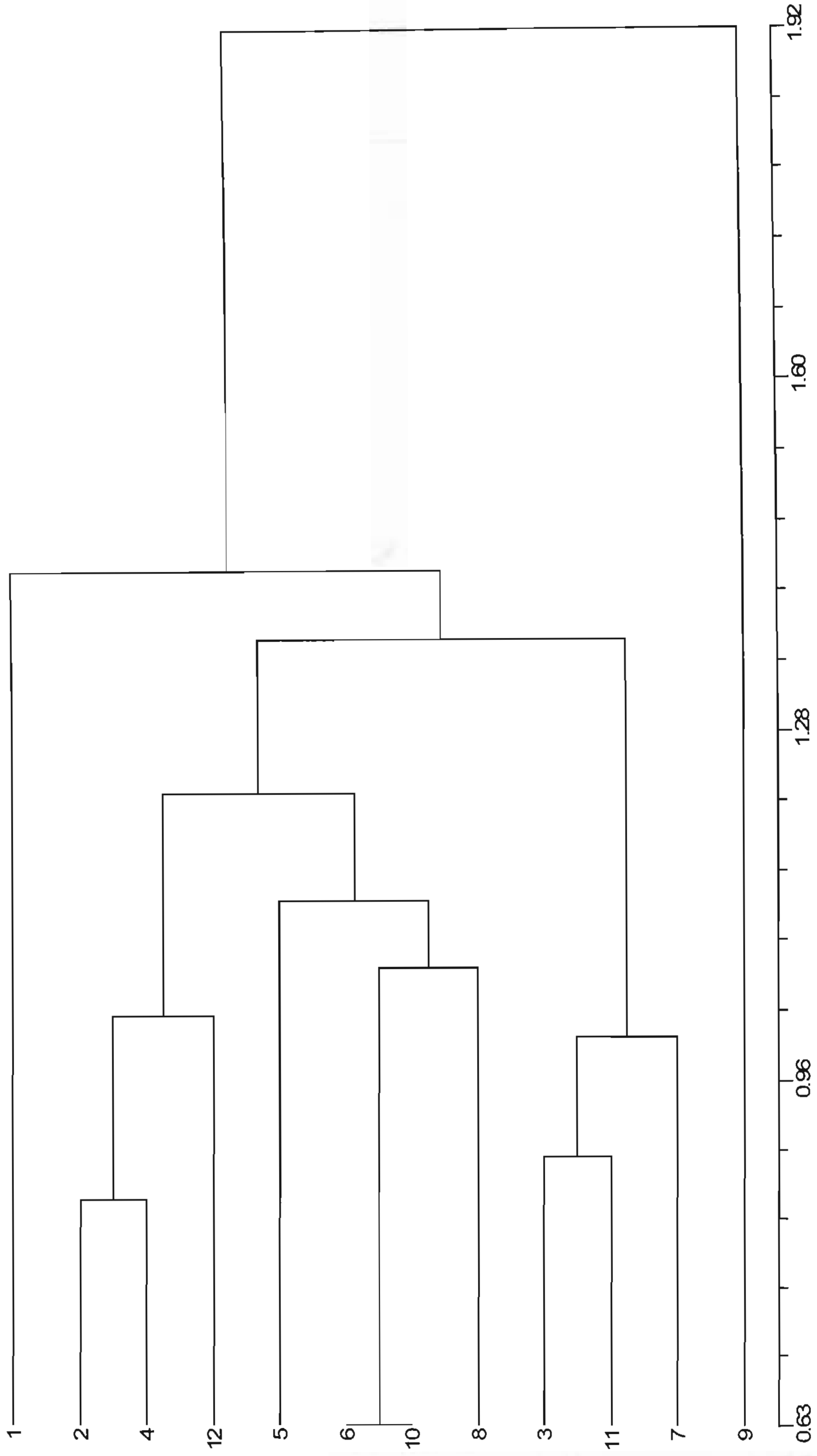


Figure 6.5 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on 12 individuals of *Hypsugo anchietae* in southern Africa. Individual numbers correspond to those in Table 6.5. Cophenetic correlation coefficient = 0.855.

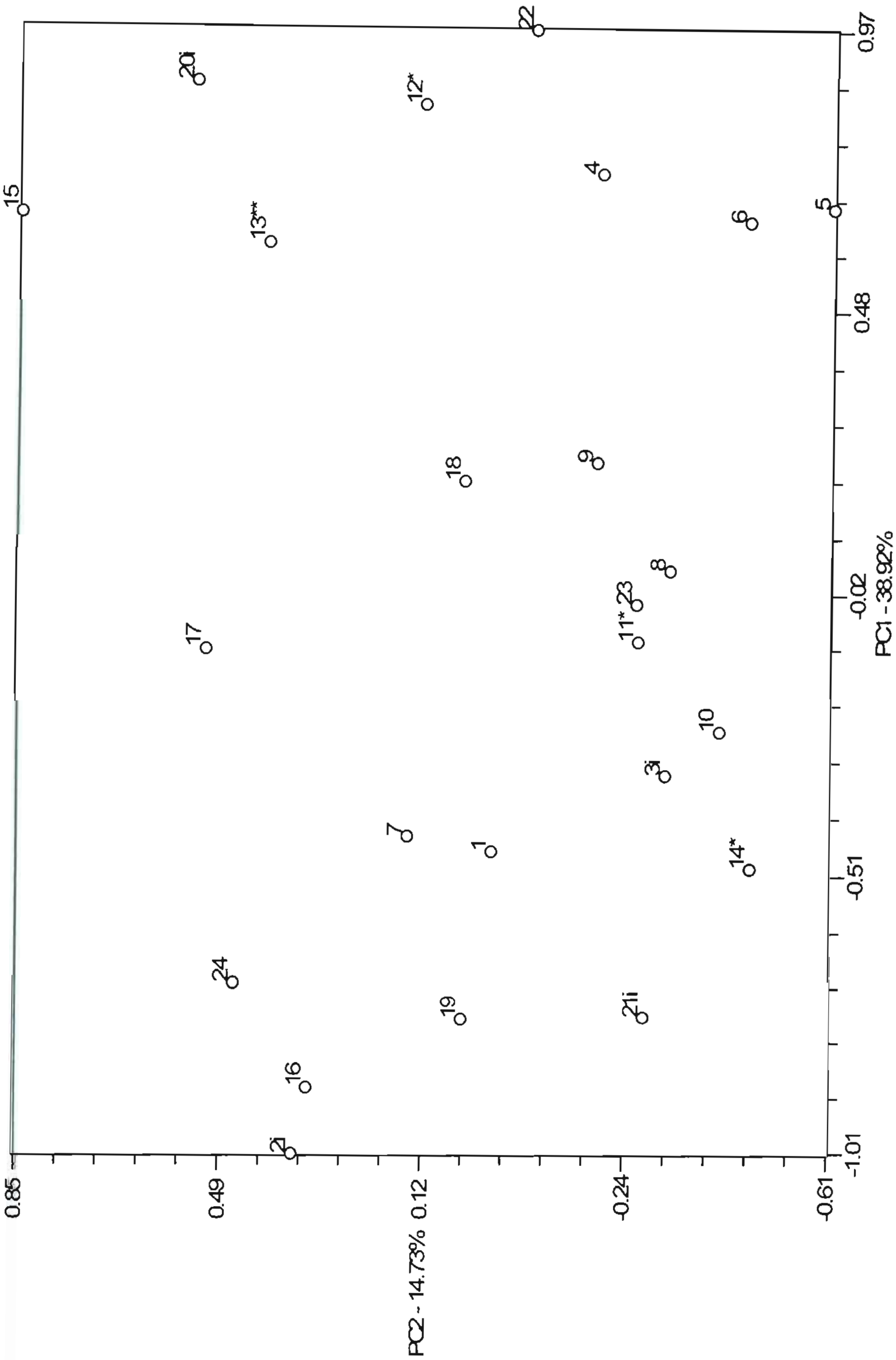


Figure 6.6 Scatterplot of the first two principal component axes based on 24 specimens of *Neoromicia capensis* from the northern part of the Fynbos biome in southern Africa. OTU numbers correspond to those in Appendix 6.1; ** = type specimen; * = topotypes; i = known identity specimen.

Table 6.5 Five OTUs of single and pooled localities for *Hypsugo anchietae* from southern Africa arranged in relation to occurrence from north to south, and east to west, with associated numbering of individuals in each OTU (IC), and number of specimens included in each OTU (*n*). For details on the localities and specimens used see Appendix 6.1.

OTU	IC	Locality	*n*
1	1	Zimbabwe: Gwayi River	1
2	2-4	South Africa: Limpopo Province; Kruger National Park	3
3	5-6	South Africa: KwaZulu-Natal Province; St Lucia; False Bay Park and Sobenghu Lodge	2
4	7-9	South Africa: KwaZulu-Natal Province; Harold Johnson Nature Reserve	3
5	10-12	South Africa: KwaZulu-Natal Province; Empisini Nature Reserve and Hella-Hella Game Farm	3

Table 6.6 Eigenvector scores of principal components one and two of a PCA of 12 specimens based on 12 cranial measurements (Meas) of *Hypsugo anchietae* from southern Africa. See material and methods section of Chapter 5 for an explanation of the measurement codes. Highest and lowest scores are indicated in bold type.

Meas	PC1	PC2
CIL	0.748	0.240
BH	0.721	0.296
ZB	0.709	0.183
BB	0.695	-0.049
POW	0.644	**-0.580**
WFM	0.486	0.412
WAS	0.644	**-0.555**
WOUC	**0.854**	-0.160
WIUM1	0.578	-0.414
WUPM4	**-0.080**	0.526
LUM1	0.130	**0.806**
MAOT	0.554	0.642

Table 6.7 Basic statistics and ANOVA results to test for OTU variation in five OTUs of *Hypsugo anchietae* from southern Africa. SD = standard deviation; CV = coefficient of variation; Min = minimum value; Max = maximum value; *n* = sample size; SS = sum of squares; df = degrees of freedom; *P* = significance of *F* values; * denotes significance at *P* < 0.05. See Table 6.5 for a description of the OTU codes, and materials and methods section of Chapter 5 for an explanation of the measurement codes.

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
1	(*n* = 1)	12.18	4.72	7.07	6.38	3.34	3.22	1.32	3.69	2.46	1.00	1.32	2.87
2	**Mean**	12.50	4.66	6.97	6.46	3.62	3.11	1.51	4.04	2.46	1.01	1.30	2.88
(*n* = 3)	**SD**	0.365	0.13	0.07	0.06	0.05	0.07	0.12	0.06	0.03	0.14	0.04	0.16
	CV	3.07	2.91	1.13	1.06	1.48	2.32	8.43	1.58	1.29	14.76	3.26	5.84
	Min	12.12	4.54	6.92	6.39	3.56	3.07	1.37	3.97	2.44	0.85	1.25	2.75
	Max	12.82	4.79	7.05	6.50	3.65	3.19	1.58	4.07	2.49	1.09	1.32	3.05
3	**Mean**	12.65	4.61	7.33	6.57	3.52	3.17	1.40	3.92	2.34	0.86	1.29	2.83
(*n* = 2)	**SD**	0.15	0.21	0.06	-	-	0.11	0.04	0.07	0.07	0.07	0.05	0.04
	CV	1.32	5.01	0.98	-	-	3.77	2.89	2.07	3.46	9.36	4.19	1.43
	Min	12.54	4.46	7.28	6.57	3.52	3.09	1.37	3.87	2.29	0.81	1.25	2.80
	Max	12.75	4.75	7.37	6.57	3.52	3.24	1.43	3.97	2.39	0.92	1.32	2.85
4	**Mean**	12.68	4.71	7.45	6.63	3.68	3.19	1.63	4.07	2.51	0.83	1.29	2.87
(*n* = 3)	**SD**	0.30	0.18	0.49	0.11	0.11	0.19	0.15	0.26	0.08	0.05	0.07	0.15
	CV	2.55	4.05	7.08	1.75	3.35	6.51	10.16	6.77	3.35	6.80	5.70	5.55
	Min	12.43	4.55	7.02	6.56	3.55	2.97	1.48	3.82	2.44	0.78	1.22	2.70
	Max	13.01	4.90	7.98	6.75	3.77	3.32	1.78	4.33	2.60	0.88	1.36	2.95

Table 6.7 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
5	**Mean**	12.42	4.72	7.24	6.51	3.63	3.09	1.58	4.02	2.48	0.86	1.28	2.90
(*n* = 3)	**SD**	0.30	0.13	0.26	0.07	0.05	0.08	0.22	0.15	0.08	0.02	0.05	0.15
	CV	2.66	2.99	3.85	1.15	1.34	2.68	15.23	4.11	3.40	2.47	4.39	5.70
	Min	12.18	4.60	6.95	6.47	3.59	3.02	1.43	3.87	2.39	0.85	1.22	2.75
	Max	12.76	4.86	7.44	6.59	3.68	3.17	1.83	4.17	2.55	0.88	1.32	3.05
ANOVA	**SS**	0.256	0.022	0.401	0.068	0.102	0.026	0.117	0.133	0.037	0.069	0.001	0.008
	df	4	4	4	4	4	4	4	4	4	4	4	4
	F	0.705	0.230	1.132	2.942	5.133	0.427	1.175	1.234	2.068	2.463	0.124	0.094
	P	0.613	0.913	0.414	0.101	0.030*	0.785	0.399	0.378	0.189	0.141	0.969	0.981

Table 6.8 Pearson correlation coefficients for correlation between latitude and longitude and the principal component scores and five OTUs of 12 cranial measurements of *Hypsugo anchietae* in southern Africa. * denotes significance at $P < 0.05$; ** denotes significance at $P < 0.01$.

	PC1	PC2	CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Latitude														
Pearson Correlation	-0.967	0.041	-0.771	0.150	-0.670	-0.847	-0.863	0.573	-0.794	-0.848	-0.029	0.853	0.973	-0.005
Significance (2-tailed)	0.007**	0.948	0.127	0.810	0.216	0.070	0.060	0.313	0.108	0.070	0.963	0.066	0.005**	0.993
Longitude														
Pearson Correlation	0.780	-0.384	0.926	-0.657	0.402	0.773	0.739	-0.458	0.518	0.792	-0.327	-0.522	-0.666	-0.359
Significance (2-tailed)	0.120	0.524	0.024*	0.228	0.503	0.126	0.154	0.438	0.372	0.111	0.591	0.367	0.219	0.553

2. while the type specimen of *E. melckorum* (TM2283), a female, occurred in the cluster of larger specimens, of the other specimens collected at the same time from the same roost and also described by Roberts (1919) as *E. melckorum*, a female (TM2281) plotted with the larger specimens, and two males (TM2280, TM2284) plotted with the smaller specimens.

Furthermore, the geometric morphometric shape analysis (Chapter 3) showed a clinal size increase in *N. capensis* both to the south and the west of southern Africa.

Thirty-nine OTUs (Table 6.9) were identified from single and pooled localities, which included separate OTUs for males and females from Jagersfontein in the Free State Province of South Africa. Six specimens were not included as there were no adjacent localities close enough with which to be pooled (DM5355, BM1902.4.3.1, MM7061, TM11785, TM44210, ZM17074, NM7053, TM32567). A 39-OTU PCA scatterplot of the first two principal components showed a tendency for OTU scores to increase with increasing longitude along both the first and second principal component axes (Fig. 6.7). The first principal component which accounted for 63.96% of the variance, showed high positive loadings for all the measurements (Table 6.10) which was consistent with the first principal component accounting largely for variation in overall size. The second principal component, which accounted for 15.58% of the variance had measurement loadings of mixed signs, indicating that cranial configuration was also intra-specifically variable. The measurements that loaded highest on the first principal component axis were braincase height, condylo-incisor skull length, and braincase breadth. The measurements that loaded highest and lowest on the second principal component were width of the upper fourth premolar, length between the condylar and the coronoid processes of the mandible, and greatest width of the articular surface. Although there were too many individuals (353) in the PCA scatterplot of the first two principal components (Fig. 6.8) to allow an assessment of the patterns of relationship between the localities, the results of the PCA of individuals was similar to that of the OTUs since the important measurements identified on the first and second principal components of each were similar (Table 6.10).

A scatterplot of the second and third principal component axes (Fig. 6.9) identified three outlier OTUs (OTU 3 from Botswana, OTU 9 from Gauteng Province in South Africa and OTU 28 from Deelfontein and Hanover in the Eastern Cape) among the smaller individuals on the third principal component axis. Among the other specimens, the separation appears to have some pattern in relation to longitude. The second principal component separated several OTUs among the larger individuals, however, there was no discernible pattern of variation along this axis in relation to latitude or longitude. The third principal component axis explained 6.00% and the measurements with the highest and lowest eigenvector scores were post-orbital width and width of the upper fourth premolar. The distance phenogram based on 39 OTUs of *N. capensis* revealed a similar geographic structure to that observed in the PCA of the first two principal components (Fig. 6.10).

Table 6.11 gives the basic statistics and the results of the one-way ANOVAs between OTUs for each measurement, which showed significant variation in all 12 measurements between the different OTUs. The maximally non-significant subsets identified by the post-hoc Tukey tests for each of the 12 cranial measurements (Appendix 6.2 B) showed geographically discernible patterns of change in five measurements: condylo-incisor skull length, braincase height, zygomatic and braincase breadths and width across the outer surfaces of the upper canines, where the pattern of OTU order indicated a north-east to south-west size increase. In the other seven measurements, the pattern in OTU order was not as obviously geographically meaningful, although there was still some indication of increasing size from north to south.

Nine of the 12 cranial measurement showed significant negative correlations between the 39 different OTUs and latitude (i.e. increase in measurement with increasing latitude); eight of the 12 cranial measurement showed significant negative correlations between the 39 different OTUs and longitude (i.e. decrease in measurement with increasing longitude), and first principal component scores were significantly negatively correlated with both latitude and longitude, whereas second principal component scores were only significantly negatively correlated with latitude (Table 6.12). Hence, these results indicated a clinal continuum of overall size change in the 12 cranial measurements of *N. capensis*, with specimens from western and southern OTUs being larger than specimens from northern and eastern OTUs and this concurs with the findings of the shape morphometric analysis, albeit the actual changes in size are not easily compared with those identified in the shape analysis. This clinal geographic variation associated with latitude and longitude does not support the subspecies identified by Thorn (1988) or Koopman (1994).

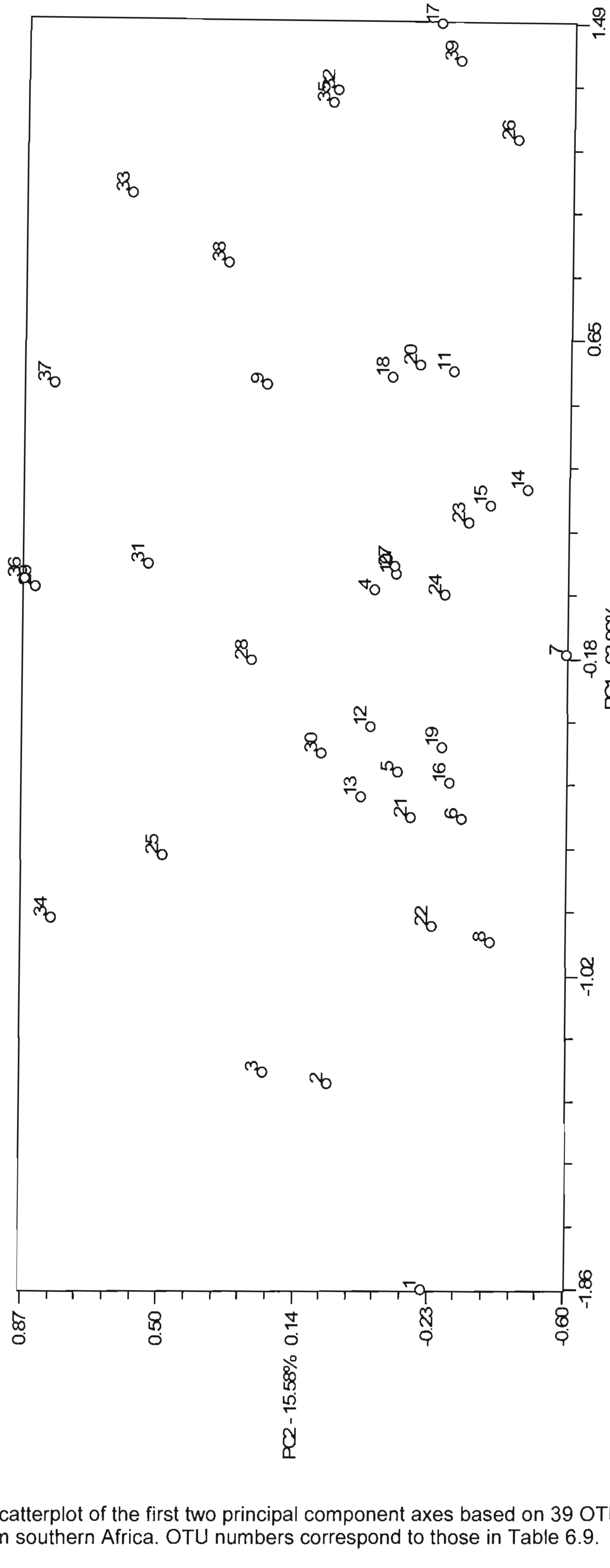
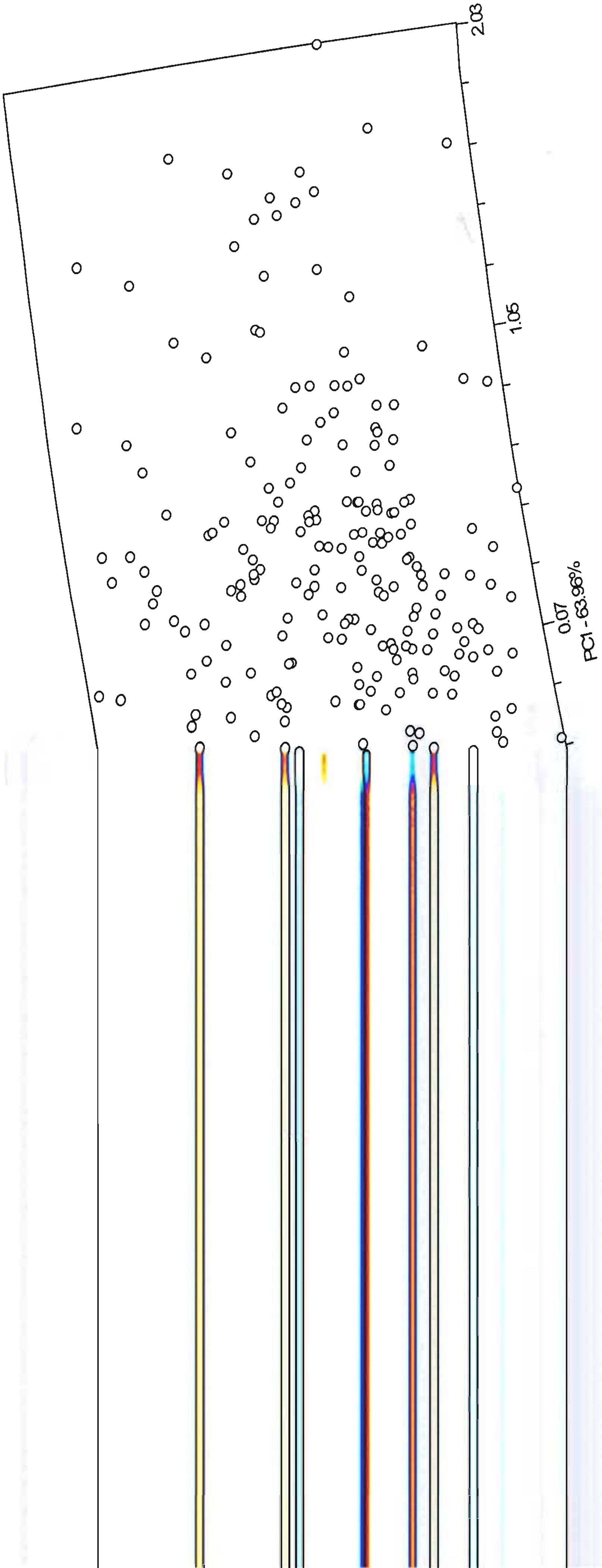


Figure 6.7 Scatterplot of the first two principal component axes based on 39 OTUs of *Neoromicia capensis* from southern Africa. OTU numbers correspond to those in Table 6.9.


2.03
1.05
0.07
PC1 - 63.96%

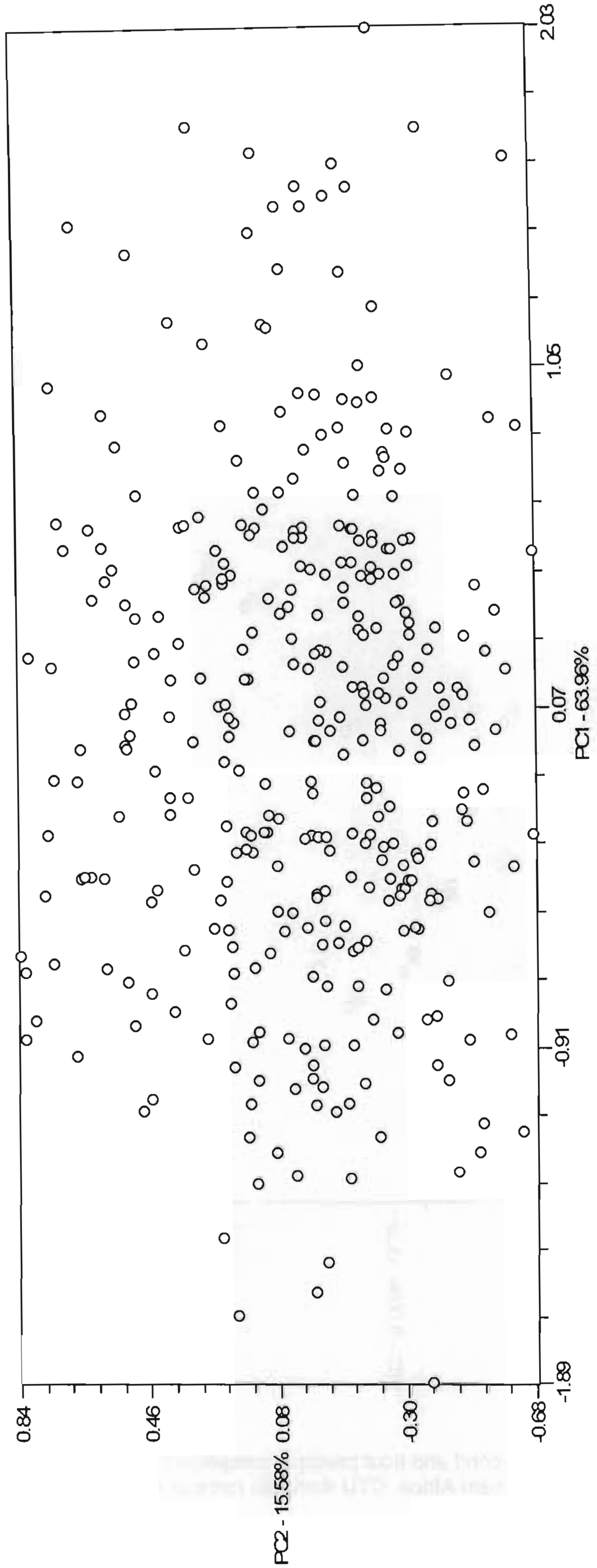


Figure 6.8 Scatterplot of the first two principal component axes based on 353 specimens of *Neoromicia capensis* from localities across southern Africa.

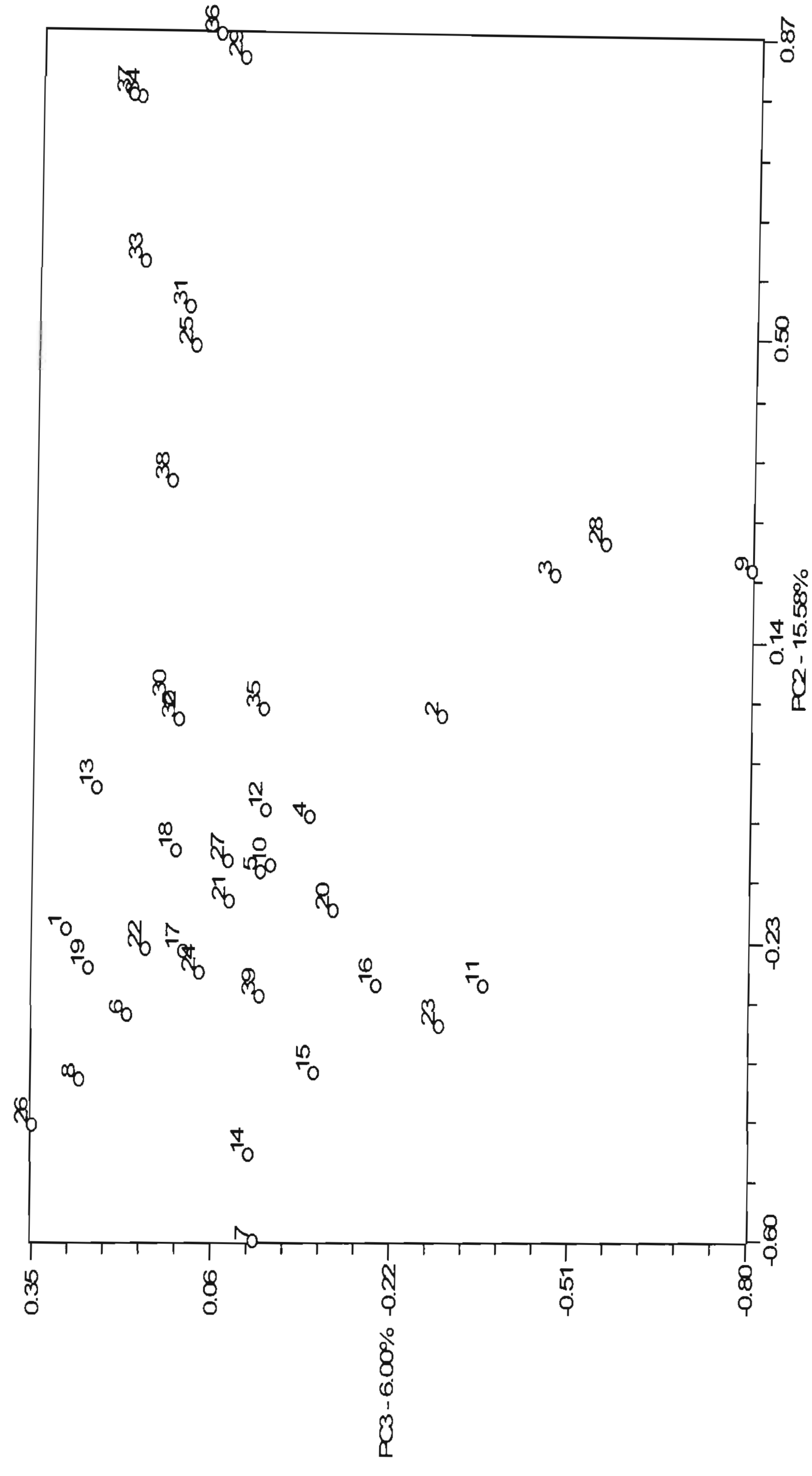


Figure 6.9 Scatterplot of the second and third principal component axes based on 39 OTUs of *Neoromicia capensis* from southern Africa. OTU numbers correspond to those in Table 6.9.

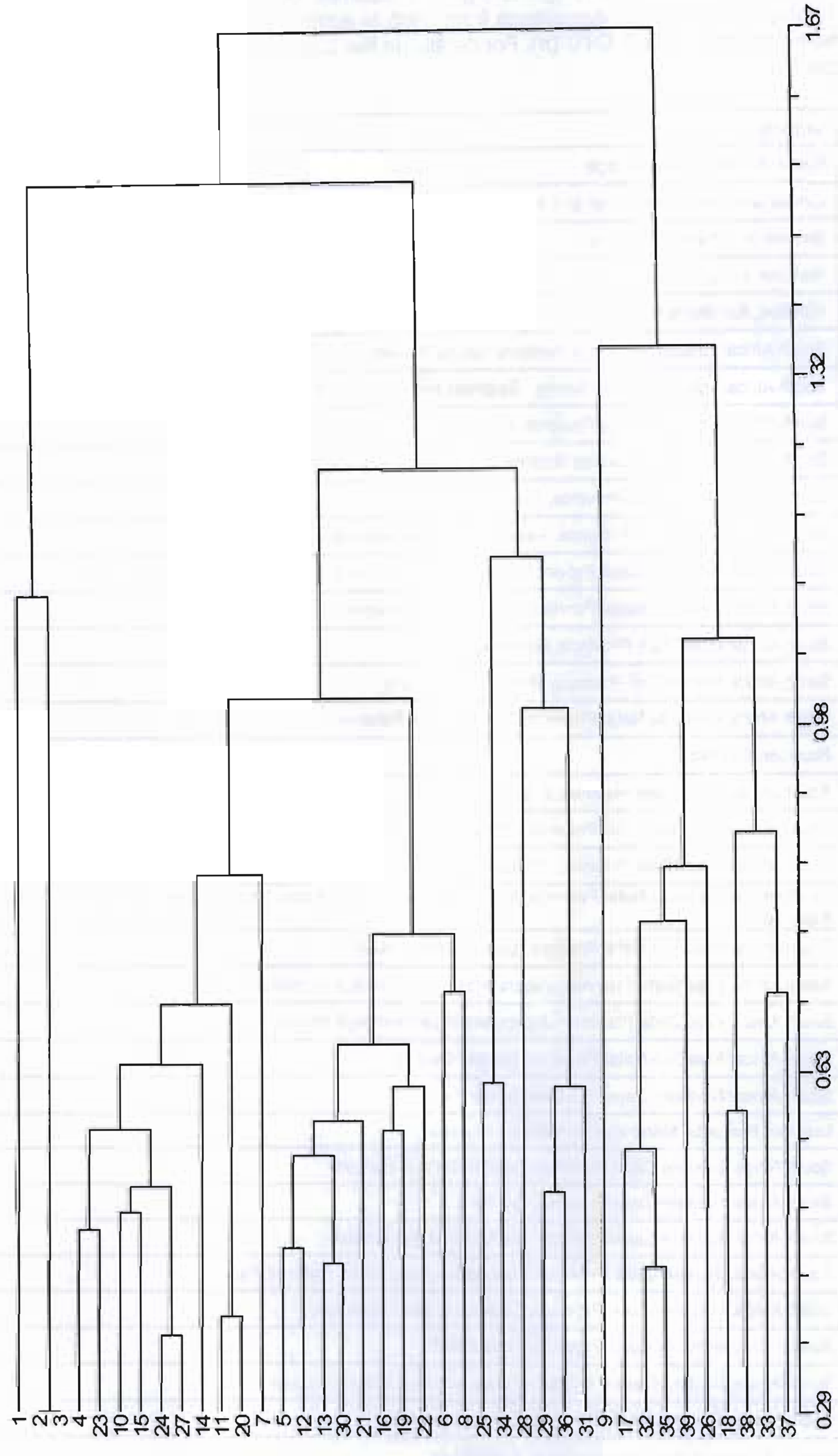


Figure 6.10 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on 39 OTUs of *Neoromicia capensis* from southern Africa. OTU numbers correspond to those in Table 6.9. Cophenetic correlation coefficient = 0.687.

Table 6.9 Thirty-nine OTUs of single and pooled localities for *Neoromicia capensis* from southern Africa arranged in relation to occurrence from north to south, and east to west, with number of specimens included in each OTU (*n*). For details on the localities and specimens used see Appendix 6.1

OTU	Locality	*n*
1	Namibia: Ssannakanu Village	8
2	Zimbabwe: Near Gwayi River and Sengwa	12
3	Botswana: Nthane and Nkate	10
4	Namibia: Lilbig's Ranch, Okahandja, and Outja	3
5	Namibia: Sandfontein and Gobabis Farm	14
6	South Africa: Limpopo Province; Messina Nature Reserve and Pafuri	4
7	South Africa: Mpumalanga Province; Badplaas and Rhenosterkoppies	5
8	South Africa: Northern Cape Province; Marie se Gat and Mata Mata	18
9	South Africa: Gauteng Province; Krugersdorp and Suikerbos Nature Reserve	3
10	South Africa: North West Province; Ratsegaai Farm	13
11	South Africa: Free State Province; Aasvogelrand-oost and Helena	11
12	South Africa: Northern Cape Province; Kuruman, Wonderwerk Cave, Molopo Nature Reserve	5
13	South Africa: KwaZulu-Natal Province; Ithala Game Reserve	7
14	South Africa: Free State Province; Hoopstad	8
15	South Africa: North West Province; Bloemhof-Christiana	10
16	South Africa: KwaZulu-Natal Province; Mkuze Game Reserve	13
17	Namibia: Swartkop	7
18	South Africa: Free State Province; Brandfort	5
19	South Africa: KwaZulu-Natal Province; Royal Natal National Park	3
20	South Africa: Free State Province; Florisbad	18
21	South Africa: KwaZulu-Natal Province; Mooi River, Nottingham Road, New Hanover, and Weenan Game Reserve	6
22	South Africa: KwaZulu-Natal Province; Loteni Game Reserve	11
23	South Africa: Free State Province; Jagersfontein Commonage (females)	7
24	South Africa: Free State Province; Jagersfontein Commonage (males)	32
25	South Africa: KwaZulu-Natal Province; Greater Durban	4
26	South Africa: Northern Cape Province; Narap Farm	4
27	Lesotho: Botsoela, Marakabei, and Mount Moorosi	11
28	South Africa: Eastern Cape Province; Deelfontein and Hanover	3
29	South Africa: Eastern Cape Province; Gouna	6
30	South Africa: Eastern Cape Province; Bedford and Jamestown	7
31	South Africa: Eastern Cape Province; Murraysburg and Karoo National Park	18
32	South Africa: Western Cape Province; Cederberg and Clanwilliam	5
33	South Africa: Western Cape Province; Groote Drift	5
34	South Africa: Eastern Cape Province; Blaney and King William's Town	15
35	South Africa: Western Cape Province; Kersefontein Farm	14
36	South Africa: Western Cape Province; Buffel River	4
37	South Africa: Western Cape Province; Zeekoegats	5
38	South Africa: Western Cape Province; Vrolijkheid Nature Reserve	6
39	South Africa: Western Cape Province; Stilbaai	5

Table 6.10 Eigenvector scores of principal components A) one to three of a PCA of 39 OTUs and B) principal components one and two of a PCA of 353 specimens of 12 cranial measurements (Meas) of *Neoromicia capensis* from southern Africa. See the methods and material of Chapter 5 for an explanation of the measurement codes. Highest and lowest scores are indicated in bold type.

	A)				B)	
Meas	**PC1**	**PC2**	**PC3**		**PC1**	**PC2**
CIL	**0.924**	0.140	0.127		**0.862**	0.082
BH	**0.933**	0.134	0.075		0.800	0.084
ZB	0.922	0.031	0.008		**0.823**	0.047
BB	**0.924**	0.288	0.027		**0.822**	0.264
POW	0.771	0.406	**0.136**		0.618	0.387
WFM	0.833	0.009	0.022		0.635	-0.023
WAS	0.601	-0.648	-0.250		0.526	**-0.504**
WOUC	0.886	-0.248	0.132		0.816	-0.209
WIUM1	0.886	-0.204	-0.170		0.746	-0.111
WUPM4	0.066	**0.724**	**-0.680**		0.117	**0.692**
LUM1	0.806	0.335	0.095		0.586	0.241
MAOT	0.609	**-0.651**	-0.315		0.577	**-0.559**

Table 6.11 Basic statistics and ANOVA results to test for variation in 39 OTUs of *Neoromicia capensis* in southern Africa. SD = standard deviation; CV = coefficient of variation; Min = minimum value; Max = maximum value; n = sample size; SS = sum of squares; df = degrees of freedom; P = significance of F values; *** denotes significance at $P < 0.001$. See Table 6.9 for a description of the OTU codes, and material and methods section of Chapter 5 for an explanation of the measurement codes.

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
1	**Mean**	12.79	4.54	7.47	6.49	3.44	3.38	1.48	4.24	2.53	0.93	1.22	2.95
(*n* = 8)	**SD**	0.25	0.11	0.26	0.10	0.17	0.12	0.09	0.19	0.15	0.08	0.06	0.18
	CV	2.02	2.41	3.58	1.56	5.03	3.59	6.12	4.53	6.28	8.76	4.72	6.38
	Min	12.45	4.41	6.99	6.35	3.26	3.19	1.37	4.02	2.34	0.81	1.15	2.55
	Max	13.06	4.72	7.80	6.65	3.65	3.54	1.63	4.53	2.80	1.05	1.29	3.16
2	**Mean**	12.98	4.59	7.53	6.58	3.47	3.39	1.56	4.32	2.56	1.01	1.32	3.13
(*n* = 12)	**SD**	0.24	0.10	0.13	0.16	0.11	0.12	0.07	0.17	0.10	0.12	0.10	0.15
	CV	1.87	2.19	1.74	2.43	3.23	3.50	4.60	4.07	3.85	12.02	7.75	5.00
	Min	12.51	4.43	7.28	6.28	3.25	3.23	1.43	4.08	2.42	0.85	1.15	2.90
	Max	13.27	4.75	7.74	6.82	3.65	3.58	1.68	4.68	2.75	1.25	1.49	3.41
3	**Mean**	12.97	4.52	7.58	6.64	3.50	3.36	1.51	4.27	2.62	1.10	1.35	3.16
(*n* = 10)	**SD**	0.28	0.13	0.17	0.17	0.12	0.22	0.06	0.15	0.11	0.08	0.06	0.09
	CV	2.24	2.84	2.35	2.55	3.57	6.73	3.73	3.65	4.26	7.08	4.31	2.99
	Min	12.45	4.32	7.32	6.43	3.34	2.97	1.45	4.08	2.49	0.93	1.28	2.98
	Max	13.49	4.70	7.82	6.87	3.65	3.71	1.61	4.58	2.84	1.18	1.49	3.26
4	**Mean**	13.80	4.83	8.04	6.96	3.70	3.41	1.61	4.62	2.72	1.02	1.38	3.33
(*n* = 3)	**SD**	0.31	0.04	0.37	0.12	0.13	0.16	0.13	0.30	0.19	0.16	0.20	0.16
	CV	2.43	0.90	4.95	1.86	3.66	5.14	8.61	7.00	7.69	16.55	15.61	5.07
	Min	13.60	4.79	7.62	6.86	3.57	3.22	1.48	4.28	2.49	0.88	1.15	3.16
	Max	14.16	4.87	8.28	7.09	3.82	3.50	1.73	4.84	2.85	1.19	1.53	3.46

Table 6.11 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
5	Mean	13.68	4.84	7.85	6.86	3.48	3.52	1.60	4.45	2.64	1.00	1.34	3.19
(*n* = 14)	SD	0.30	0.14	0.25	0.23	0.10	0.16	0.13	0.11	0.11	0.08	0.06	0.16
	CV	3.86	5.23	5.67	6.01	5.26	8.16	14.41	4.44	7.69	14.63	7.62	9.06
	Min	13.19	4.64	7.28	6.48	3.34	3.16	1.32	4.23	2.44	0.85	1.22	2.85
	Max	14.06	5.09	8.13	7.39	3.69	3.72	1.78	4.63	2.85	1.12	1.46	3.46
6	Mean	13.32	4.70	7.99	6.64	3.51	3.49	1.58	4.59	2.69	0.95	1.34	3.12
(*n* = 4)	SD	0.56	0.16	0.26	0.24	0.13	0.17	0.00	0.08	0.09	0.06	0.09	0.06
	CV	4.45	3.55	3.47	3.88	3.79	5.04	0.00	1.77	3.44	6.93	6.77	2.18
	Min	12.78	4.53	7.69	6.38	3.33	3.27	1.58	4.53	2.60	0.88	1.22	3.05
	Max	13.99	4.85	8.31	6.88	3.62	3.62	1.58	4.68	2.80	1.02	1.42	3.21
7	Mean	13.79	4.84	7.97	6.85	3.56	3.56	1.61	4.55	2.74	0.94	1.29	3.44
(*n* = 5)	SD	0.37	0.16	0.19	0.15	0.16	0.14	0.06	0.15	0.13	0.08	0.08	0.09
	CV	2.81	3.40	2.44	2.34	4.62	4.10	3.79	3.38	4.86	8.61	6.48	2.60
	Min	13.37	4.62	7.73	6.67	3.36	3.37	1.53	4.43	2.65	0.85	1.22	3.31
	Max	14.26	5.03	8.20	7.01	3.75	3.76	1.68	4.73	2.90	1.02	1.39	3.51
8	Mean	13.40	4.66	7.65	6.69	3.45	3.51	1.55	4.40	2.58	0.91	1.35	3.23
(*n* = 18)	SD	0.33	0.11	0.23	0.16	0.14	0.09	0.11	0.11	0.11	0.08	0.05	0.13
	CV	2.48	2.31	2.97	2.41	4.10	2.52	7.23	2.58	4.23	8.31	3.93	3.92
	Min	12.92	4.46	7.29	6.48	3.15	3.38	1.32	4.17	2.39	0.81	1.25	3.05
	Max	13.88	4.80	7.98	7.08	3.69	3.66	1.78	4.58	2.75	1.09	1.42	3.51

Table 6.11 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
9	**Mean**	13.73	4.89	8.04	7.19	3.75	3.74	1.72	4.40	2.87	1.15	1.40	3.33
(*n* = 3)	**SD**	0.46	0.12	0.14	0.10	0.20	0.14	0.09	0.12	0.09	0.14	0.04	0.07
	CV	3.59	2.70	1.84	1.44	5.84	4.06	5.35	3.07	3.42	13.48	2.80	2.32
	Min	13.23	4.75	7.93	7.09	3.52	3.58	1.63	4.28	2.77	0.98	1.36	3.29
	Max	14.12	4.97	8.19	7.28	3.88	3.85	1.78	4.53	2.94	1.25	1.42	3.41
10	**Mean**	13.60	4.87	7.96	7.00	3.66	3.61	1.58	4.63	2.71	1.00	1.35	3.34
(*n* = 13)	**SD**	0.31	0.14	0.28	0.19	0.12	0.15	0.10	0.22	0.17	0.10	0.07	0.14
	CV	2.35	2.91	3.56	2.81	3.34	4.10	6.58	4.77	6.36	10.51	4.88	4.22
	Min	13.05	4.62	7.46	6.64	3.47	3.39	1.43	4.33	2.49	0.88	1.25	3.16
	Max	14.15	5.10	8.27	7.28	3.85	3.82	1.83	4.94	3.00	1.29	1.49	3.61
11	**Mean**	14.13	4.96	8.10	7.08	3.64	3.62	1.73	4.70	2.75	1.05	1.40	3.45
(*n* = 11)	**SD**	0.25	0.14	0.27	0.16	0.14	0.23	0.09	0.15	0.18	0.16	0.07	0.06
	CV	1.78	2.91	3.41	2.33	3.99	6.37	5.01	3.18	6.64	15.18	4.99	1.85
	Min	13.70	4.68	7.76	6.86	3.46	3.16	1.63	4.43	2.55	0.85	1.25	3.36
	Max	14.53	5.15	8.64	7.31	4.00	3.97	1.88	4.94	3.15	1.35	1.49	3.56
12	**Mean**	13.69	4.74	7.88	7.01	3.59	3.49	1.65	4.47	2.61	1.00	1.37	3.18
(*n* = 5)	**SD**	0.33	0.11	0.26	0.14	0.16	0.12	0.10	0.11	0.08	0.16	0.08	0.17
	CV	2.53	2.36	3.43	2.02	4.64	3.69	6.41	2.57	3.06	17.16	6.47	5.72
	Min	13.39	4.67	7.61	6.82	3.39	3.36	1.49	4.33	2.49	0.88	1.29	2.95
	Max	14.20	4.92	8.29	7.18	3.78	3.69	1.73	4.58	2.70	1.28	1.49	3.41

Table 6.11 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
13	Mean	13.35	4.75	7.77	6.89	3.67	3.53	1.56	4.47	2.55	0.96	1.36	3.21
(*n* = 7)	SD	0.27	0.14	0.16	0.12	0.06	0.10	0.12	0.10	0.17	0.09	0.08	0.12
	CV	2.11	3.11	2.17	1.79	1.75	3.03	7.96	2.30	7.00	9.15	5.79	3.80
	Min	12.88	4.53	7.56	6.80	3.58	3.43	1.37	4.33	2.39	0.88	1.25	3.00
	Max	13.73	5.00	8.06	7.11	3.78	3.73	1.73	4.58	2.90	1.12	1.49	3.36
14	Mean	13.81	4.87	8.03	7.05	3.70	3.47	1.67	4.74	2.83	0.96	1.33	3.38
(*n* = 8)	SD	0.16	0.20	0.28	0.09	0.13	0.13	0.10	0.17	0.11	0.09	0.07	0.15
	CV	1.16	4.24	3.65	1.27	3.50	3.80	6.15	3.62	3.96	9.90	5.57	4.54
	Min	13.53	4.61	7.46	6.92	3.52	3.25	1.58	4.38	2.70	0.81	1.22	3.21
	Max	14.03	5.18	8.37	7.22	3.90	3.63	1.83	4.94	3.00	1.12	1.46	3.61
15	Mean	13.85	4.82	7.91	7.09	3.67	3.59	1.70	4.67	2.74	0.99	1.35	3.38
(*n* = 10)	SD	0.27	0.19	0.28	0.18	0.17	0.09	0.10	0.12	0.13	0.07	0.04	0.13
	CV	2.02	3.93	3.67	2.55	4.66	2.49	6.00	2.69	4.70	6.74	3.31	3.86
	Min	13.41	4.56	7.57	6.81	3.40	3.41	1.53	4.48	2.55	0.88	1.29	3.21
	Max	14.20	5.05	8.33	7.45	3.94	3.70	1.88	4.84	2.90	1.09	1.42	3.61
16	Mean	13.30	4.77	7.67	6.89	3.61	3.43	1.69	4.51	2.67	1.01	1.33	3.23
(*n* = 13)	SD	0.33	0.15	0.38	0.19	0.13	0.11	0.11	0.12	0.09	0.08	0.08	0.10
	CV	2.54	3.29	4.99	2.84	3.54	3.37	6.88	2.73	3.42	7.68	6.07	3.25
	Min	12.73	4.48	7.10	6.60	3.42	3.26	1.53	4.280	2.49	0.88	1.19	3.05
	Max	13.81	4.91	8.31	7.17	3.83	3.63	1.93	4.73	2.80	1.12	1.42	3.41

Table 6.11 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
17	**Mean**	14.82	5.15	8.52	7.38	3.79	3.67	1.72	4.87	2.86	0.97	1.44	3.48
(*n* = 7)	**SD**	0.25	0.14	0.24	0.17	0.12	0.16	0.10	0.14	0.13	0.06	0.11	0.24
	CV	1.72	2.79	2.86	2.45	3.17	4.52	5.81	2.93	4.70	6.49	8.05	7.15
	Min	14.49	5.00	8.24	7.10	3.66	3.38	1.58	4.68	2.65	0.85	1.29	3.16
	Max	15.18	5.35	8.93	7.59	3.94	3.86	1.83	5.09	3.05	1.02	1.59	3.8
18	**Mean**	14.21	4.89	7.98	7.13	3.72	3.71	1.66	4.65	2.72	0.98	1.45	3.36
(*n* = 5)	**SD**	0.24	0.13	0.40	0.14	0.14	0.17	0.12	0.07	0.09	0.07	0.11	0.08
	CV	1.79	2.76	5.29	2.07	3.83	4.92	7.76	1.54	3.57	7.01	8.21	2.52
	Min	13.95	4.75	7.41	6.93	3.58	3.52	1.53	4.58	2.60	0.88	1.29	3.26
	Max	14.51	5.09	8.40	7.25	3.89	3.99	1.78	4.73	2.80	1.05	1.56	3.46
19	**Mean**	13.52	4.84	7.70	6.86	3.67	3.41	1.65	4.46	2.66	0.93	1.38	3.21
(*n* = 3)	**SD**	0.12	0.04	0.02	0.19	0.17	0.09	0.06	0.16	0.15	0.10	0.04	0.09
	CV	0.97	0.93	0.29	3.05	4.86	2.77	3.87	3.97	5.98	11.44	3.08	2.98
	Min	13.39	4.79	7.68	6.72	3.57	3.35	1.58	4.28	2.49	0.81	1.36	3.11
	Max	13.63	4.87	7.72	7.08	3.86	3.51	1.68	4.58	2.75	0.98	1.42	3.26
20	**Mean**	13.99	4.96	8.13	7.11	3.69	3.57	1.70	4.70	2.75	1.01	1.44	3.41
(*n* = 18)	**SD**	0.30	0.15	0.23	0.12	0.16	0.14	0.11	0.13	0.11	0.06	0.05	0.17
	CV	0.02	0.03	0.03	0.02	0.04	0.04	0.06	0.03	0.04	0.06	0.04	0.05
	Min	13.41	4.62	7.70	6.91	3.38	3.32	1.53	4.48	2.60	0.88	1.36	3.11
	Max	14.41	5.24	8.53	7.42	3.96	3.81	1.83	4.99	3.00	1.12	1.53	3.77

Table 6.11 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
21	**Mean**	13.20	4.74	7.66	6.87	3.59	3.60	1.64	4.33	2.63	0.97	1.36	3.18
(*n* = 6)	**SD**	0.43	0.10	0.41	0.24	0.13	0.14	0.11	0.30	0.21	0.09	0.05	0.21
	CV	3.42	2.14	5.63	3.70	3.90	3.90	7.22	7.27	8.23	9.17	4.03	6.89
	Min	12.55	4.64	7.13	6.62	3.35	3.41	1.48	3.92	2.34	0.85	1.29	2.85
	Max	13.75	4.89	8.25	7.25	3.73	3.72	1.78	4.68	2.80	1.05	1.42	3.36
22	**Mean**	13.00	4.61	7.59	6.76	3.63	3.38	1.62	4.43	2.63	0.94	1.37	3.14
(*n* = 11)	**SD**	0.27	0.24	0.32	0.15	0.16	0.22	0.13	0.19	0.16	0.07	0.07	0.14
	CV	2.09	5.42	4.33	2.22	4.60	6.75	8.24	4.44	6.15	7.50	5.10	4.57
	Min	12.66	4.07	6.79	6.62	3.37	3.02	1.43	4.02	2.34	0.81	1.25	2.90
	Max	13.63	4.97	7.95	7.11	3.85	3.73	1.83	4.79	2.85	1.02	1.49	3.41
23	**Mean**	13.89	4.80	8.04	6.97	3.63	3.46	1.72	4.65	2.76	1.03	1.40	3.39
(*n* = 7)	**SD**	0.24	0.12	0.16	0.08	0.11	0.12	0.11	0.17	0.11	0.08	0.06	0.11
	CV	1.76	2.65	2.05	1.24	3.25	3.49	6.33	3.81	4.05	7.57	4.46	3.46
	Min	13.56	4.63	7.75	6.89	3.45	3.34	1.53	4.38	2.60	0.88	1.32	3.26
	Max	14.14	4.97	8.24	7.13	3.75	3.68	1.83	4.84	2.90	1.09	1.46	3.56
24	**Mean**	13.71	4.82	7.91	7.00	3.63	3.52	1.66	4.58	2.70	0.96	1.40	3.29
(*n* = 32)	**SD**	0.22	0.12	0.23	0.19	0.13	0.12	0.10	0.15	0.12	0.07	0.06	0.12
	CV	1.61	2.52	2.93	2.76	3.71	3.55	6.25	3.38	4.46	7.48	4.40	3.65
	Min	13.27	4.53	7.27	6.52	3.35	3.24	1.48	4.17	2.44	0.81	1.29	3.00
	Max	14.15	5.14	8.29	7.40	3.90	3.76	1.88	4.99	2.95	1.12	1.56	3.56

Table 6.11 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
25	**Mean**	13.00	4.72	7.89	6.93	3.82	3.42	1.54	4.37	2.56	1.03	1.35	3.00
(*n* = 4)	**SD**	0.60	0.29	0.50	0.16	0.16	0.22	0.17	0.15	0.13	0.04	0.03	0.17
	CV	4.92	6.50	6.71	2.46	4.33	6.69	11.61	3.70	5.56	4.50	2.56	6.06
	Min	12.19	4.32	7.47	6.72	3.66	3.20	1.32	4.17	2.44	0.98	1.32	2.80
	Max	13.64	4.94	8.61	7.11	3.99	3.64	1.73	4.53	2.70	1.09	1.39	3.21
26	**Mean**	14.89	5.13	8.15	7.26	3.70	3.79	1.71	4.70	2.86	0.90	1.44	3.45
(*n* = 4)	**SD**	0.30	0.16	0.21	0.25	0.22	0.20	0.12	0.32	0.14	0.04	0.26	0.19
	CV	2.16	3.21	2.69	3.69	6.26	5.47	7.55	7.25	5.20	5.18	18.99	5.92
	Min	14.51	4.97	7.92	7.04	3.53	3.61	1.58	4.23	2.70	0.85	1.12	3.26
	Max	15.14	5.34	8.42	7.61	4.02	4.00	1.83	4.94	3.00	0.95	1.70	3.72
27	**Mean**	13.75	4.92	7.82	6.88	3.67	3.53	1.63	4.64	2.73	0.99	1.42	3.29
(*n* = 11)	**SD**	0.37	0.16	0.24	0.20	0.09	0.16	0.10	0.12	0.15	0.09	0.08	0.19
	CV	2.77	3.32	3.10	2.91	2.43	4.52	6.55	2.53	5.43	9.26	5.77	5.77
	Min	13.17	4.68	7.58	6.56	3.57	3.17	1.48	4.43	2.44	0.85	1.32	2.95
	Max	14.24	5.26	8.29	7.22	3.77	3.78	1.78	4.84	2.90	1.19	1.56	3.61
28	**Mean**	13.75	4.97	7.89	7.00	3.57	3.52	1.55	4.43	2.68	1.13	1.34	3.35
(*n* = 3)	**SD**	0.24	0.19	0.34	0.24	0.15	0.07	0.06	0.09	0.08	0.15	0.07	0.14
	CV	1.85	4.12	4.64	3.77	4.67	2.00	4.42	2.18	3.15	14.29	5.46	4.50
	Min	13.52	4.76	7.51	6.72	3.40	3.46	1.48	4.33	2.60	0.98	1.29	3.26
	Max	13.99	5.13	8.15	7.16	3.70	3.59	1.59	4.48	2.75	1.28	1.42	3.51

Table 6.11 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
29	**Mean**	14.31	4.96	7.94	7.02	3.66	3.58	1.48	4.49	2.67	1.10	1.45	2.97
(*n* = 6)	**SD**	0.32	0.09	0.16	0.23	0.12	0.10	0.06	0.18	0.07	0.04	0.04	0.12
	CV	2.36	1.93	2.10	3.39	3.45	2.99	3.90	4.05	2.74	3.36	2.52	4.08
	Min	13.91	4.78	7.74	6.74	3.48	3.47	1.39	4.28	2.60	1.05	1.39	2.79
	Max	14.79	5.04	8.17	7.36	3.78	3.70	1.56	4.73	2.80	1.15	1.49	3.09
30	**Mean**	13.63	4.77	7.73	6.85	3.64	3.50	1.56	4.51	2.66	0.99	1.38	3.15
(*n* = 7)	**SD**	0.47	0.19	0.37	0.26	0.08	0.21	0.14	0.25	0.10	0.08	0.08	0.31
	CV	3.54	4.21	4.95	3.97	2.39	6.12	9.02	5.68	3.74	8.09	6.18	10.18
	Min	13.24	4.51	7.23	6.58	3.53	3.26	1.36	4.28	2.60	0.88	1.29	2.59
	Max	14.39	5.10	8.27	7.35	3.73	3.89	1.78	4.94	2.80	1.09	1.53	3.51
31	**Mean**	14.11	4.89	8.07	7.15	3.72	3.60	1.52	4.48	2.72	1.05	1.37	3.03
(*n* = 18)	**SD**	0.31	0.18	0.19	0.23	0.10	0.14	0.08	0.13	0.13	0.06	0.06	0.20
	CV	2.24	3.78	2.40	3.29	2.78	3.83	5.62	3.02	4.84	5.44	4.15	6.70
	Min	13.52	4.62	7.75	6.70	3.57	3.35	1.36	4.28	2.55	0.92	1.29	2.59
	Max	14.77	5.35	8.40	7.58	3.88	3.80	1.68	4.79	3.00	1.12	1.46	3.46
32	**Mean**	14.52	5.01	8.37	7.34	3.86	3.72	1.66	4.83	2.88	1.00	1.47	3.37
(*n* = 5)	**SD**	0.29	0.18	0.38	0.16	0.18	0.15	0.14	0.17	0.22	0.03	0.05	0.14
	CV	2.09	3.77	4.74	2.25	4.78	4.25	8.70	3.62	7.83	3.19	3.25	4.40
	Min	14.19	4.74	7.96	7.21	3.70	3.47	1.53	4.58	2.65	0.95	1.42	3.21
	Max	14.92	5.24	8.84	7.56	4.07	3.85	1.88	4.99	3.21	1.02	1.53	3.56

Table 6.11 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
33	**Mean**	14.74	5.08	8.24	7.40	3.83	3.70	1.56	4.68	2.85	1.04	1.46	3.13
(*n* = 5)	**SD**	0.46	0.10	0.27	0.19	0.22	0.06	0.06	0.05	0.08	0.04	0.04	0.09
	CV	3.29	2.15	3.49	2.74	5.95	1.57	4.27	1.14	2.97	4.45	2.99	2.99
	Min	14.26	4.96	7.89	7.28	3.61	3.63	1.49	4.63	2.75	0.98	1.42	2.99
	Max	15.25	5.17	8.58	7.74	4.14	3.76	1.63	4.73	2.95	1.09	1.53	3.19
34	**Mean**	13.43	4.82	7.86	6.96	3.70	3.37	1.46	4.28	2.54	1.05	1.35	2.85
(*n* = 15)	**SD**	0.25	0.09	0.27	0.13	0.12	0.13	0.13	0.10	0.13	0.08	0.06	0.21
	CV	1.87	1.96	3.43	1.87	3.20	3.83	9.16	2.40	5.28	7.94	4.61	7.58
	Min	12.88	4.56	7.50	6.68	3.51	3.15	1.19	4.12	2.29	0.88	1.25	2.29
	Max	13.87	4.94	8.46	7.10	3.91	3.59	1.63	4.43	2.77	1.21	1.45	3.09
35	**Mean**	14.53	5.12	8.32	7.29	3.79	3.76	1.68	4.77	2.80	1.02	1.48	3.42
(*n* = 14)	**SD**	0.36	0.11	0.24	0.13	0.09	0.20	0.09	0.23	0.10	0.06	0.07	0.15
	CV	2.53	2.10	2.90	1.78	2.45	5.36	5.13	4.80	3.61	5.65	4.98	4.32
	Min	13.87	4.92	7.92	7.06	3.65	3.37	1.53	4.53	2.70	0.88	1.39	3.16
	Max	15.15	5.28	8.69	7.52	4.01	4.09	1.83	5.19	2.97	1.12	1.63	3.67
36	**Mean**	14.27	4.89	7.81	7.19	3.79	3.54	1.48	4.51	2.63	1.09	1.43	3.063
(*n* = 4)	**SD**	0.19	0.08	0.09	0.17	0.07	0.04	0.15	0.05	0.05	0.07	0.06	0.15
	CV	1.44	1.70	1.27	2.43	1.95	1.22	11.01	1.20	1.97	6.79	4.30	5.18
	Min	14.12	4.80	7.71	6.95	3.69	3.48	1.36	4.43	2.60	1.02	1.36	2.89
	Max	14.54	4.99	7.93	7.33	3.84	3.57	1.70	4.53	2.70	1.19	1.49	3.19

Table 6.11 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
37	**Mean**	14.17	5.03	8.02	7.37	3.82	3.55	1.52	4.67	2.72	1.06	1.48	3.05
(*n* = 5)	**SD**	0.26	0.20	0.13	0.16	0.09	0.06	0.10	0.14	0.08	0.05	0.03	0.09
	CV	1.94	4.06	1.71	2.24	2.36	1.90	7.11	3.07	2.98	5.07	2.15	3.07
	Min	13.89	4.84	7.86	7.24	3.67	3.45	1.46	4.53	2.65	0.98	1.46	2.99
	Max	14.52	5.29	8.16	7.62	3.88	3.61	1.70	4.89	2.80	1.12	1.53	3.19
38	**Mean**	14.26	5.05	8.11	7.23	3.83	3.71	1.60	4.67	2.73	1.02	1.49	3.30
(*n* = 6)	**SD**	0.53	0.15	0.38	0.16	0.19	0.16	0.15	0.20	0.15	0.06	0.11	0.18
	CV	3.89	3.05	4.91	2.33	5.15	4.56	9.75	4.35	5.58	5.95	7.78	5.79
	Min	13.56	4.85	7.66	6.97	3.53	3.55	1.32	4.43	2.55	0.95	1.32	3.00
	Max	14.99	5.29	8.74	7.39	4.05	3.98	1.73	4.89	2.95	1.12	1.63	3.56
39	**Mean**	14.39	5.20	8.29	7.32	3.84	3.63	1.82	4.77	2.97	0.98	1.44	3.33
(*n* = 5)	**SD**	0.28	0.18	0.25	0.12	0.04	0.17	0.08	0.14	0.16	0.11	0.07	0.16
	CV	2.01	3.55	3.10	1.72	1.20	4.88	4.82	3.11	5.63	11.36	5.40	5.15
	Min	14.08	4.98	8.00	7.21	3.80	3.39	1.73	4.58	2.80	0.81	1.32	3.05
	Max	14.76	5.46	8.65	7.49	3.89	3.86	1.93	4.94	3.11	1.09	1.53	3.46
ANOVA	**SS**	83.275	8.558	18.654	15.864	4.092	4.087	2.297	8.525	3.058	0.860	1.030	8.561
	df	38	38	38	38	38	38	38	38	38	38	38	38
	F	22.765	10.521	7.240	13.693	6.191	4.963	5.488	8.935	4.958	3.282	5.017	9.438
	P	0.00E-16***	0.00E-16***	0.00E-16***	0.00E-16***	0.00E-16***	0.00E-16***	0.00E-16***	0.00E-16***	0.44E-16***	5.30E-16***	0.22E-16***	0.00E-16***

Table 6.12 Pearson correlation coefficients for correlation between latitude and longitude and the principal component scores and 39 OTUs within the 12 cranial measurements of *Neoromicia capensis* from southern Africa. ** denotes significance at $P < 0.01$; *** denotes significance at $P < 0.001$.

	PC1	PC2	CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Latitude														
Pearson Correlation	-0.604	-0.420	-0.595	-0.672	-0.481	-0.725	-0.756	-0.473	-0.128	-0.43	-0.381	-0.171	-0.684	-0.013
Significance (2-tailed)	4.75E-05***	0.008**	6.48E-06***	2.79E-06***	0.002**	1.49E-07***	1.27E-08***	0.002**	0.438	0.006**	0.017*	0.299	1.57E-06***	0.939
Longitude														
Pearson Correlation	-0.488	-0.187	-0.646	-0.524	-0.509	-0.497	-0.290	-0.409	-0.013	-0.408	-0.384	-0.038	-0.463	-0.133
Significance (2-tailed)	0.002**	0.255	8.86E-06***	0.001**	0.001**	0.001**	0.074	0.01*	0.939	0.01*	0.016*	0.818	0.003**	0.420

6.3.1.4 *Neoromicia* cf. *melckorum*

An initial PCA and DFA of 23 *N.* cf. *melckorum* specimens re-assigned one specimen (TM36778) to *N. zuluensis*, and this specimen was removed from further analyses of *N.* cf. *melckorum*. The remaining 22 specimens were allocated to five OTUs (Table 6.13). A PCA scatterplot of the first two principal components based on the 22 specimens of *N.* cf. *melckorum* (Fig. 6.11) showed no clear geographic pattern in the distribution of the specimens. The first principal component axis described 29.98% of the variation and the eigenvector loadings were, with the exception of one negative value, all positive. The largest and smallest loadings on the first principal component axis were zygomatic breadth and width of the upper fourth premolar. The second principal component axis described 17.80% of the variance, and the largest and smallest of the mixed sign eigenvector scores were length of the upper first molar and post-orbital width (Table 6.14). The distance phenogram based on 22 specimens of *N.* cf. *melckorum* also revealed no geographic structure within the clusters (Fig. 6.12).

Table 6.15 lists the basic statistics and the results of the one-way ANOVAs between OTUs for each measurement and shows that one measurement, width across the outer surfaces of the upper canines, was significantly different among OTUs. A post-hoc Tukey test identified two significantly different subsets separating the Zimbabwe locality from the South African localities (Appendix 6.2C). Three measurements, width across the outer surfaces of the upper canine, width between the inner surfaces of the upper first molar and length of the upper first molar, were significantly positively correlated with latitude and negatively correlated with longitude (Table 6.16). All three measurements show a considerable size difference between the South African and the Zimbabwe specimens, with the Zimbabwe specimens being larger. However, neither the first nor the second principal component scores were significantly correlated with either latitude or longitude. Hence while some of the12 cranial measurements showed significant clinal latitudinal and longitudinal variation, overall variation of the 12 skull measurements of *N.* cf. *melckorum* from the limited number of localities was not significantly correlated with latitudinal and, or longitudinal clinal variation.

6.3.1.5 *Neoromicia africanus*

Initial PCA, UPGMA and DFA of 105 specimens allocated to five manageable groups based on geographic proximity, identified 16 outliers, 14 of which were removed from further analyses (TM34973, NMBZ64001, NMBZ29607, TM39467, TM41621, TM39643, TM39642, TM39621, TM38317, DM4555, NMBZ64007, TM39826, TM39817, TM39199), and two were re-assigned to *P. rusticus* (BM1906.8.2.37, BM1906. 8.2.34). The remaining 89 specimens were separated into 11 OTUs (Table 6.17). The type specimen (TM1076) of *N. a. meesteri* (Kock, 2001c), proposed as a replacement of the preoccupied name of *australis* (Roberts, 1913), was included in OTU 11 with other specimens collected at the same time as TM1076 from Port St Johns in the Eastern Cape Province of South Africa. A scatterplot of the first two principal components and a UPGMA distance phenogram (Fig. 6.13) show the relationship between the type specimen of *N. a. meesteri* from Port St Johns and other specimens of *N. africanus* from the same locality and other coastal localities north of Port St Johns, including a specimen from Malvern [although not the specimen compared by Roberts (1913)]. These analyses, which included specimens of known species identity based on baculum morphology and/or chromosome diploid number, showed no obvious difference between the type specimen and other specimens from the same locality or specimens from localities further north.

A PCA scatterplot of the first two principal components based on 11 OTUs of *N. africanus* (Fig.6.14), identified OTU 3 (specimens from the most westerly locality of Sentinel Ranch in Zimbabwe) as an outlier among the smaller individuals on the first principal component axis. Among the other OTUs there was some geographic pattern in their distribution, given the tendency for OTU scores to increase along the second principal component axis with increasing latitude. The first principal component axis explained 35.04% of the variation, and unusually for the first principal component axis the eigenvector scores were both negative and positive. The most positive and negative scores on the first principal component axis were, width across the outer surfaces of the upper canines and braincase breadth. The second principal component axis explained 20.63% of the variance and the largest and smallest of the mixed sign eigenvector scores were, greatest width of the foramen magnum and length of the upper first molar (Table 6.18). The distance phenogram based on 11 OTUs of *N. africanus* also identified OTU 3 (specimens from Sentinel Ranch in Zimbabwe) as an outlier, although among the remaining OTUs, there was little geographically discernible pattern (Fig. 6.15). Besides the outlier of OTU 3,

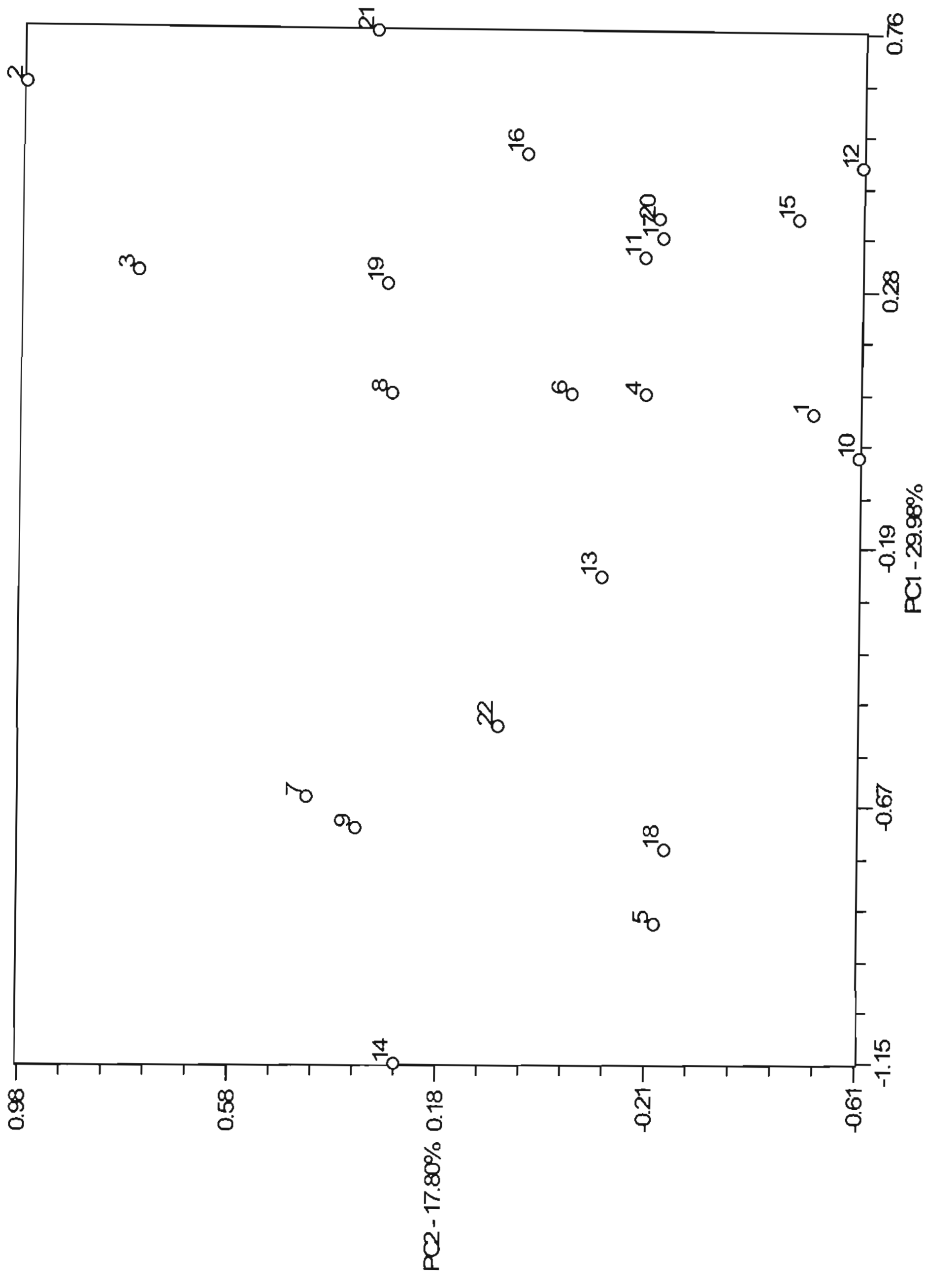


Figure 6.11 Scatterplot of the first two principal component axes based on 22 specimens of *Neoromicia* cf. *melckorum* in southern Africa. Individual numbers correspond to those in Table 6.13.

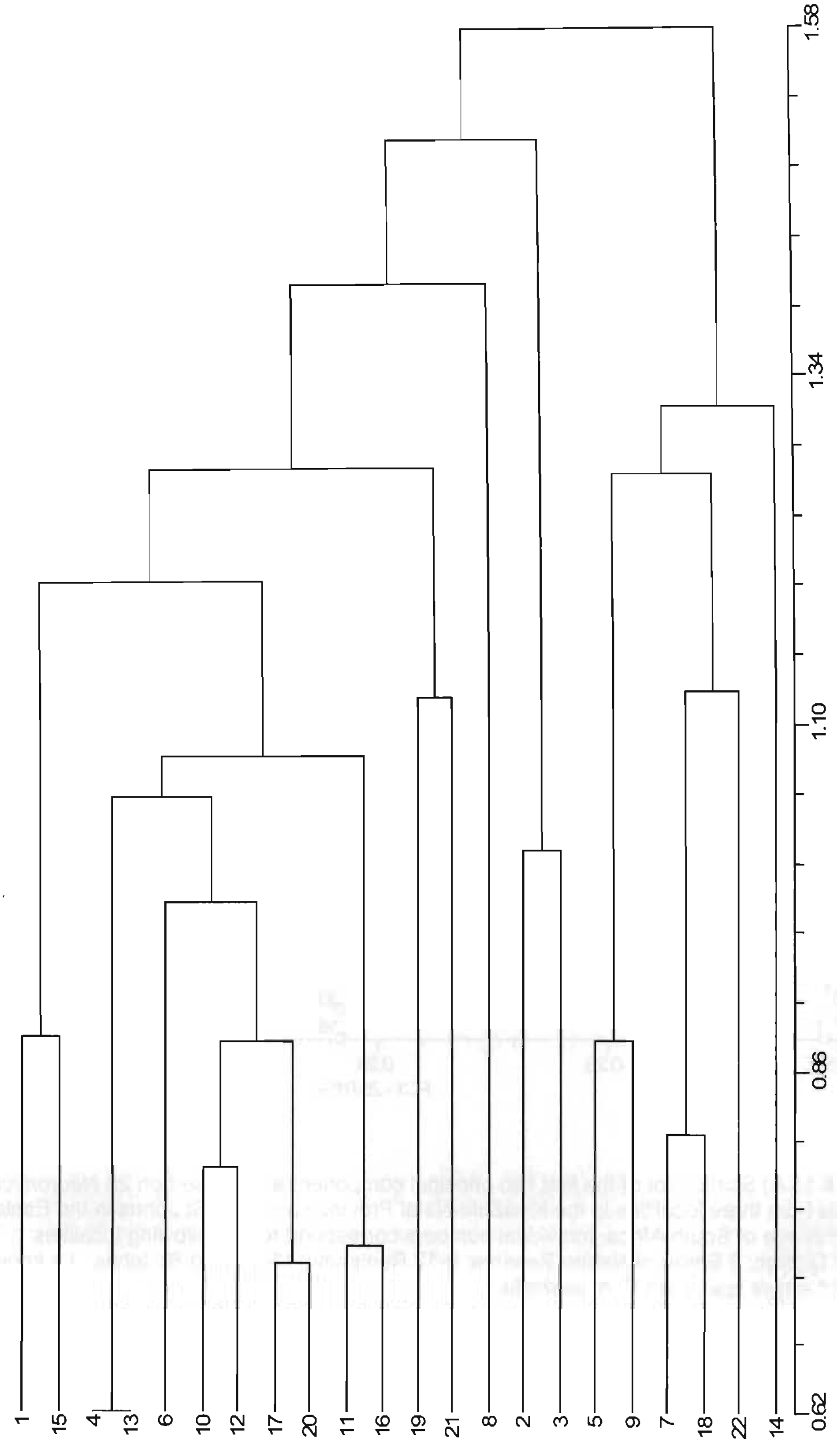


Figure 6.12 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on 22 *Neoromicia* cf. *melckorum* from southern Africa. Individual numbers correspond to those in Table 6.13. Cophenetic correlation coefficient = 0.717.

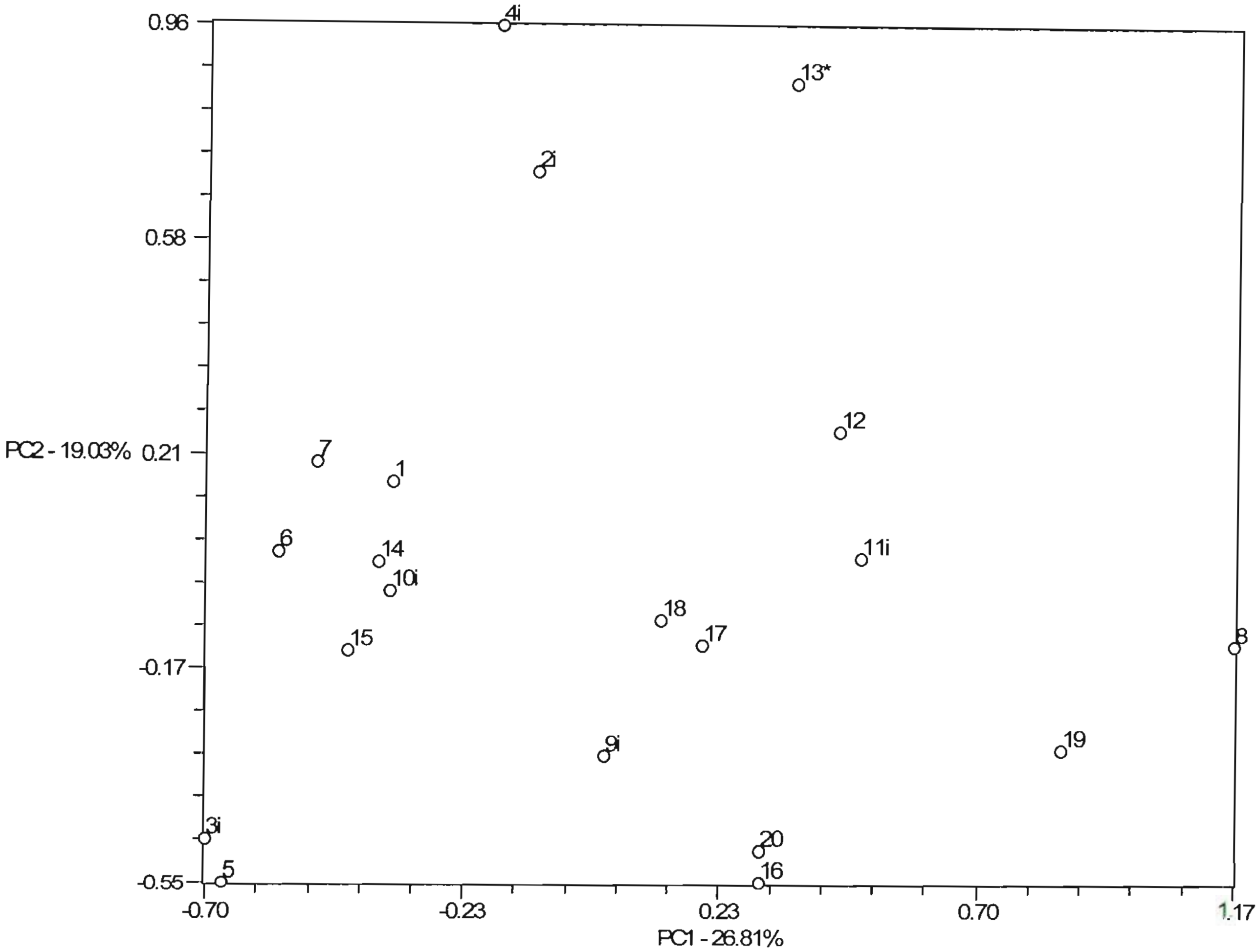


Figure 6.13 A) Scatterplot of the first two principal component axes based on 20 *Neoromicia africanus* from three localities in the KwaZulu-Natal Province and Port St Johns in the Eastern Cape Province of South Africa. Individual numbers correspond to the following localities: 1-7 Greater Durban; 8 Empisini Nature Reserve; 9-12 Renishaw; 13-20 Port St Johns. i = known identity; * = type specimen *P. n. australis.*

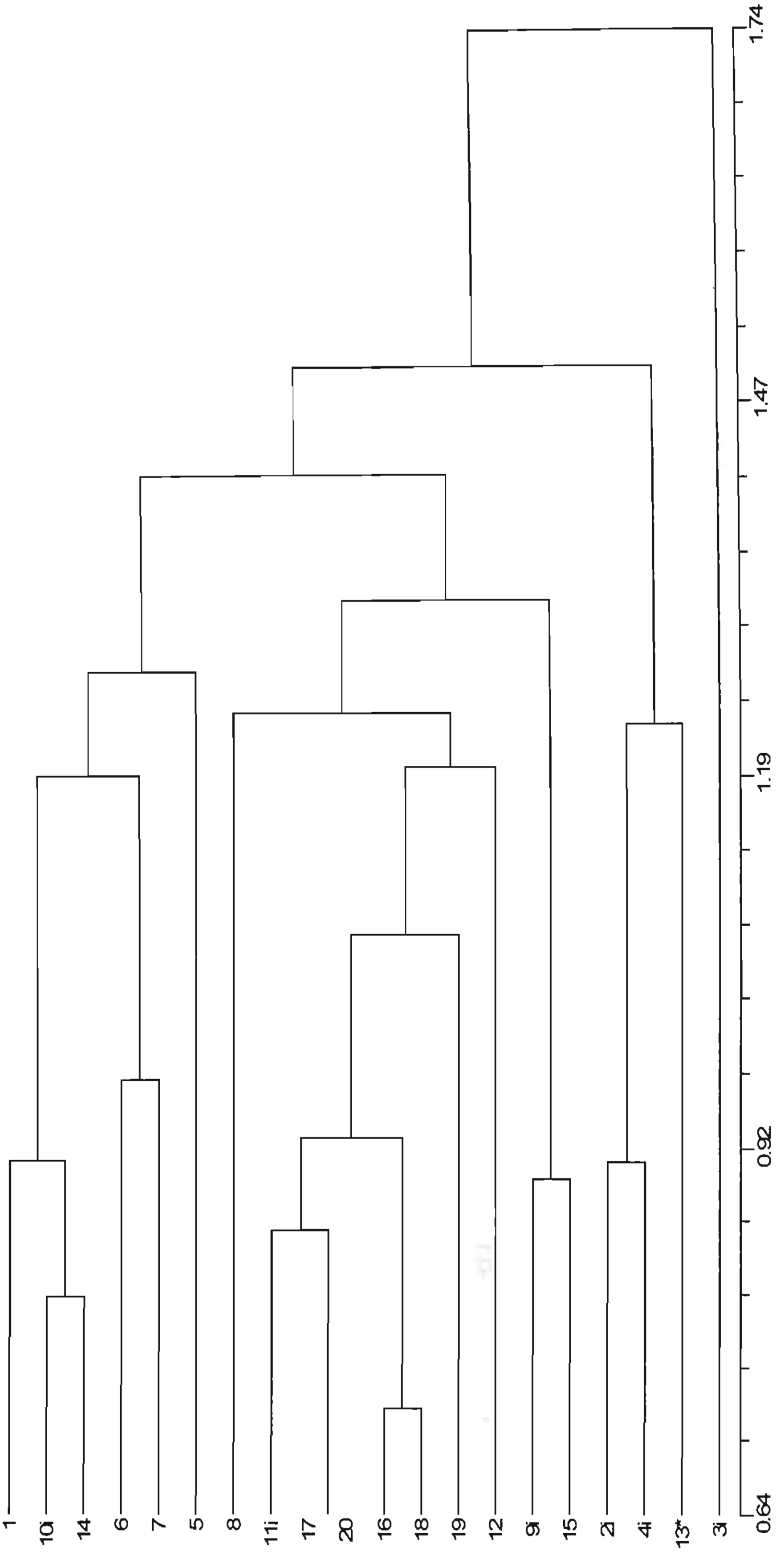


Figure 6.13 B) Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on 20 *Neoromicia africanus* from three localities in the KwaZulu-Natal Province and Port St Johns in the Eastern Cape Province of South Africa. Cophenetic correlation coefficient = 0.665. Individual numbers correspond to the following localities: 1-7 Greater Durban; 8 Empisini Nature Reserve; 9-12 Renishaw; 13-20 Port St Johns. i = known identity; * = type specimen *P. n. australis*.

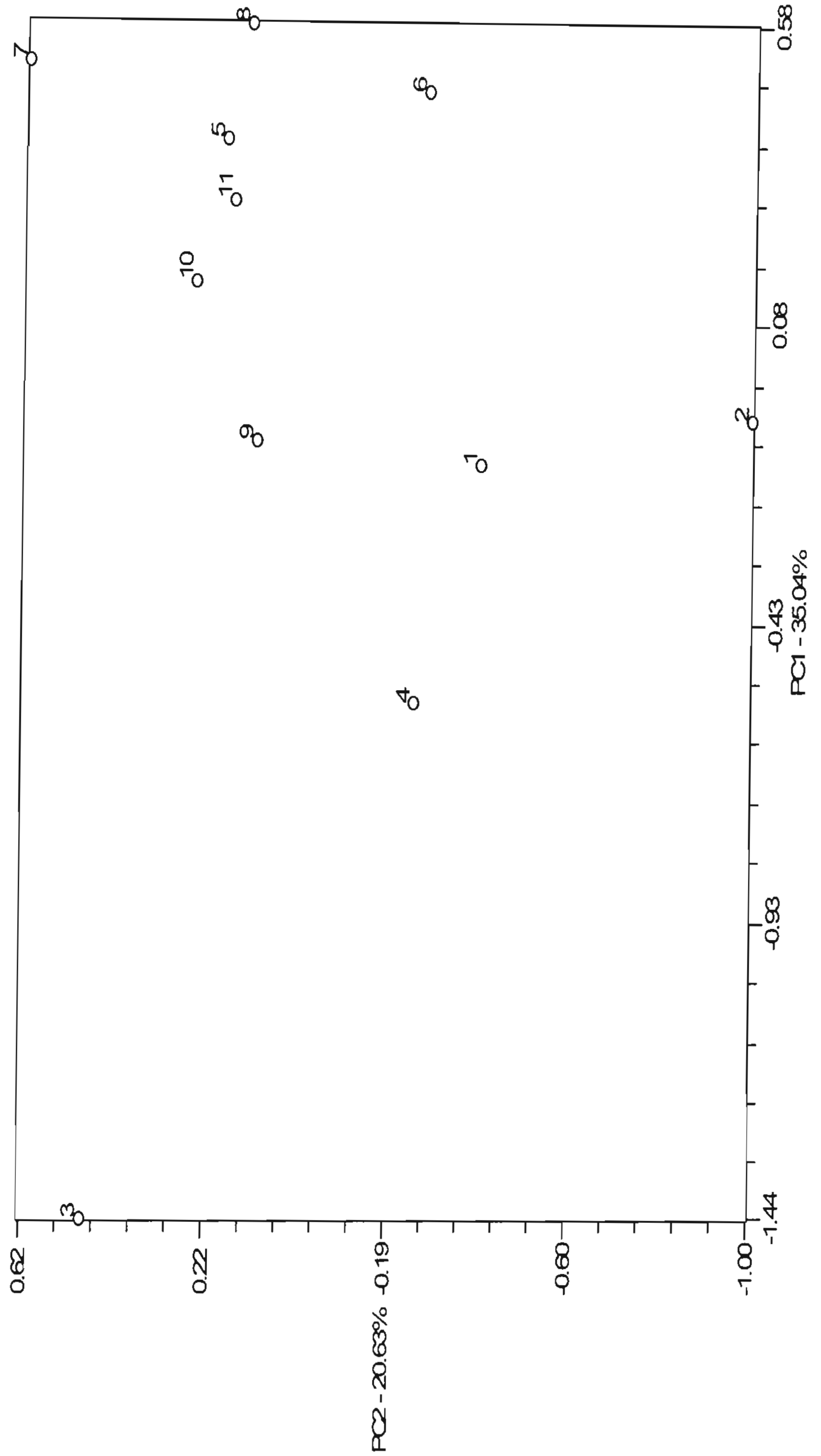


Figure 6.14 Scatterplot of the first two principal component axes based on 11 OTUs of *Neoromicia africanus* from southern Africa. OTU numbers correspond to those in Table 6.17.

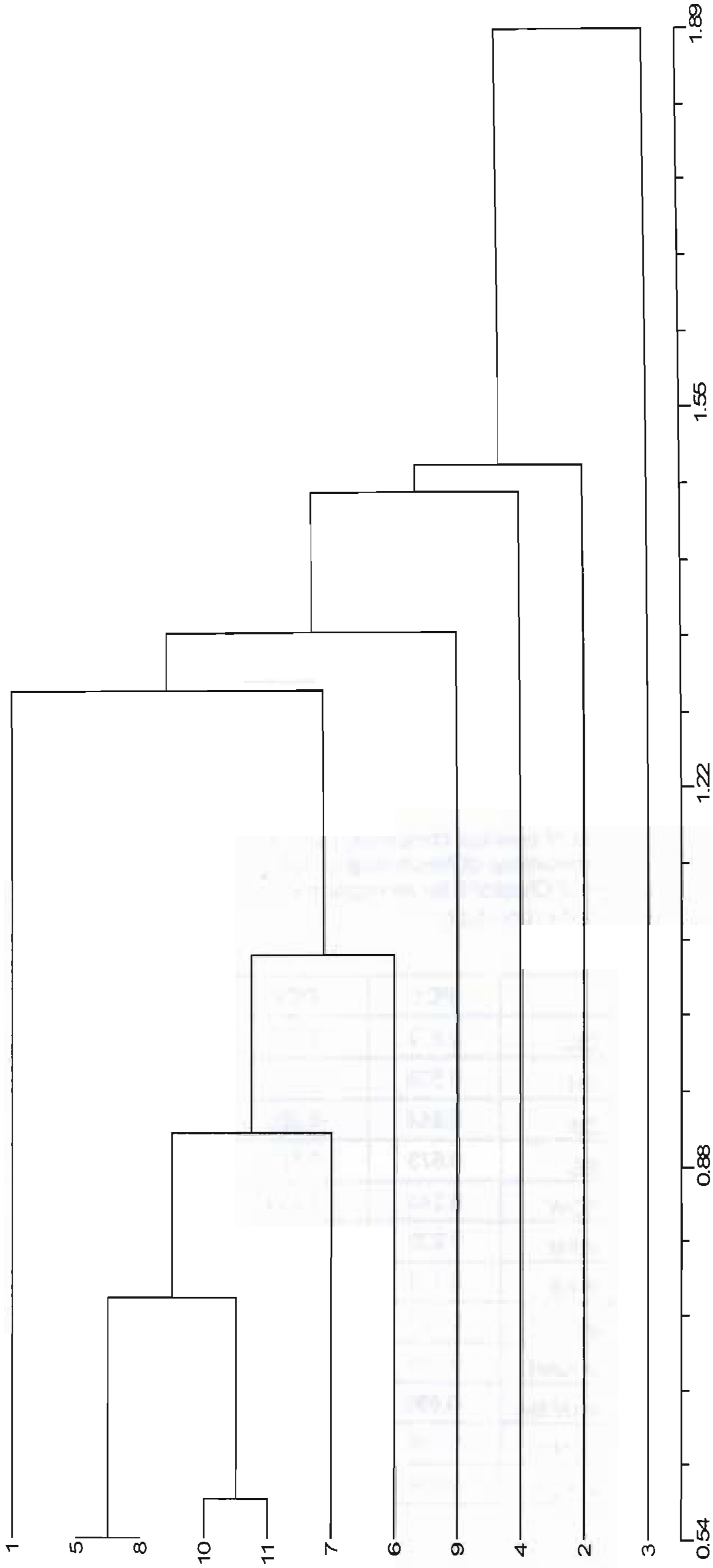


Figure 6.15 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on 11 OTUs of *Neoromicia africanus* from southern Africa. OTU numbers correspond to those in Table 6.17. Cophenetic correlation coefficient = 0.917.

Table 6.13 Five OTUs of single and pooled localities for *Neoromicia* cf. *melckorum* from southern Africa arranged in relation to occurrence from north to south, and east to west, with associated numbering of individuals in each OTU (IC), and number of specimens included in each OTU (*n*). For details on the localities and specimens used see Appendix 6.1.

OTU	IC	Locality	n
1	1-3	Zimbabwe: Mana Pools	3
2	4-7	South Africa: Limpopo Province; Pafuri; Anthrax Camp and Mauxeba Windmill	4
3	8-11	South Africa: Limpopo Province; Pafuri; Culling Camp and Fig Tree Forest, left bank	4
4	12-18	South Africa: Limpopo Province; Pafuri; Fig Tree Forest, New Fig Tree Forest, Old Picnic Site, and the Mockford's Garden	7
5	19-22	South Africa: Limpopo Province; Pafuri; Levuvhu Hippo Pool	4

Table 6.14 Eigenvector scores of principal components one and two of a PCA based on 12 cranial measurements of 22 specimens of *Neoromicia* cf. *melckorum* from southern Africa. See material and methods section of Chapter 5 for an explanation of the measurement codes. Highest and lowest scores are indicated in bold type.

	PC1	PC2
CIL	0.672	0.065
BH	0.538	-0.371
ZB	**0.814**	-0.205
BB	0.673	-0.563
POW	0.243	**-0.514**
WFM	0.203	-0.143
WAS	0.724	-0.097
WOUC	0.628	0.466
WIUM1	0.585	0.587
WUPM4	**-0.096**	0.135
LUM1	0.056	**0.757**
MAOT	0.604	0.433

Table 6.15 Basic statistics and ANOVA results to test for variation in five OTUs of N. cf. *melckorum* in southern Africa. SD = standard deviation; CV = coefficient of variation; Min = minimum value; Max = maximum value; *n* = sample size; SS = sum of squares; df = degrees of freedom; *P* = significance of *F* values; *** denotes significance at *P* < 0.001. See Table 6.14 for a description of the OTU codes, and materials and methods of Chapter 5 for an explanation of the measurement codes.

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
1	Mean	14.77	4.94	8.58	7.24	3.80	3.80	1.73	5.04	2.85	1.11	1.50	3.44
(*n* = 3)	SD	0.21	0.21	0.25	0.10	0.18	0.11	0.10	0.09	0.18	0.02	0.10	0.21
	CV	1.54	4.69	3.12	1.56	5.13	3.21	6.37	1.90	6.70	1.92	7.47	6.67
	Min	14.53	4.75	8.35	7.16	3.62	3.67	1.63	4.94	2.65	1.09	1.39	3.21
	Max	14.93	5.17	8.84	7.36	3.98	3.87	1.83	5.09	2.95	1.12	1.59	3.61
2	Mean	14.4	4.82	8.37	7.26	3.74	3.75	1.68	4.75	2.70	1.07	1.43	3.44
(*n* = 4)	SD	0.24	0.08	0.35	0.19	0.21	0.18	0.07	0.06	0.08	0.09	0.03	0.16
	CV	1.76	1.75	4.48	2.76	5.88	5.21	4.55	1.43	3.27	8.92	2.41	4.89
	Min	14.23	4.73	7.98	7.04	3.54	3.55	1.63	4.68	2.60	0.95	1.39	3.21
	Max	14.76	4.92	8.76	7.43	3.99	3.99	1.78	4.84	2.80	1.15	1.46	3.56
3	Mean	14.64	4.81	8.50	7.31	3.62	3.86	1.77	4.72	2.67	1.07	1.42	3.50
(*n* = 4)	SD	0.24	0.27	0.32	0.19	0.16	0.14	0.10	0.06	0.07	0.03	0.06	0.09
	CV	1.73	6.00	4.00	2.76	4.56	3.73	5.79	1.44	2.61	3.37	4.62	2.64
	Min	14.45	4.43	8.03	7.03	3.46	3.70	1.63	4.63	2.60	1.02	1.36	3.41
	Max	14.95	5.06	8.71	7.45	3.80	4.03	1.83	4.79	2.75	1.09	1.49	3.61
4	Mean	14.58	4.85	8.58	7.38	3.77	3.75	1.77	4.69	2.68	1.09	1.43	3.44
(*n* = 7)	SD	0.31	0.18	0.28	0.25	0.16	0.16	0.11	0.12	0.12	0.07	0.05	0.12
	CV	2.20	3.80	3.32	3.52	4.26	4.53	6.14	2.63	4.50	6.34	3.38	3.63
	Min	14.25	4.48	8.09	6.93	3.61	3.48	1.63	4.48	2.49	1.02	1.39	3.26
	Max	15.00	4.99	8.81	7.68	4.04	3.94	1.88	4.79	2.85	1.19	1.53	3.56

Table 6.15 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
5	**Mean**	14.87	4.98	8.40	7.26	3.70	3.85	1.78	4.81	2.75	1.11	1.42	3.63
(*n* = 4)	**SD**	0.25	0.16	0.21	0.26	0.13	0.16	0.04	0.05	0.07	0.07	0.07	0.21
	CV	1.80	3.44	2.59	3.84	3.58	4.36	2.48	1.12	2.78	6.69	5.47	6.13
	Min	14.59	4.82	8.14	6.90	3.57	3.69	1.73	4.73	2.65	1.02	1.32	3.36
	Max	15.09	5.20	8.57	7.51	3.83	4.06	1.83	4.84	2.80	1.19	1.49	3.87
ANOVA	**SS**	0.462	0.090	0.165	0.074	0.079	0.049	0.028	0.280	0.075	0.007	0.014	0.110
	df	4	4	4	4	4	4	4	4	4	4	4	4
	F	1.641	0.636	0.506	0.381	0.735	0.503	0.889	8.930	1.650	0.401	0.943	1.153
	P	0.210	0.644	0.732	0.819	0.581	0.734	0.492	4.49E-04***	0.208	0.805	0.463	0.366

Table 6.16 Pearson correlation coefficients for correlation between latitude and longitude and principal component scores and five OTUs within the 12 cranial measurements of *Neoromicia* cf. *melckorum* from southern Africa. ** denotes significance at $P < 0.01$; *** denotes significance at $P < 0.001$.

	PC1	PC2	CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Latitude														
Pearson Correlation	0.774	-0.514	0.351	0.433	0.540	-0.452	0.606	-0.018	-0.203	0.948	0.916	0.480	0.991	-0.311
Significance (2-tailed)	0.124	0.376	0.562	0.467	0.348	0.445	0.278	0.977	0.743	0.014*	0.029*	0.414	0.001**	0.610
Longitude														
Pearson Correlation	-0.793	0.493	-0.372	-0.461	-0.496	0.499	-0.595	-0.002	0.212	-0.964	-0.932	-0.490	-0.986	0.274
Significance (2-tailed)	0.109	0.399	0.537	0.434	0.396	0.392	0.290	0.997	0.732	0.008**	0.021*	0.402	0.002**	0.655

Table 6.17 Eleven OTUs of single and pooled localities for *Neoromicia africanus* in southern Africa arranged in relation to occurrence from north to south, and east to west, with number of specimens included in each OTU (n). For details on the localities and specimens used see Appendix 6.1

OTU	Locality	*n*
1	Mozambique: Nabaunama River and Mount Gorongoza	5
2	Zimbabwe: Rusito Forest, Chirinda Forest, and Mount Silinda	4
3	Zimbabwe: Sentinal Ranch	9
4	South Africa: Limpopo Province; Pafuri	28
5	South Africa: Mpumalanga Province; Kruger National Park and Legogot	8
6	Swaziland: near Simunye; SA: KwaZulu-Natal Province; Jozini Dam Wall and Ithala Game Reserve	4
7	South Africa: KwaZulu-Natal Province; Ngome Forest Reserve, Hluhluwe Game Reserve	7
8	South Africa: KwaZulu-Natal Province; Vuma Farm	4
9	South Africa: KwaZulu-Natal Province; Malvern and Stainbank Nature Reserve	4
10	South Africa: KwaZulu-Natal Province; Umkomaas, Empisini Nature Reserve, and Renishaw	8
11	South Africa: Eastern Cape Province; Port St Johns	8

Table 6.18 Eigenvector scores of principal components one and two of a PCA based on 12 cranial measurements (Meas) of 11 OTUs of *N. africanus* from southern Africa. See material and methods section of Chapter 5 for an explanation of the measurement codes. Highest and lowest scores are indicated in bold type.

Meas	PC1	PC2
CIL	0.766	0.180
BH	0.792	0.193
ZB	0.612	0.663
BB	**-0.581**	0.537
POW	-0.048	0.378
WFM	-0.116	**0.717**
WAS	0.279	-0.374
WOUC	**0.908**	0.279
WIUM1	0.841	-0.111
WUPM4	-0.157	0.456
LUM1	0.215	**-0.751**
MAOT	0.762	-0.139

neither the PCA scatterplot nor the distance phenogram identified any distinction between OTUs 11 (Port St Johns), 9 and 10 (localities north of Port St Johns that were included in the PCA and UPGMA analyses in Figure 6.13) and the other OTUs of *N. africanus* analysed. This supports *N. a. meesteri* as a synonym of the nominate subspecies *N. a. africanus* on the basis of the 12 cranial measurements used in this analysis.

Table 6.19 reports the basic statistics and the results of the one-way ANOVAs between OTUs for each measurement, which showed eight of the 12 measurements were significantly different between the different OTUs. Post-hoc Tukey tests identified different significantly different subsets for each of the measurements (Appendix 6.2 D), which also showed little geographically discernible pattern, other than in width across the outer surfaces of the upper canines and braincase height. These measurements showed some indication of size increase in OTUs from north to south. Not surprisingly, width across the outer surfaces of the upper canines (the measurement that loaded highest on the first principal axis) was also the most significantly different measurement between the different OTUs and was smallest in the OTU from Sentinel Ranch in Zimbabwe.

Although many of the measurements were significantly different among OTUs, significantly negative correlations between OTUs and latitude (i.e. increased size from OTUs in the north to OTUs in the south) were only observed in three measurements: braincase height, zygomatic breadth and width across the outer surfaces of the upper canines (Table 6.20). Significantly negative and positive correlations between longitude and the significantly different OTUs were identified in two measurements which also loaded highest on the second principal component axis, greatest width of the foramen magnum (increased in size from east to west) and length of the upper first molar (decreased in size from east to west). There was no significant correlation between scores of the first or the second principal component axes and either latitude or longitude. Although *N. africanus* in southern Africa showed considerable geographic variation in the 12 cranial measurements, only a few measurements showed that this variation was clinal in relation to latitude and longitude. There was no significant overall clinal variation in the 12 cranial measurements of *N. africanus* in relation to latitude or longitude. Unfortunately, this analysis did not include any specimens from north-western Namibia to be able to test the geographic variation relative to the described subspecies from north-western Namibia *N. a. fouriei* and *N. a. meesteri* from Port St Johns in the Eastern Cape Province of South Africa.

6.3.1.6 *Neoromicia rendalli*

Neoromicia rendalli is another species known only from a few localities within the subregion and poorly represented in museum collections. The specimens examined were too few to allow more than a cursory assessment of individual differences. Only five specimens from two localities with the Zimbabwe locality were represented by a single specimen (Table 6.21). A PCA scatterplot of the first two principal components (Fig. 6.16) showed considerable separation between the individuals, with the specimen from Zimbabwe being smallest on the first principal component axis. The first principal component axis accounted for 67.53% of the variance and of the all positive eigenvector scores, those with the highest scores were width across the outer surfaces of the upper canines and length between the condylar and the coronoid processes of the mandible (Table 6.22). The second principal component axis showed variation in the sign of the eigenvector scores of which, the highest and lowest were width of the upper fourth premolar and greatest width of the articular surface (Table 6.22). A scatterplot of the second and third principal component axes (Fig. 6.17), was different to the plot of the first and second principal component in that, a male of tooth wear class A from Bonamanzi in KwaZulu-Natal was separated from all other individuals on the third principal component axis, while the separation between the Zimbabwean and South African specimens from KwaZulu Natal was no longer distinct. The third principal component axis explained 11.70% of the variation and the measurements with the highest and lowest eigenvector scores were length of the upper first molar and width of the upper fourth premolar (Table 6.22).

The clustering pattern of the distance phenogram based on the five individuals (Fig. 6.18) was not in relation to geographic locality, sex, or tooth wear class. Values for each measurement of the Zimbabwe specimen relative to the mean for the South African specimens of *N. rendalli* were smaller in all but one measurement, in which the values were the same between the two localities (Table 6.23). Only further analyses with more specimens from additional localities will clarify whether this is a reflection of clinal longitudinal variation in size between the localities, possibly associated with change in altitude, in which specimens from south-easterly localities are

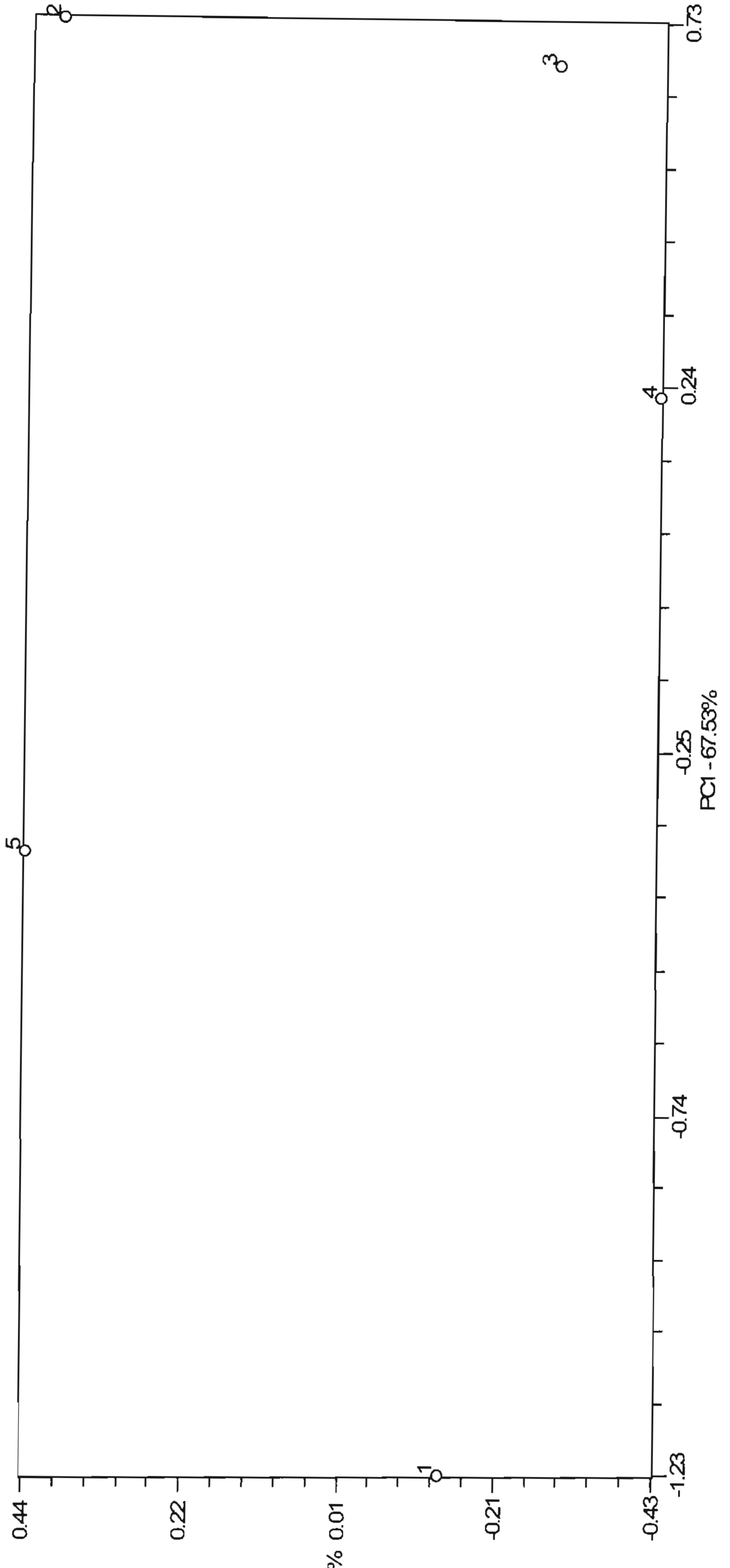


Figure 6.16 Scatterplot of the first two principal component axes based on five specimens of *Neoromicia rendalli* from southern Africa. Individual numbers correspond to those in Table 6.21.

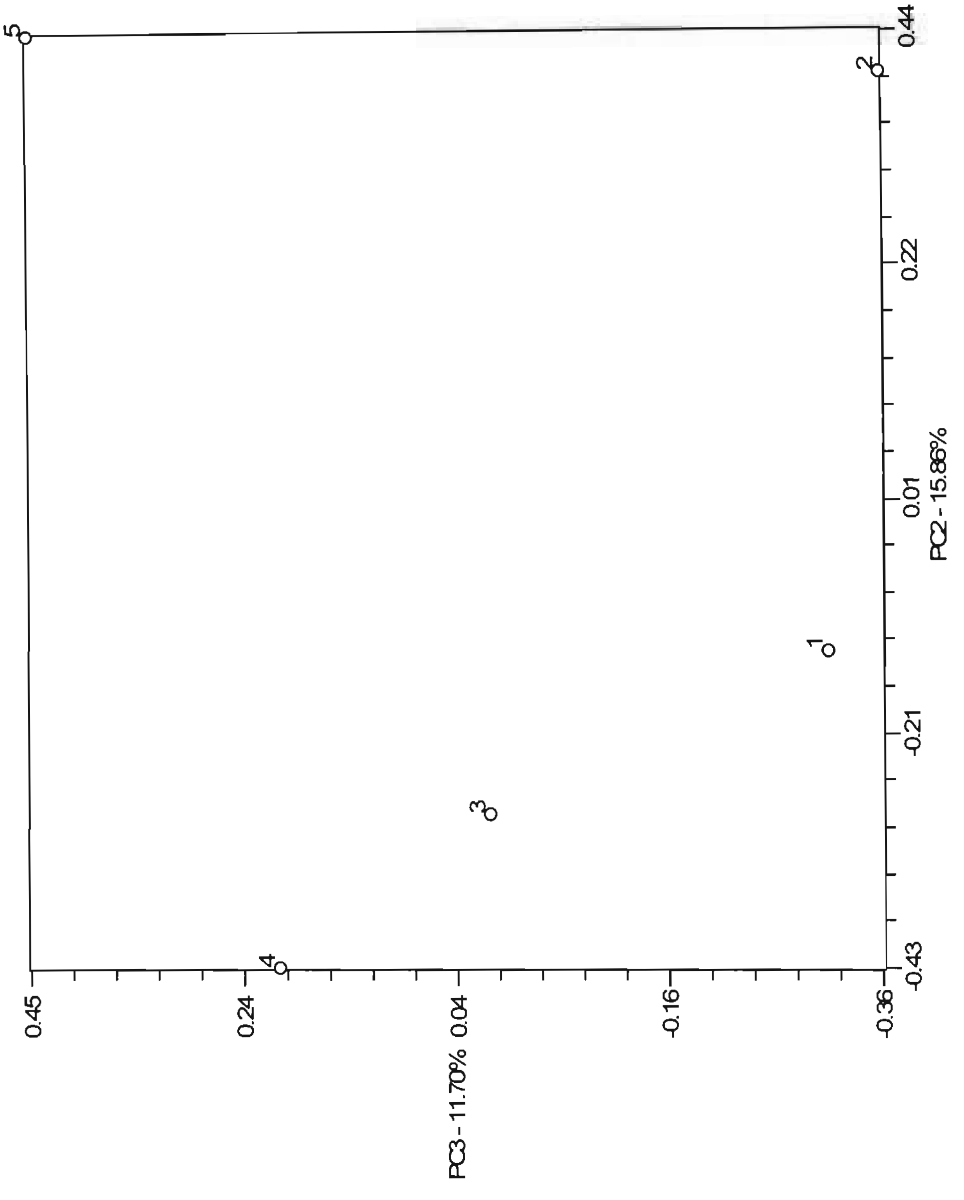


Figure 6.17 Scatterplot of the second and third principal component axes based on five specimens of *Neoromicia rendalli* from southern Africa. Individual numbers correspond to those in Table 6.21.

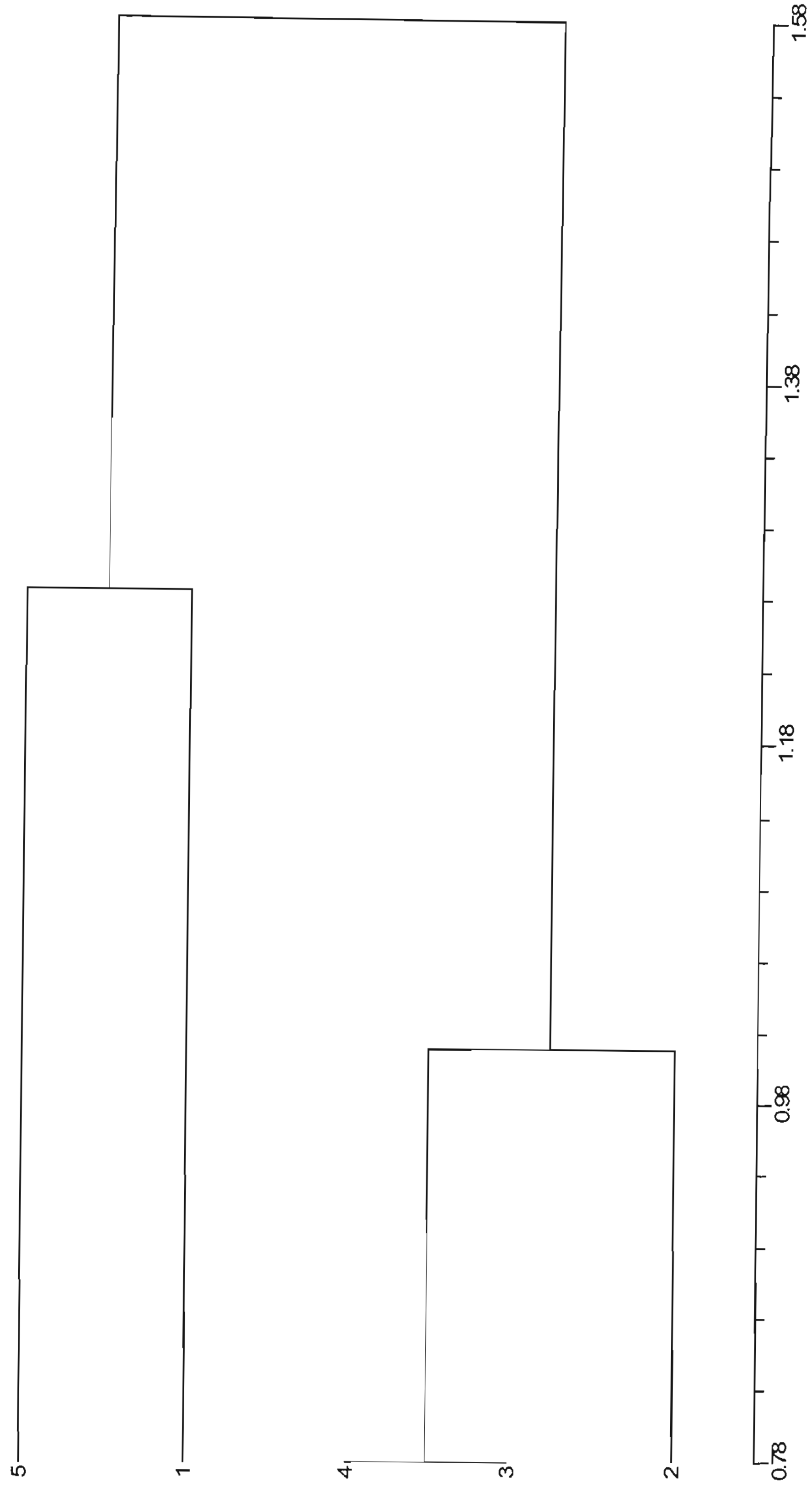


Figure 6.18 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on five specimens of *Neoromicia rendalli* from southern Africa. Individual numbers correspond to those in Table 6.21. Cophenetic correlation coefficient = 0.757.

Table 6.19 Basic statistics and ANOVA results to test for variation in 11 OTUs of *Neoromicia africanus* in southern Africa. SD = standard deviation; CV = coefficient of variation; Min = minimum value; Max = maximum value; *n* = sample size; SS = sum of squares; df = degrees of freedom; *P* = significance of *F* values; * denotes significance at $P < 0.05$; *** denotes significance at $P < 0.001$. See Table 6.18 for a description of the OTU codes, and materials and methods section of Chapter 5 for an explanation of the measurement codes.

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
1	**Mean**	11.19	4.39	6.41	6.10	3.43	3.03	1.19	3.41	2.45	0.84	1.10	2.35
(*n* = 5)	**SD**	0.16	0.07	0.22	0.10	0.05	0.11	0.13	0.09	0.12	0.09	0.05	0.07
	CV	1.47	1.64	3.57	1.78	1.66	3.68	11.25	2.77	5.18	11.17	4.72	2.90
	Min	11.01	4.33	6.23	5.92	3.34	2.91	1.04	3.29	2.28	0.68	1.04	2.28
	Max	11.37	4.47	6.78	6.17	3.47	3.14	1.37	3.51	2.60	0.90	1.14	2.46
2	**Mean**	10.95	4.35	6.27	5.89	3.35	3.11	1.16	3.53	2.41	0.72	1.12	2.44
(*n* = 4)	**SD**	0.22	0.08	0.11	0.11	0.08	0.08	0.05	0.11	0.05	0.03	0.03	0.08
	CV	2.16	2.06	1.79	1.94	2.49	2.78	4.47	3.16	2.15	4.78	2.63	3.62
	Min	10.71	4.28	6.19	5.80	3.27	3.05	1.12	3.41	2.34	0.68	1.09	2.34
	Max	11.24	4.47	6.42	6.04	3.42	3.23	1.22	3.67	2.44	0.75	1.15	2.55
3	**Mean**	10.90	4.21	6.39	6.22	3.43	3.20	1.11	3.30	2.22	0.81	1.03	2.25
(*n* = 9)	**SD**	0.17	0.13	0.19	0.07	0.06	0.08	0.08	0.14	0.08	0.06	0.04	0.09
	CV	0.04	0.08	0.08	0.03	0.04	0.07	0.20	0.11	0.10	0.21	0.10	0.12
	Min	10.64	4.00	6.17	6.14	3.35	3.12	1.02	3.16	2.09	0.68	0.98	2.09
	Max	11.09	4.43	6.87	6.32	3.54	3.34	1.27	3.61	2.34	0.85	1.09	2.39
4	**Mean**	11.01	4.17	6.39	6.17	3.43	3.16	1.22	3.43	2.33	0.70	1.05	2.44
(*n* = 28)	**SD**	0.23	0.17	0.22	0.15	0.12	0.14	0.10	0.15	0.08	0.09	0.06	0.09
	CV	2.12	4.07	3.50	2.37	3.47	4.35	8.59	4.43	3.39	12.98	5.22	3.71
	Min	10.46	3.82	5.85	5.88	3.22	2.90	1.02	2.90	2.19	0.54	0.92	2.29
	Max	11.43	4.63	6.81	6.44	3.68	3.39	1.43	3.72	2.49	0.88	1.15	2.65

Table 6.19 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
5	**Mean**	11.44	4.37	6.57	6.05	3.45	3.14	1.16	3.64	2.42	0.75	1.07	2.45
(*n* = 8)	**SD**	0.31	0.18	0.20	0.09	0.06	0.06	0.05	0.17	0.17	0.10	0.06	0.13
	CV	2.78	4.30	3.10	1.44	1.65	2.01	4.54	4.82	7.20	12.98	5.85	5.55
	Min	10.97	4.16	6.31	5.92	3.36	3.03	1.07	3.36	2.14	0.64	0.98	2.19
	Max	11.93	4.66	6.87	6.19	3.52	3.22	1.22	3.82	2.66	0.93	1.14	2.65
6	**Mean**	11.35	4.48	6.54	5.97	3.39	3.08	1.21	3.65	2.38	0.68	1.05	2.41
(*n* = 4)	**SD**	0.17	0.06	0.18	0.12	0.08	0.09	0.13	0.06	0.06	0.03	0.03	0.08
	CV	1.54	1.35	2.99	2.05	2.39	2.97	11.18	1.86	2.86	4.34	2.80	3.37
	Min	11.14	4.44	6.37	5.84	3.31	2.97	1.07	3.56	2.29	0.64	1.02	2.34
	Max	11.54	4.56	6.79	6.10	3.46	3.18	1.37	3.72	2.44	0.71	1.09	2.49
7	**Mean**	11.21	4.50	6.55	6.13	3.45	3.24	1.18	3.78	2.48	0.79	1.05	2.47
(*n* = 7)	**SD**	0.09	0.13	0.08	0.15	0.08	0.10	0.06	0.08	0.05	0.10	0.01	0.06
	CV	0.82	3.04	1.20	2.45	2.46	3.29	5.44	2.24	2.02	12.98	1.27	2.42
	Min	11.05	4.31	6.44	5.88	3.33	3.11	1.12	3.67	2.39	0.68	1.02	2.39
	Max	11.33	4.74	6.64	6.29	3.57	3.37	1.27	3.87	2.55	0.92	1.05	2.55
8	**Mean**	11.33	4.51	6.56	6.00	3.42	3.12	1.16	3.69	2.44	0.75	1.05	2.46
(*n* = 4)	**SD**	0.10	0.01	0.20	0.12	0.11	0.15	0.05	0.03	-	0.05	-	0.08
	CV	0.95	0.30	3.24	2.10	3.38	5.00	4.47	0.85	-	6.83	-	3.30
	Min	11.22	4.49	6.31	5.88	3.34	2.98	1.12	3.67	2.44	0.68	1.05	2.39
	Max	11.46	4.52	6.80	6.15	3.57	3.32	1.22	3.72	2.44	0.78	1.05	2.55

Table 6.19 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
9	**Mean**	10.92	4.52	6.56	5.99	3.32	3.143	1.18	3.61	2.32	0.75	1.02	2.32
(*n* = 4)	**SD**	0.13	0.12	0.20	0.15	0.10	0.066	0.15	0.07	0.07	0.06	0.03	0.09
	CV	1.23	2.88	3.19	2.68	3.23	2.232	13.65	2.12	3.02	7.89	2.89	4.05
	Min	10.79	4.43	6.29	5.79	3.18	3.070	0.97	3.56	2.24	0.68	0.98	2.19
	Max	11.07	4.69	6.73	6.12	3.41	3.220	1.32	3.72	2.39	0.81	1.05	2.39
10	**Mean**	11.15	4.46	6.52	6.01	3.41	3.155	1.15	3.61	2.41	0.85	1.06	2.42
(*n* = 8)	**SD**	0.22	0.11	0.17	0.15	0.06	0.089	0.09	0.20	0.07	0.10	0.03	0.10
	CV	2.02	2.56	2.71	2.59	1.88	2.897	7.98	5.67	3.18	11.90	2.53	4.30
	Min	10.85	4.29	6.29	5.74	3.31	2.990	0.97	3.39	2.34	0.71	1.02	2.29
	Max	11.46	4.58	6.76	6.22	3.47	3.310	1.27	3.97	2.55	0.97	1.11	2.55
11	**Mean**	11.25	4.44	6.52	6.02	3.35	3.190	1.16	3.67	2.40	0.79	1.06	2.44
(*n* = 8)	**SD**	0.21	0.11	0.14	0.10	0.05	0.103	0.04	0.07	0.06	0.08	0.06	0.10
	CV	1.89	2.54	2.25	1.65	1.38	3.333	3.95	2.09	2.75	10.77	5.90	4.25
	Min	10.92	4.20	6.22	5.91	3.29	3.080	1.12	3.56	2.34	0.71	0.93	2.29
	Max	11.61	4.54	6.69	6.15	3.44	3.400	1.22	3.82	2.49	0.92	1.12	2.55
ANOVA	**SS**	2.417	1.679	0.670	0.761	0.119	0.192	0.116	1.754	0.424	0.256	0.042	0.365
	df	10	10	10	10	10	10	10	10	10	10	10	10
	F	5.489	8.799	1.837	4.821	1.510	1.611	1.400	9.703	5.602	3.694	1.974	4.256
	P	3.93E-06***	1.72E-09***	0.068	2.20E-05***	0.152	0.119	0.196	2.58E-10***	2.95E-06***	4.45E-04***	0.047*	9.78E-05***

Table 6.20 Pearson correlation coefficients for correlation between latitude and longitude and principal component scores and 11 OTUs within the 12 cranial measurements of *Neoromicia africanus* from southern Africa. ** denotes significance at $P < 0.01$; *** denotes significance at $P < 0.001$.

	PC1	PC2	CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Latitude														
Pearson Correlation	-0.501	-0.554	-0.278	-0.639	-0.764	0.28	0.323	-0.473	0.096	-0.73	-0.107	-0.04	0.551	-0.258
Significance (2-tailed)	0.116	0.077	0.407	0.034*	0.006**	0.405	0.333	0.142	0.778	0.011*	0.754	0.907	0.079	0.444
Longitude														
Pearson Correlation	0.202	-0.597	0.129	0.102	-0.315	-0.17	0.163	-0.728	0.417	-0.122	0.535	0.018	0.671	0.121
Significance (2-tailed)	0.551	0.052	0.706	0.766	0.346	0.618	0.632	0.011*	0.202	0.721	0.09	0.958	0.024*	0.722

Table 6.21 Two localities for *Neoromicia rendalli* in southern Africa arranged in relation to occurrence from north to south, with associated numbering of individuals in each locality (IC) and number of specimens included in each locality (*n*). For details on the localities and specimens used see Appendix 6.1

IC	Locality	*n*
1	Zimbabwe: Mana Pools Nature Reserve	4
2-5	South Africa: KwaZulu-Natal; Bonamanzi Game Reserve	1

Table 6.22 Eigenvector scores of principal components one to three of a PCA based on 12 cranial measurements (Meas) of five specimens of *Neoromicia rendalli* from southern Africa. See the material and methods section of Chapter 5 for an explanation of the measurement codes. Highest and lowest scores are indicated in bold type.

Meas	PC1	PC2	PC3
CIL	0.803	0.385	0.193
BH	0.928	0.297	-0.220
ZB	0.969	-0.223	0.089
BB	0.799	-0.477	-0.366
POW	0.833	-0.306	-0.444
WFM	0.838	0.417	0.104
WAS	0.685	**-0.684**	-0.003
WOUC	**0.978**	0.032	0.201
WIUM1	0.941	0.128	0.020
WUPM4	0.174	**0.785**	**-0.591**
LUM1	0.571	0.144	**0.761**
MAOT	**0.979**	0.017	-0.006

Table 6.23 Basic statistics of *Neoromicia rendalli* from two localities in southern Africa. SD = standard deviation; CV = coefficient of variation; Min = minimum value; Max = maximum value; *n* = sample size. See Table 6.22 for a description of the OTU codes, and the material and methods section of Chapter 5 for an explanation of the measurement codes.

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
1	(*n* = 1)	12.75	5.04	7.77	6.92	3.91	3.47	1.63	4.28	2.75	1.02	1.29	2.80
2	**Mean**	13.65	5.17	8.46	7.16	4.09	3.74	1.81	4.63	3.08	1.02	1.37	3.18
(*n* = 4)	**SD**	0.34	0.06	0.26	0.28	0.20	0.10	0.20	0.07	0.11	0.07	0.02	0.13
	CV	2.63	1.28	3.21	4.19	5.17	2.95	11.59	1.65	3.66	7.65	1.52	4.28
	Min	13.17	5.11	8.10	6.74	3.80	3.60	1.58	4.53	2.95	0.95	1.36	3.00
	Max	13.95	5.25	8.71	7.37	4.24	3.82	2.04	4.68	3.21	1.12	1.39	3.31

larger than specimens from north-westerly localities.

6.3.1.7 *Neoromicia rueppellii*

Another poorly known species in southern Africa, the analysis of *P. rueppellii* was based on eight specimens from four localities. Included in the analysis was the type specimen (TM6546) of *Pipistrellus vernayi* (Roberts,1932) from Maun in Botswana, which is currently synonymised with *N. rueppellii*. The sample was divided into four OTUs (Table 6.24). A PCA scatterplot of the first two principal components based on eight *N. rueppellii* from four localities (Fig. 6.19) identified the specimen (MM7047) from the most south-westerly locality (Augrabies Falls National Park in the Northern Cape Province) as an outlier. However, the DFA with known identity specimens, confirmed the identity of all eight specimens and the specimen from Augrabies Falls was retained for the analysis of geographic variation. Besides the separation of the Augrabies Falls specimen from the others, the PCA scatterplot of the first two principal components shows little separation of the specimens in relation to locality. The eigenvector scores on the first principal component axis, which describes 56.56% of the variation were in all but one measurement, positive. The measurements loading highest and lowest on the first principal component axis, were braincase breadth and width of the articular surface. The second principal component axis explained 18.46% of the variation The signs of the eigenvector scores were mixed and the measurements with the largest positive and negative scores were width of the foramen magnum and length of the first upper molar (Table 6.25). The distance phenogram based on the eight individuals revealed a similar clustering to that observed in the PCA (Fig. 6.20).

Table 6.26 gives the basic statistics and the results of the one-way ANOVAs between OTUs for each measurement, which showed significant variation in two measurements, braincase height and zygomatic breadth (at $P < 0.05$). Observations of the values of these measurements identified that OTU 4 was smaller than the other OTUs, and OTU 1 was largest in BH and OTU 2 was largest in ZB. No measurements showed a significant correlation between OTU and latitude or longitude, or between first and second principal component scores and latitude and longitude (Table 6.27). Thus, although this was a very small sample and although the specimens from the most south-westerly locality was separated from the other localities in the PCA, there was no geographic variation in the 12 cranial measurements of the *N. rueppellii* from the four localities analysed.

6.3.1.8 *Neoromicia zuluensis*

For initial PCA, UPGMA and DFA analyses to identify potential outliers and misidentified specimens, 60 specimens of *N. zuluensis* from various localities in southern Africa were split into four more manageable groups based on geographic proximity. Thirteen outlier and possibly misidentified specimens were removed from further analyses (NMBZ83881, NMBZ58889, NMBZ64065, TM19372, TM24752, TM3678, TM37436, TM38169, TM36572, TM36574, TM6458, KM8083, KM8089), and four specimens were re-assigned to *N. capensis* (NMBZ31973, NMBZ31988, NMBZ11190, TM44210). Of the remaining 43 specimens, four were individuals from localities that could not be pooled. However, since these represented specimens that added to the geographic extent of the area analysed, and two were type specimens of *Neoromicia zuluensis* Roberts, 1924 and *Neoromicia zuluensis vansoni* (Roberts, 1932), two separate analyses were run, one on six OTUs that were created, the other on the OTUs together with the individual specimens from the additional four localities (Table 6.28).

A PCA scatterplot of six OTUs (Fig. 6.21) showed a tendency for OTU scores to increase with decreasing longitude along the first principal component axis and, with the exception of OTU 6, OTU scores increased with decreasing latitude on the second principal component. A similar pattern was observed in the PCA scatterplot of the 39 individuals on which the six OTUs were based (Fig. 6.22). However, the important measurements on the first and second principal component axes were, with one exception, different (Table 6.29). In the analysis of OTUs, the measurements with mixed sign which loaded highest and lowest on the first principal component axis, which accounted for 50.25% of the variation, were width of the upper fourth premolar and greatest width of the foramen magnum. In the analysis of all individuals, the first principal component axis accounted for 25.86% of the variation and the measurements of mixed sign which loaded highest and lowest were width of the upper fourth premolar and post-orbital width. On the second principal component axes which accounted for 29.35% and 17.53% of the variation in the analysis of the OTUs and individuals respectively, the measurements that loaded highest and lowest were moment arm of the temporal and braincase height, in the analysis of

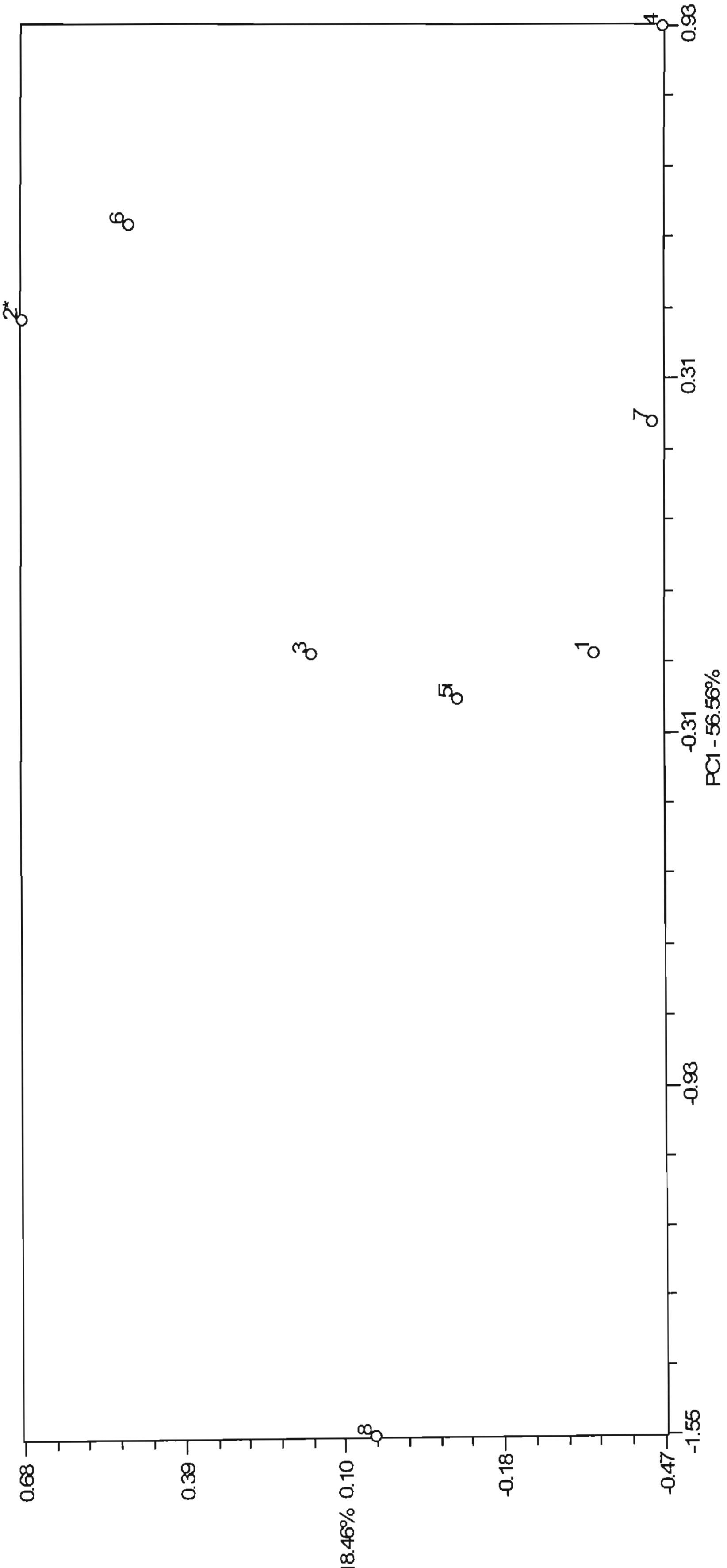


Figure 6.19 Scatterplot of the first two principal component axes based on eight specimens of *Neoromicia rueppellii* from southern Africa. Individual numbers correspond to those in Table 6.24; * = type specimen; i = known identity specimen.

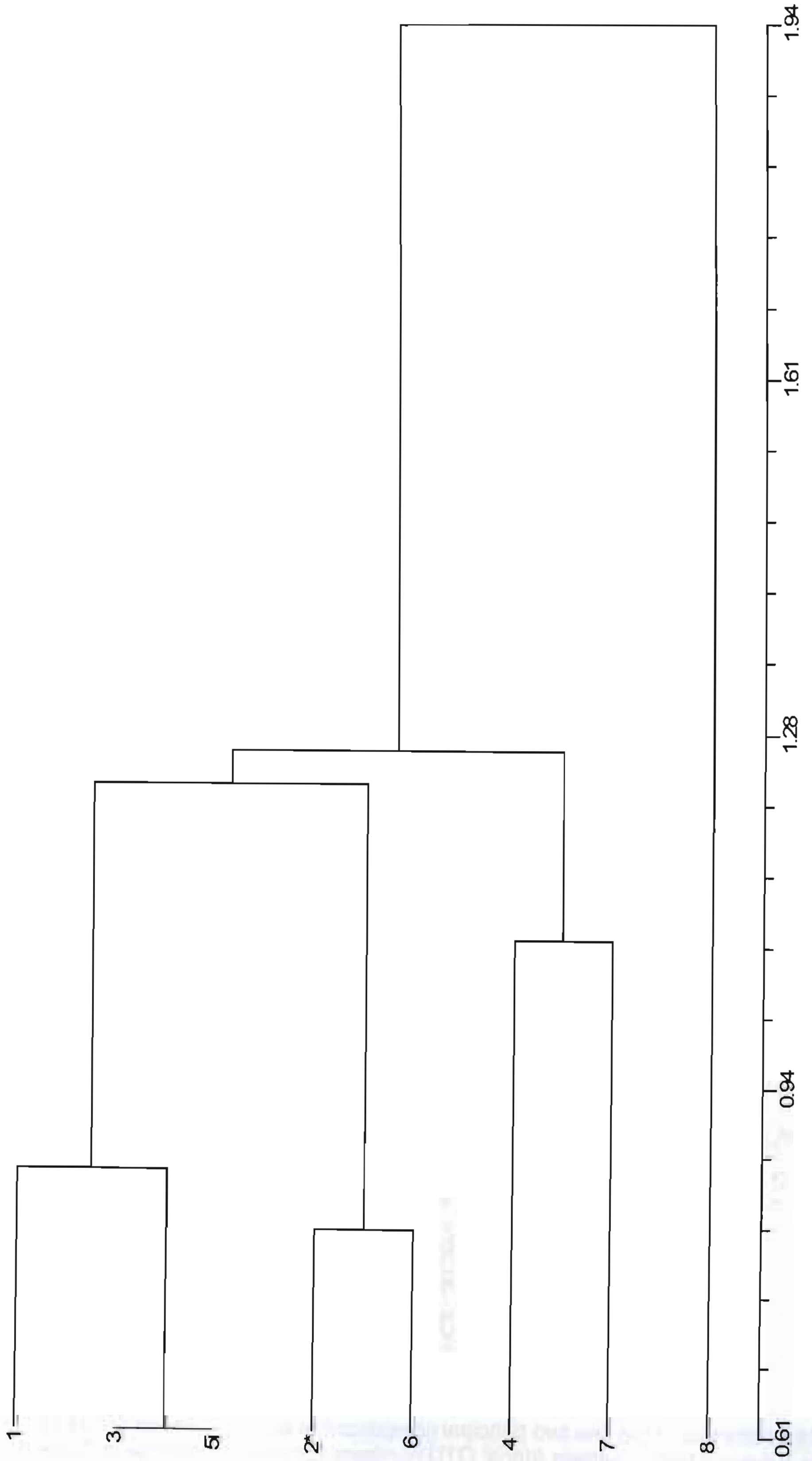


Figure 6.20 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on eight individual *Neoromicia rueppellii* from southern Africa. Individual numbers correspond to those in Table 6.24; * = type specimen; i = known identity specimen. Cophenetic correlation coefficient = 0.878.

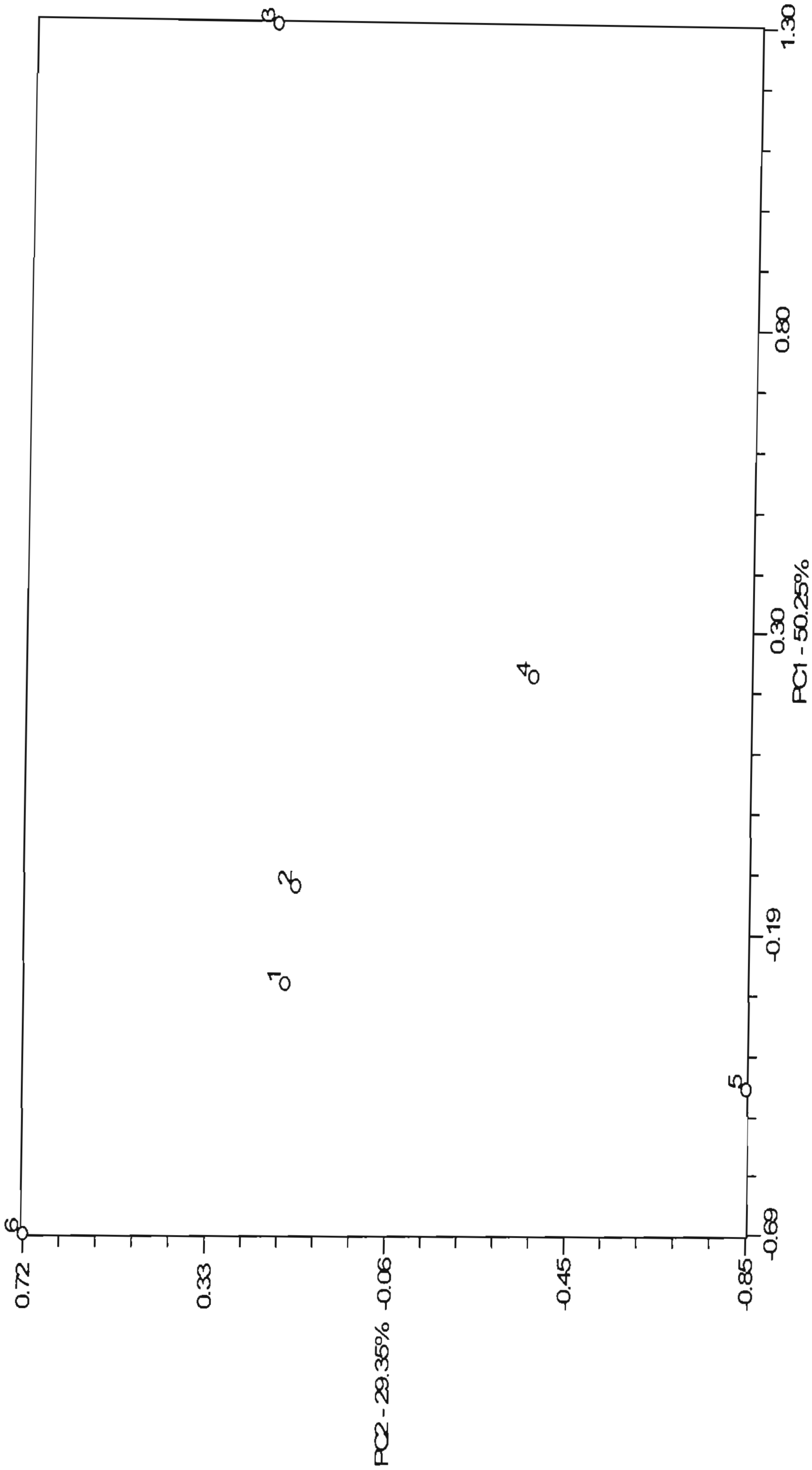


Figure 6.21 Scatterplot of the first two principal component axes based on six OTUs of *Neoromicia zuluensis* from southern Africa. OTU numbers correspond to those in Table 6.28.

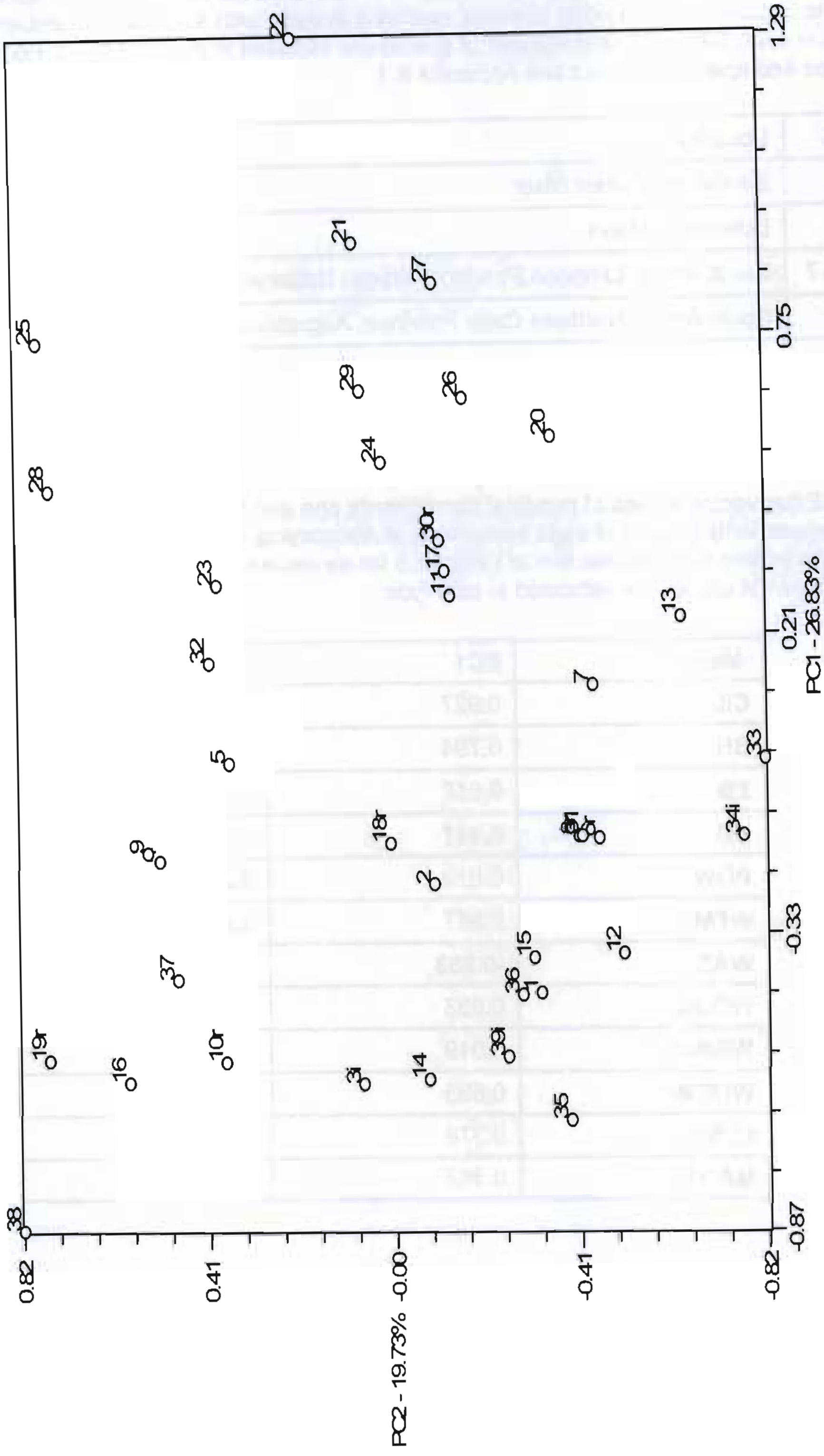


Figure 6.22 Scatterplot of the first two principal component axes based on 39 individuals of *Neoromicia zuluensis* from southern Africa. Individual numbers correspond to those in Table 6.28; i = known identity; r = possibly karyotyped by Rautenbach *et al.* (1993).

Table 6.24 Four OTUs of single and pooled localities for *Neoromicia rueppellii* in southern Africa in relation to occurrence from north to south, and east to west, with associated numbering of individuals in each OTU (IC), and number of specimens included in each OTU (*n*). For details on the localities and specimens used see Appendix 6.1.

OTU	IC	Locality	*n*
1	1	Zimbabwe: Gwayi River	1
2	2	Botswana: Maun	1
3	3- 7	South Africa: Limpopo Province; Kruger National Park; Pafuri	5
4	8	South Africa: Northern Cape Province; Augrabies Fall National Park	1

Table 6.25 Eigenvector scores of principal components one and two of a PCA based on 12 cranial measurements (Meas) of eight specimens of *Neoromicia rueppellii* from southern Africa. See the material and methods section of Chapter 5 for an explanation of the measurement codes. Highest and lowest scores are indicated in bold type.

Meas	PC1	PC2
CIL	0.927	0.308
BH	0.794	-0.246
ZB	0.816	0.379
BB	**0.947**	-0.061
POW	0.513	0.209
WFM	0.567	**0.661**
WAS	**-0.253**	-0.448
WOUC	0.933	-0.198
WIUM1	0.919	-0.043
WUPM4	0.693	-0.669
LUM1	0.379	**-0.858**
MAOT	0.863	0.088

Table 6.26 Basic statistics and ANOVA results to test for OTU variation in four OTUs of *Neoromicia rueppellii* in southern Africa. SD = standard deviation; CV = coefficient of variation; Min = minimum value; Max = maximum value; *n* = sample size; SS = sum of squares; df = degrees of freedom; *P* = significance of *F* values; * denotes significance at $P < 0.05$. See Table 6.25 for a description of the OTU codes, and the material and methods section of Chapter 5 for an explanation of the measurement codes.

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
1	(*n* = 1)	13.18	5.39	7.48	7.48	4.56	3.52	1.49	4.08	3.01	1.04	1.32	2.77
2	(*n* = 1)	13.81	5.36	8.11	7.58	4.25	3.83	1.46	4.19	3.21	0.83	1.18	3.12
3	**X**	13.46	5.38	7.90	7.59	4.39	3.59	1.53	4.34	3.07	0.99	1.28	3.02
(*n* = 5)	**SD**	0.29	0.10	0.13	0.19	0.22	0.14	0.10	0.23	0.18	0.09	0.07	0.15
	CV	2.29	1.97	1.66	2.60	5.30	3.96	7.00	5.61	6.10	9.65	5.79	5.09
	Min	13.04	5.23	7.71	7.35	4.09	3.36	1.37	4.02	2.90	0.92	1.22	2.80
	Max	13.75	5.47	8.04	7.75	4.70	3.70	1.63	4.58	3.36	1.12	1.39	3.16
4	(*n* = 1)	12.62	4.81	7.31	7.14	3.94	3.40	1.53	3.67	2.75	0.71	1.22	2.70
ANOVA	**SS**	0.836	0.282	0.487	0.176	0.227	0.099	0.005	0.393	0.122	0.086	0.011	0.150
	df	3	3	3	3	3	3	3	3	3	3	3	3
	F	3.227	9.240	10.351	1.656	1.542	1.790	0.145	2.446	1.276	3.453	0.769	2.330
	P	0.144	0.029*	0.023*	0.312	0.334	0.288	0.928	0.204	0.396	0.131	0.568	0.216

Table 6.27 Pearson correlation coefficients for correlation between latitude and longitude and principal component scores and four OTUs within the 12 cranial measurements of *Neoromicia rueppellii* from southern Africa. ** denotes significance at $P < 0.01$; *** denotes significance at $P < 0.001$.

	PC1	PC2	CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Latitude														
Pearson Correlation	0.86	0.312	0.769	0.942	0.554	0.85	0.879	0.647	-0.731	0.756	0.836	0.756	0.323	0.508
Significance (2-tailed)	0.14	0.688	0.231	0.058	0.446	0.15	0.121	0.353	0.269	0.244	0.164	0.244	0.677	0.492
Longitude														
Pearson Correlation	0.588	0.685	0.434	0.758	0.343	0.728	0.804	0.134	0.155	0.823	0.46	0.901	0.691	0.352
Significance (2-tailed)	0.412	0.315	0.566	0.242	0.657	0.272	0.196	0.866	0.845	0.177	0.54	0.099	0.309	0.648

Table 6.28 Six OTUs of single and pooled localities, and 10 localities of OTUs and single specimens (LOC) for *Neoromicia zuluensis* from southern Africa in relation to occurrence from north to south, and east to west, with associated numbering of individuals in each OTU (IC) and locality (LOC IC), and number of specimens included in each OTU (*n*). For details on the localities and specimens used see Appendix 6.1.

OTU	IC	LOC	LOC IC	Locality	*n*
-	-	1	1	Botswana: Zweizwi River Waterhole	1
-	-	2	2	Namibia: Ssannakanu Village	1
1	1-4	3	3-6	South Africa: Limpopo Province; Messina and Farm Urk	4
2	5-19	4	7-21	South Africa: Limpopo Province; Pafuri	15
3	20-30	5	22-32	Namibia: Gobabeb	11
4	31-33	6	33-35	South Africa: Limpopo Province; Lapalala and Vaalwater	3
5	34-36	7	36-38	South Africa: Limpopo Province; Sheila Farm 10, Mpumalanga Province; Kruger National Park	3
6	37-39	8	39-41	South Africa: Mpumalanga Province; Kruger National Park and Acornhoek	3
-	-	9	42	South Africa: KwaZulu-Natal Province; Mkuze Game Reserve	1
-	-	10	43	South Africa: KwaZulu-Natal Province; Umfolozi Game Reserve	1

Table 6.29 Eigenvector scores of principal components one and two of PCAs based on 12 cranial measurements of A) six OTUs, B) 39 individuals, C) six OTUs and four individuals, and D) 43 individuals of *Neoromicia zuluensis* from southern Africa. See the material and methods section of Chapter 5 for an explanation of the measurement codes. Highest and lowest scores are indicated in bold type.

	A)		B)		C)		D)	
Meas	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**	**PC1**	**PC2**
CIL	0.794	0.315	0.128	0.631	**0.882**	0.398	0.278	0.732
BH	0.491	**-0.701**	0.268	-0.158	0.734	0.003	0.051	0.155
ZB	-0.647	0.396	-0.508	0.282	**0.910**	-0.212	0.668	0.127
BB	-0.833	-0.068	-0.573	0.021	0.877	-0.445	0.715	-0.081
POW	-0.860	-0.368	**-0.785**	**-0.231**	0.859	-0.405	**0.766**	**-0.346**
WFM	**-0.876**	-0.073	-0.493	-0.122	0.545	**-0.455**	0.491	-0.182
WAS	-0.149	0.884	-0.069	0.576	0.825	-0.191	0.423	0.374
WOUC	-0.738	0.607	-0.615	**0.662**	0.802	0.239	0.728	0.388
WIUM1	-0.746	0.571	-0.632	0.410	0.333	0.229	0.599	0.084
WUPM4	**0.925**	0.231	**0.811**	0.217	0.248	**0.820**	**-0.517**	0.639
LUM1	0.630	0.548	0.457	0.617	0.360	0.625	-0.142	**0.767**
MAOT	0.403	**0.894**	0.189	0.655	0.487	0.589	0.094	0.679

OTUs, and width across the outer surfaces of the upper canines and post-orbital width, in the analysis of individuals (Table 6.29). Neither of the distance phenograms based on the six OTUs (Fig. 6.23) or 39 individuals (Fig. 6.24) identified the same pattern of geographic variation observed in the PCAs, although both showed the distinction of specimens from Gobabeb in Namibia from the other localities.

The addition of individuals from four different localities to the analyses of the six OTUs, introduced latitudinal variation into the analyses and the pattern along the first principal component axis of both PCA scatterplots of OTUs and individuals (Fig. 6.25) and 43 individuals (Fig. 6.26) indicates separation of the localities due to latitude, as well as longitude. The type specimen of *N. zuluensis* from Umfolosi Game Reserve in KwaZulu-Natal Province of South Africa was separated more from the other OTUs and specimens than an individual (number 42) added from Mkuze Game Reserve in KwaZulu-Natal. The distribution along the second principal component axes is not in relation to either latitude or longitude, but separated the type specimen of *N. z. vansoni* from the other OTUs and specimens (Fig. 6.25). Although the distribution patterns of the PCAs were similar, the most important measurements on each of the principal component axes were different (Table 6.29). The distance phenograms based on the six OTUs and four individuals (Fig. 6.27) and the 43 individuals (Fig. 6.28) were slightly different in their emphasis of the distinction of the type specimen of *N. z. vansoni* and the specimen from Grootfontein in Namibia from the other specimens in the analysis. However, both phenograms indicated the distinction of the type specimen of *N. zuluensis* and the specimens from Gobabeb in Namibia from all other specimens.

Table 6.30 gives the basic statistics and the results of the one-way ANOVAs between the six OTUs for each measurement, which identified six measurements as significantly different between different OTUs. Post-hoc Tukey tests identified only one subset for zygomatic breadth and width of the foramen magnum, whereas two significantly different subsets were identified for width across the outer surfaces of the upper canines, width of the upper fourth premolar, and length of the upper first molar, and three significantly different subsets were identified for post-orbital width (Appendix 6.2 E). The significantly different subsets were different for each measurement although the general pattern in each case was to separate localities longitudinally. In three of the four measurements the significantly different subsets overlapped, but width of the upper fourth premolar was significantly larger in the Namibian OTU than any of the other OTUs.

In the analyses of six OTUs, no measurements were significantly correlated with latitude, but two measurements, condylo-incisor skull length and width of the upper fourth premolar, were significantly negatively correlated with longitude (i.e. increasing in size from east to west). In analyses with both OTUs and individuals, seven measurements showed significantly negative correlations with latitude (i.e. increasing in size from north to south), and four measurements showed significantly positive correlations with longitude (i.e. decreasing in size from east to west) (Table 6.31). In both analyses of six OTUs and the OTUs with individuals, the first principal component scores were significantly positively correlated with longitude (Table 6.31). However, in the analysis of OTUs with individuals, the first principal component axis was more significantly correlated with latitude, whereas there was no significant correlation between latitude and the first principal component axis in the analysis of OTUs only. Hence, with or without the additional localities, the analyses showed clinal longitudinal variation in the overall size of the 12 cranial measurements of *N. zuluensis* with OTUs in the east being larger than OTUs in the west, whereas clinal latitudinal variation with increasing size in more southerly OTUs was only observed when the additional specimens from more northerly and southerly localities were added. Since single individuals were representative of the more northerly and southerly localities, the observed pattern of latitudinal clinal change in overall size of the 12 skull measurements of *N. zuluensis* will need to be tested with further specimens to confirm that this is not just due to outlier individuals.

6.3.1.9 *Pipistrellus hesperidus*

For the initial PCA, UPGMA and DFA analyses to identify potential outliers and misidentified specimens, a sample of 56 specimens of *P. hesperidus* from various localities in southern Africa was split into three manageable groups based on geographic proximity. Nine outlier and possibly misidentified specimens were removed from further analyses (TM34757, TM34768, TM34634, TM11403, DM4692, TM40457, TM40014, DM6893, TM1073), while one specimen was re-assigned to *P. rusticus* (TM36440). Of the remaining 46 specimens, there were sufficient individuals from most of the localities in KwaZulu-Natal Province of South Africa to allow the formation of six OTUs, whereas six specimens from five localities were sufficiently far apart as

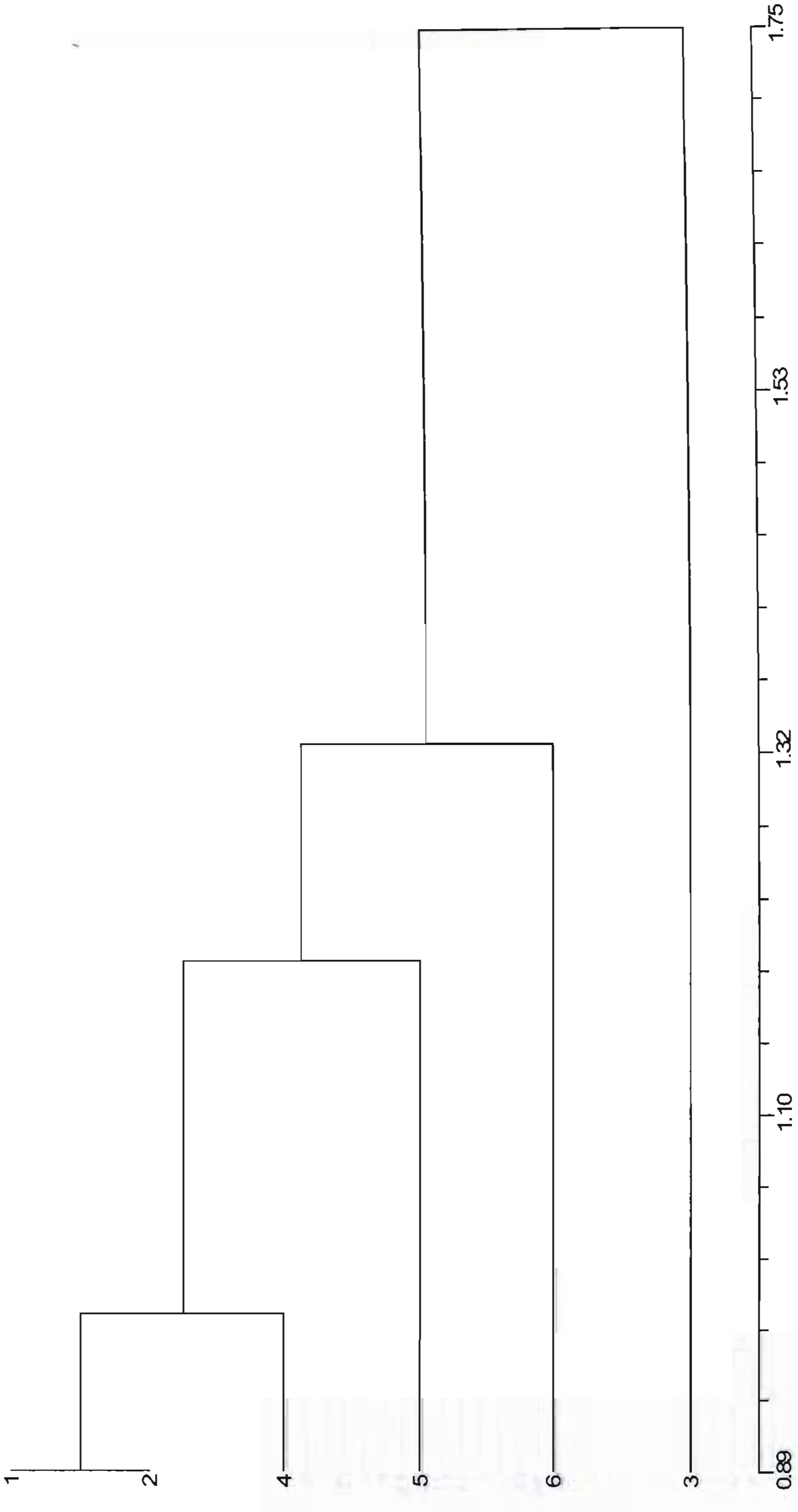


Figure 6.23 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on six OTUs of *Neoromicia zuluensis* from southern Africa. OTU numbers correspond to those in Table 6.28. Cophenetic correlation coefficient = 0.822.

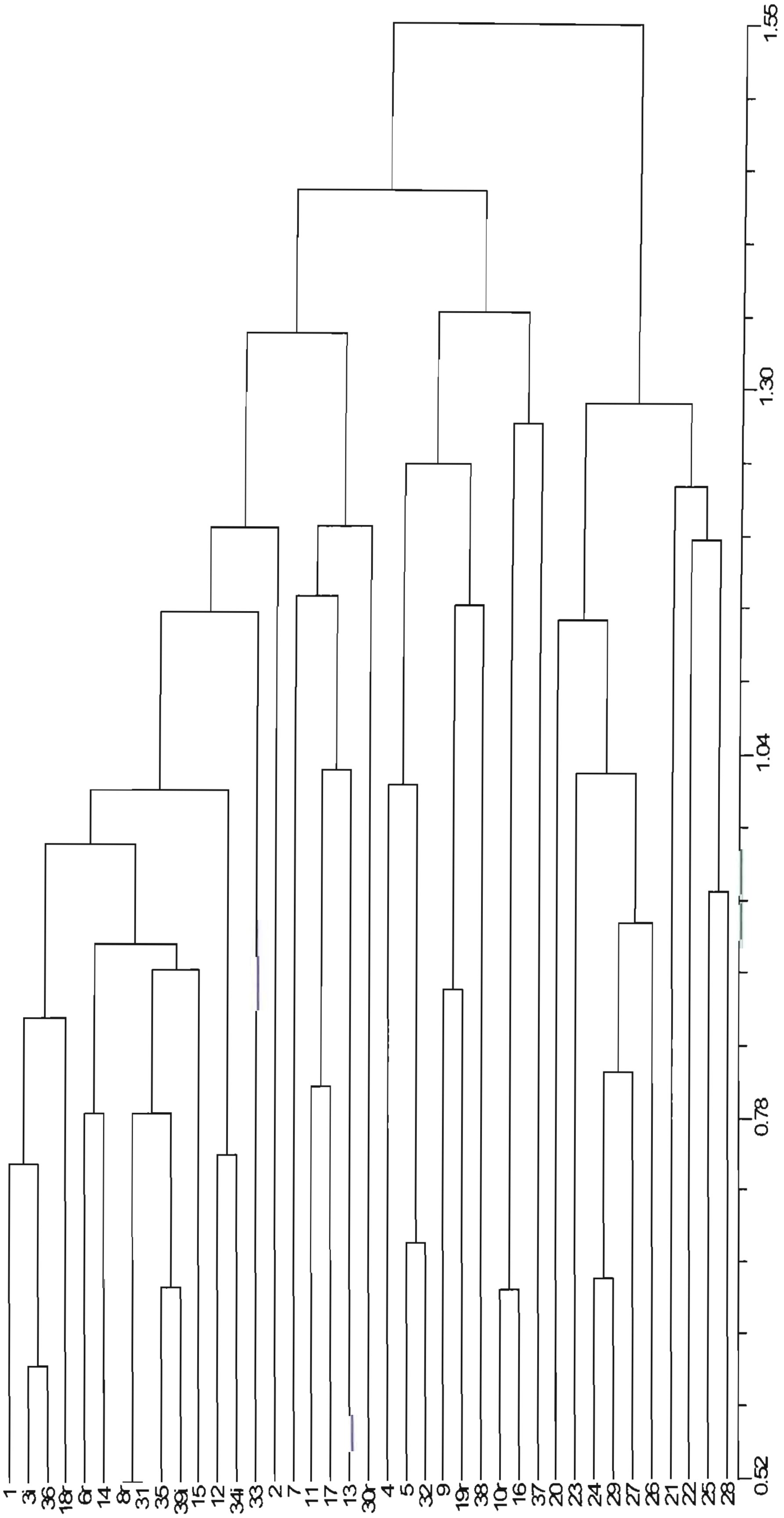


Figure 6.24 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on 39 individuals of *Neoromicia zuluensis* from southern Africa. Individual numbers correspond to those in Table 6.28; i = known identity; r = possibly karyotyped by Rautenbach *et al.* (1993). Cophenetic correlation coefficient = 0.665.

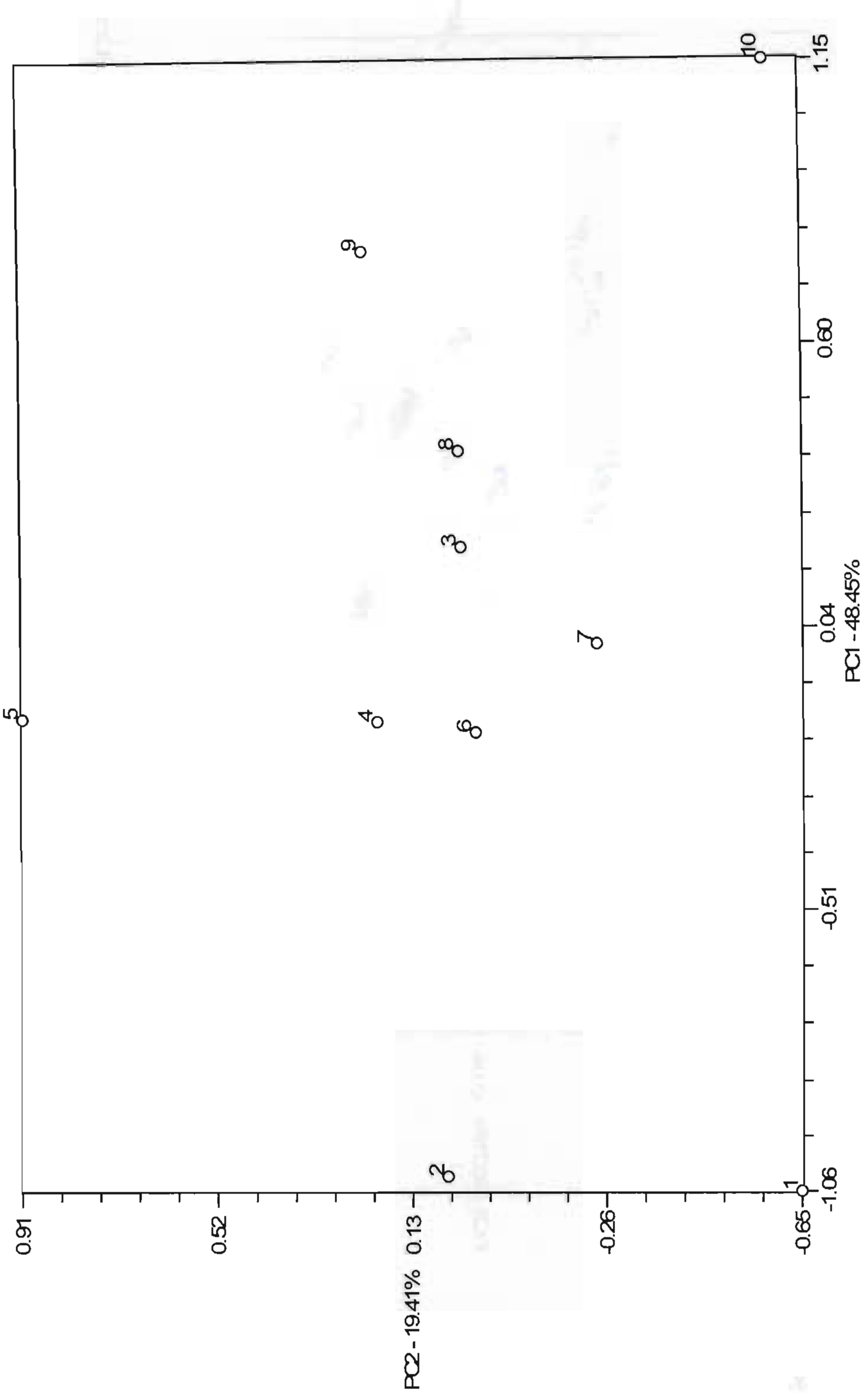


Figure 6.25 Scatterplot of the first two principal component axes based on six OTUs and four individuals of *Neoromicia zuluensis* from southern Africa. OTU and individual numbers correspond to those in Table 6.28.

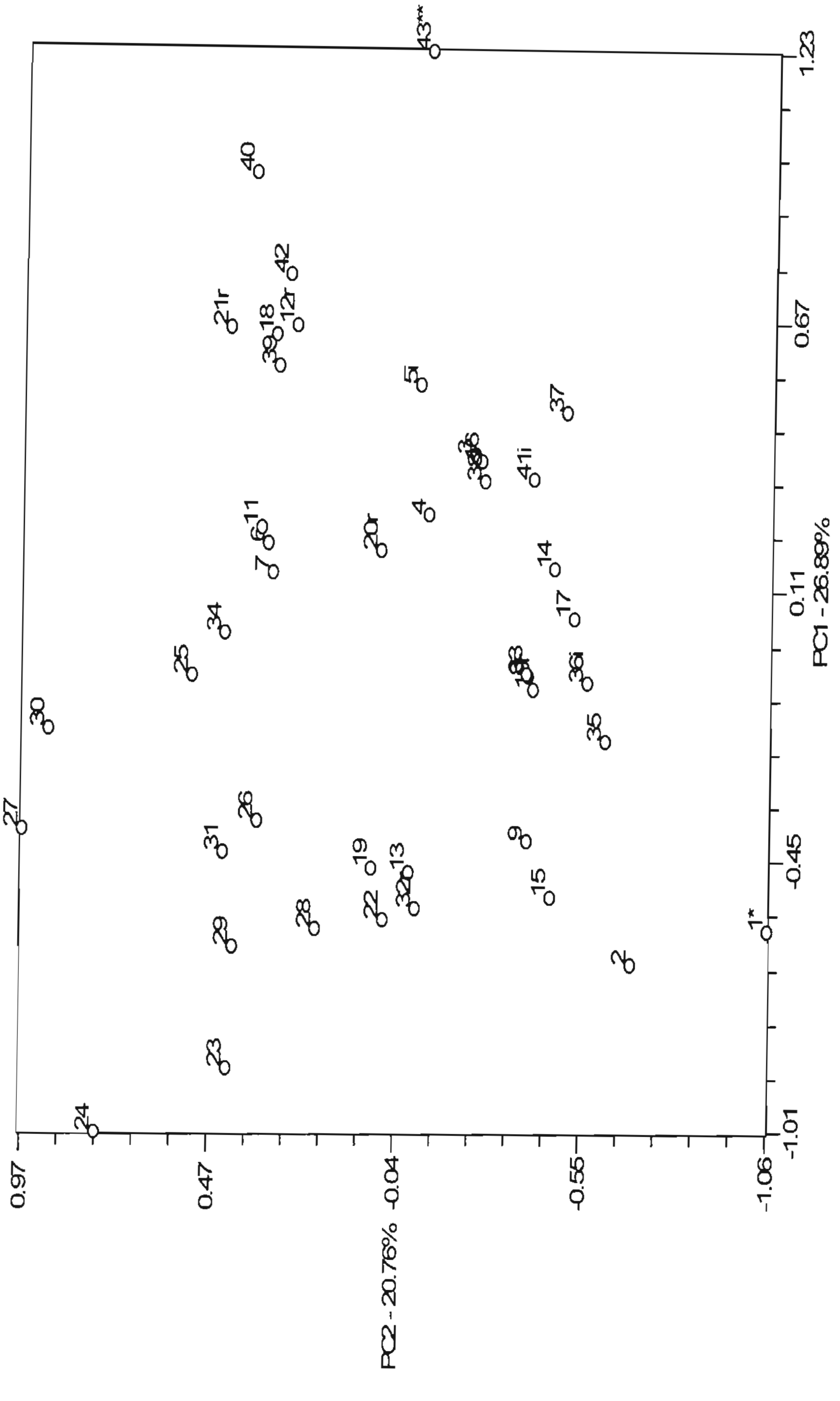


Figure 6.26 Scatterplot of the first two principal component axes based on 43 individuals of *Neoromicia zuluensis* from southern Africa. Individual numbers correspond to those in Table 6.28; i = known identity; r = possibly karyotyped by Rautenbach *et al.* (1993), * = type of *Neoromicia vansoni*; ** = type of *Eptesicus zuluensis*.

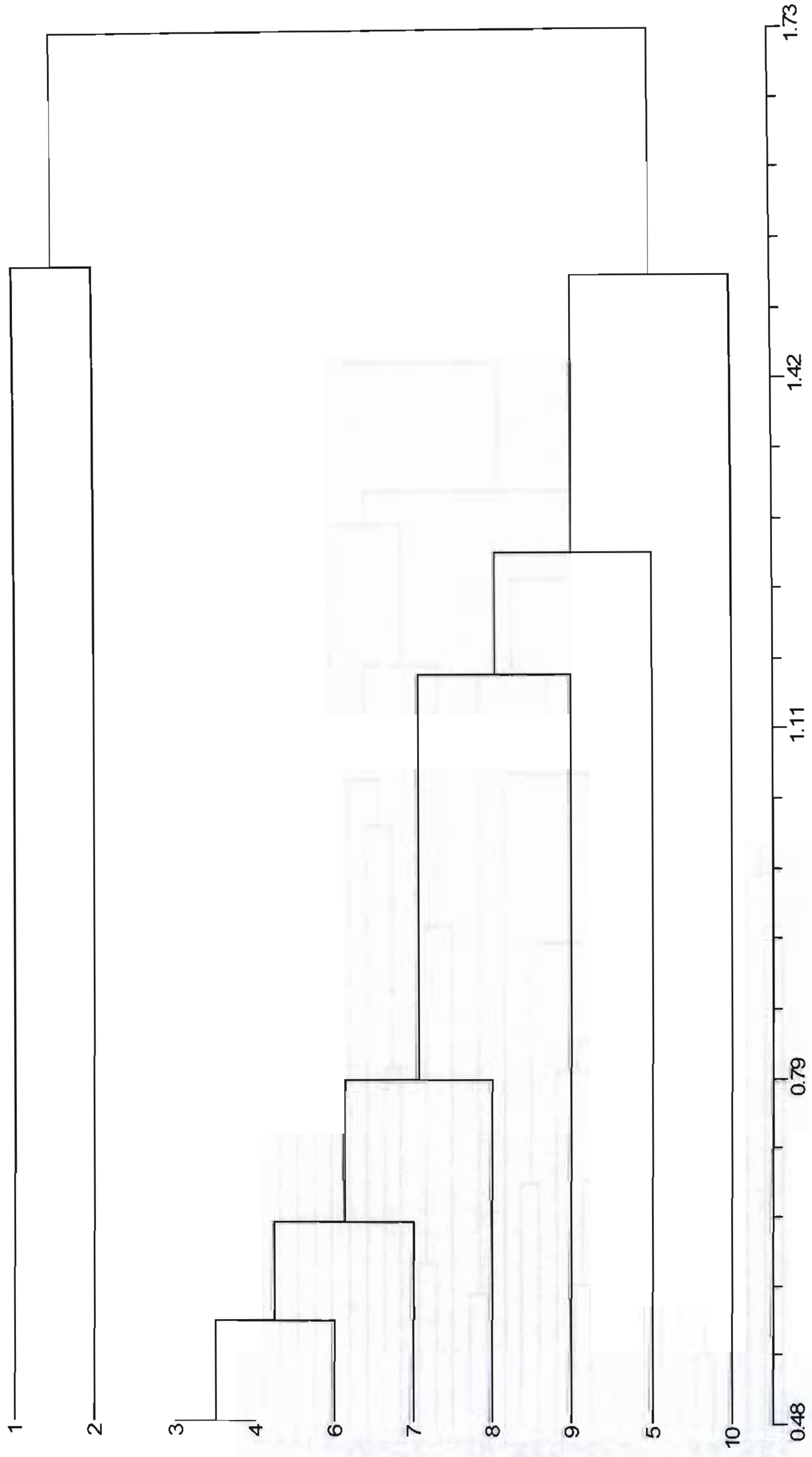


Figure 6.27 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on six OTUs and four individuals of *Neoromicia zuluensis* from southern Africa. Numbers correspond to those in Table 6.28. Cophenetic correlation coefficient = 0.853.

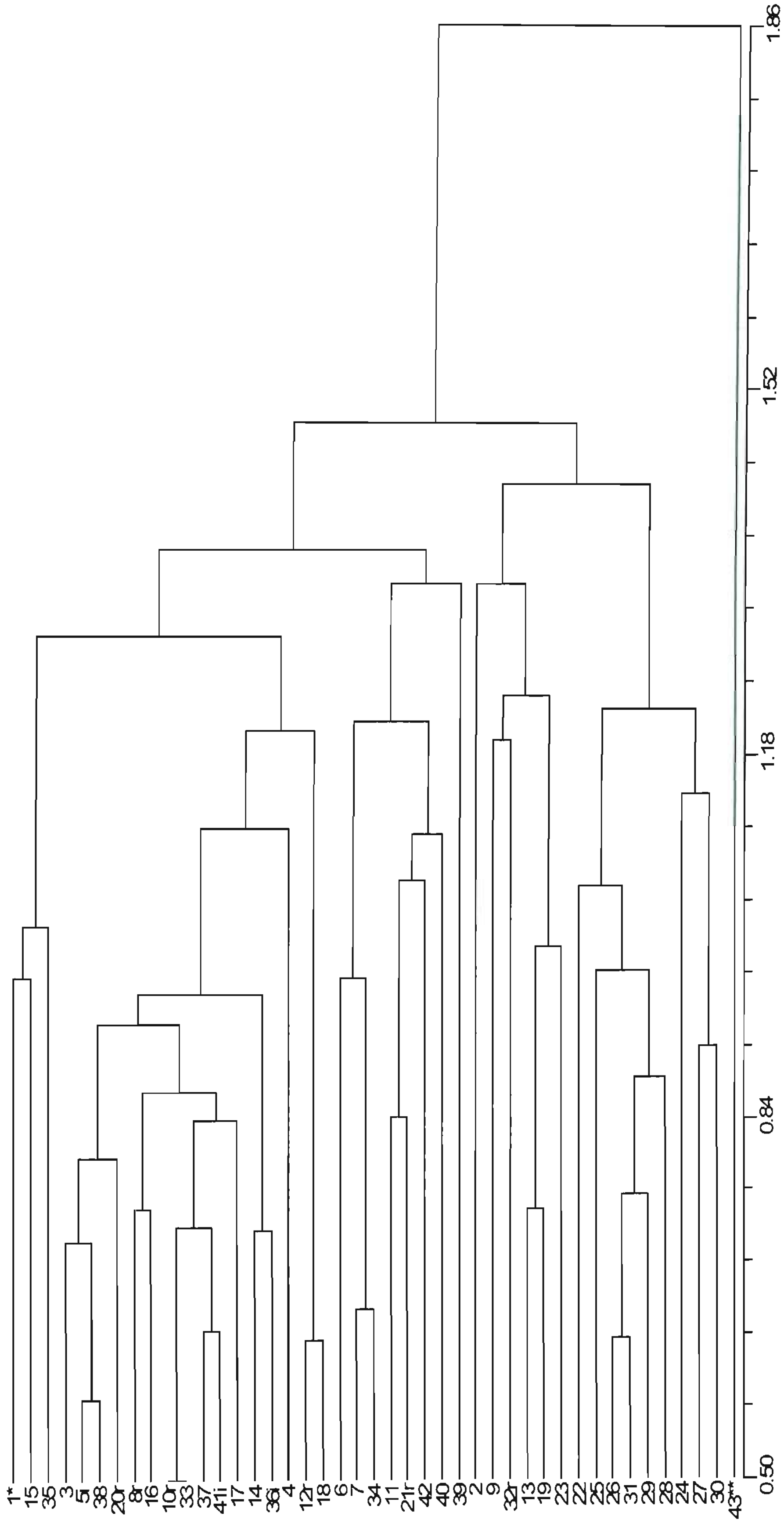


Figure 6.28 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on 43 individuals of *Neoromicia zuluensis* in southern Africa. Individual numbers correspond to those in Table 6.28. Cophenetic correlation coefficient = 0.649. i = known identity; r = possibly karyotyped by Rautenbach *et al.* (1993), * = type of *Neoromicia vansoni*; ** = type of *Eptesicus zuluensis*.

Table 6.30 Basic statistics and ANOVA results to test for OTU variation in six OTUs of *Neoromicia zuluensis* in southern Africa. SD = standard deviation; CV = coefficient of variation; Min = minimum value; Max = maximum value; n = sample size; SS = sum of squares; df = degrees of freedom; P = significance of F values; * denotes significance at $P < 0.05$; ** denotes significance at $P < 0.01$. See Table 6.29 for a description of the OTU codes, and the material and methods section of Chapter 5 for an explanation of the measurement codes.

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
1	**Mean**	11.98	4.57	7.10	6.35	3.47	3.22	1.40	3.75	2.41	0.80	1.24	2.72
(n = 4)	**SD**	0.16	0.16	0.16	0.17	0.11	0.13	0.10	0.11	0.03	0.07	0.08	0.07
	CV	1.44	3.63	2.38	2.83	3.38	4.28	7.40	2.97	1.12	8.66	6.93	2.56
	Min	11.78	4.37	6.96	6.12	3.33	3.10	1.32	3.67	2.39	0.75	1.19	2.65
	Max	12.17	4.71	7.33	6.51	3.60	3.40	1.53	3.87	2.44	0.88	1.36	2.80
2	**Mean**	11.90	4.52	6.98	6.21	3.40	3.09	1.37	3.79	2.41	0.82	1.18	2.72
(n = 15)	**SD**	0.24	0.07	0.18	0.17	0.10	0.15	0.11	0.14	0.09	0.08	0.08	0.09
	CV	2.04	1.65	2.54	2.74	3.04	4.84	8.13	3.72	3.96	9.69	6.87	3.36
	Min	11.41	4.38	6.66	5.91	3.22	2.77	1.22	3.56	2.24	0.68	1.02	2.60
	Max	12.37	4.62	7.24	6.50	3.58	3.26	1.58	4.07	2.60	0.95	1.32	2.85
3	**Mean**	12.04	4.62	6.76	6.18	3.26	3.02	1.40	3.66	2.31	1.02	1.32	2.78
(n = 11)	**SD**	0.31	0.14	0.19	0.12	0.13	0.09	0.06	0.08	0.09	0.11	0.07	0.08
	CV	2.65	3.02	2.85	2.05	4.21	3.04	4.32	2.18	4.10	10.57	5.32	3.04
	Min	11.53	4.35	6.45	5.97	3.07	2.85	1.28	3.59	2.18	0.78	1.14	2.60
	Max	12.63	4.79	7.04	6.40	3.47	3.19	1.49	3.79	2.46	1.21	1.42	2.87
4	**Mean**	11.98	4.60	6.87	6.24	3.37	3.18	1.39	3.68	2.31	0.80	1.15	2.70
(n = 3)	**SD**	0.27	0.01	0.23	0.19	0.08	0.17	0.12	0.15	0.08	0.05	0.09	0.09
	CV	2.44	0.14	3.54	3.23	2.68	5.73	9.15	4.32	3.65	6.99	8.43	3.54
	Min	11.78	4.59	6.68	6.04	3.30	3.05	1.32	3.51	2.24	0.75	1.05	2.65
	Max	12.29	4.60	7.12	6.41	3.46	3.37	1.53	3.77	2.39	0.85	1.22	2.80

Table 6.30 continued.

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
5	Mean	11.87	4.63	6.84	6.38	3.62	3.24	1.31	3.73	2.36	0.78	1.16	2.66
(*n* = 3)	SD	0.11	0.06	0.12	0.16	0.05	0.08	0.06	0.06	0.03	0.10	0.09	0.03
	CV	0.97	1.30	1.88	2.65	1.35	2.56	4.87	1.71	1.35	14.13	7.94	1.20
	Min	11.79	4.57	6.70	6.24	3.57	3.17	1.27	3.67	2.34	0.68	1.09	2.65
	Max	11.99	4.68	6.91	6.55	3.66	3.32	1.37	3.77	2.39	0.88	1.25	2.70
6	Mean	11.92	4.52	6.98	6.38	3.49	3.27	1.51	3.95	2.44	0.79	1.22	2.77
(*n* = 3)	SD	0.16	0.04	0.05	0.09	0.12	0.14	0.08	0.19	0.14	0.052	0.06	0.18
	CV	1.41	1.05	0.70	1.46	3.70	4.52	5.58	5.28	5.97	7.092	5.21	7.00
	Min	11.77	4.49	6.93	6.29	3.36	3.15	1.43	3.82	2.34	0.746	1.19	2.60
	Max	12.08	4.57	7.02	6.46	3.59	3.42	1.58	4.17	2.60	0.848	1.29	2.95
ANOVA	SS	0.151	0.092	0.513	0.222	0.412	0.288	0.071	0.260	0.094	0.365	0.152	0.044
	df	5	5	5	5	5	5	5	5	5	5	5	5
	F	0.484	1.767	3.422	1.926	6.692	3.517	1.680	3.525	2.371	10.009	5.173	1.047
	P	0.786	0.147	0.013*	0.117	2.10E-04***	0.012*	0.167	0.012*	0.061	6.78E-06***	0.001**	0.407

Table 6.31 Pearson correlation coefficients for correlation between latitude and longitude, and principal component scores and A) six OTUs, and B) six OTUs and four individuals, within the 12 cranial measurements of *Neoromicia zuluensis* from southern Africa. ** denotes significance at $P < 0.01$; *** denotes significance at $P < 0.001$.

A)	PC1	PC2	CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Latitude														
Pearson Correlation	-0.190	-0.018	0.145	-0.139	0.412	-0.411	-0.252	-0.455	-0.408	-0.360	0.077	0.106	0.114	-0.082
Significance (2-tailed)	0.719	0.974	0.784	0.793	0.417	0.419	0.629	0.365	0.422	0.484	0.885	0.841	0.830	0.878
Longitude														
Pearson Correlation	0.951	-0.147	-0.818	-0.495	0.629	0.659	0.781	0.770	-0.012	0.590	0.627	-0.975	-0.811	-0.562
Sig. (2-tailed)	0.004**	0.781	0.046*	0.319	0.181	0.155	0.067	0.073	0.981	0.218	0.183	0.001**	0.050	0.246
B)														
Latitude														
Pearson Correlation	-0.959	-0.068	-0.901	-0.818	-0.800	-0.808	-0.826	-0.421	-0.791	-0.763	-0.318	-0.313	-0.321	-0.493
Significance (2-tailed)	1.18E-05***	0.852	3.75E-04***	0.004**	0.005**	0.005**	0.003**	0.225	0.006**	0.010*	0.371	0.378	0.365	0.148
Longitude														
Pearson Correlation	0.637	-0.463	0.406	0.220	0.739	0.707	0.772	0.629	0.424	0.683	0.226	-0.415	0.096	-0.041
Sig. (2-tailed)	0.048*	0.178	0.244	0.541	0.015*	0.022*	0.009**	0.051	0.222	0.03*	0.530	0.233	0.792	0.911

to not allow pooling with another locality (Table 6.32). Unfortunately, these specimens were from three distinct Zimbabwean localities, a locality in the Limpopo Province of South Africa, and the most westerly locality in KwaZulu-Natal. Since these specimens would have greatly extended the geographic coverage of the analysis, two separate analyses were undertaken one of the six KwaZulu-Natal OTUs, and another of the six OTUs together with the specimens from five additional localities (Table 6.32). Both specimens of *P. hesperidus* marked as TM1085 (one from Tzaneen in the Limpopo Province and one from Malvern in the KwaZulu-Natal Province) were included in the analysis. Sharing the same accession number had caused some confusion as to which had been designated the type of *P. k. broomi* (Roberts, 1948). However, Smithers *et al.* (1987) formally confirmed the original designation of the individual from Malvern as correct.

A PCA scatterplot based on six OTUs (Fig. 6.29) showed a tendency for the OTU scores to increase with increasing latitude, along the first principal component axis, and to increase with increasing longitude, along the second principal component axis. The first principal component described 52.25% of the variation, and as with several other species, one of the eigenvectors was negative. The measurements that loaded highest and lowest were zygomatic breadth and width of the upper fourth premolar. The second principal component described 26.89% of the variation and braincase breadth and width of the foramen magnum loaded highest and lowest. A similar pattern was present in the PCA scatterplot of the 40 specimens making up the six OTUs (Fig. 6.30), although the specimens of OTU 5 do not follow the progression of larger first principal component score with increasing latitude, and specimens of OTU 6 span the entire range of the first principal component. The important measurements on the first and second principal component axes were also different to those based on OTUs (Table 6.33). The distance phenogram based on six OTUs revealed a similar pattern of variation between the specimens as that observed in the PCA (Fig. 6.31), while the distance phenogram based on 40 individuals showed little clustering in relation to different geographic localities (Fig. 6.32). The addition of individuals changed little in the overall pattern of the PCA scatterplots of OTUs and individuals (Fig. 6.33) and of all 46 individuals (Fig. 6.34). The patterns still roughly reflected an increase in principal component score with increasing latitude along the first principal component axis, although the association of increasing principal component score with increasing longitude on the second principal component axis was not apparent, and the important measurements on each principal component axis were different (Table 6.33). The distance phenogram based on six OTUs and individuals revealed a similar pattern of variation between the specimens as that observed in the PCA (Fig. 6.35), while the distance phenogram based on 46 individuals showed little clustering in relation to different geographic localities (Fig. 6.36).

Table 6.34 shows the basic statistics and the results of the one-way ANOVAs between OTUs for each measurement, which three measurements were significantly different between the different OTUs. A Tukey post-hoc test of moment arm of the temporal did not identify different subsets, whereas two different maximally non-significant subsets were identified for zygomatic breadth and width across the outer surfaces of the upper canines, although both identified a separation of OTUs along latitudinal lines (Appendix 6.2 F).

In the analyses of six OTUs, one measurement, width of the articular surface, was significantly negatively correlated with latitude (i.e. increase in size from north to south). In the analyses with both OTUs and individuals, six measurements, condylo-incisor skull length, braincase height, zygomatic breadth, braincase breadth, post-orbital width and width of the foramen, showed significant negative correlations with latitude (i.e. increased in size from north to south) (Table 6.35). However, there were no significant correlations in either analyses with longitude (Table 6.35). Both analyses of the six OTUs and the OTUs with individuals that the first principal component scores showed a significant negative correlation with latitude, but no significant correlation with longitude (Table 6.35). Thus, *P. hesperidus* showed significant clinal latitudinal variation in the overall size of the 12 cranial measurements with increasing size in more southerly OTUs, but no significant clinal longitudinal variation. Although this variation in size has some resemblance to a subspecies distinction between east coast *P. h. broomi* and *P. h. subtilis* from the "Interior of Caffraria" (Sundervall, 1846), however, the clinal variation in cranial size with latitude precludes the subspecies distinction.

6.3.1.10 *Pipistrellus rusticus*

For the initial PCA and UPGMA analyses to identify potential outliers and misidentified specimens, the 52 specimens of *P. rusticus* from various localities were allocated to three

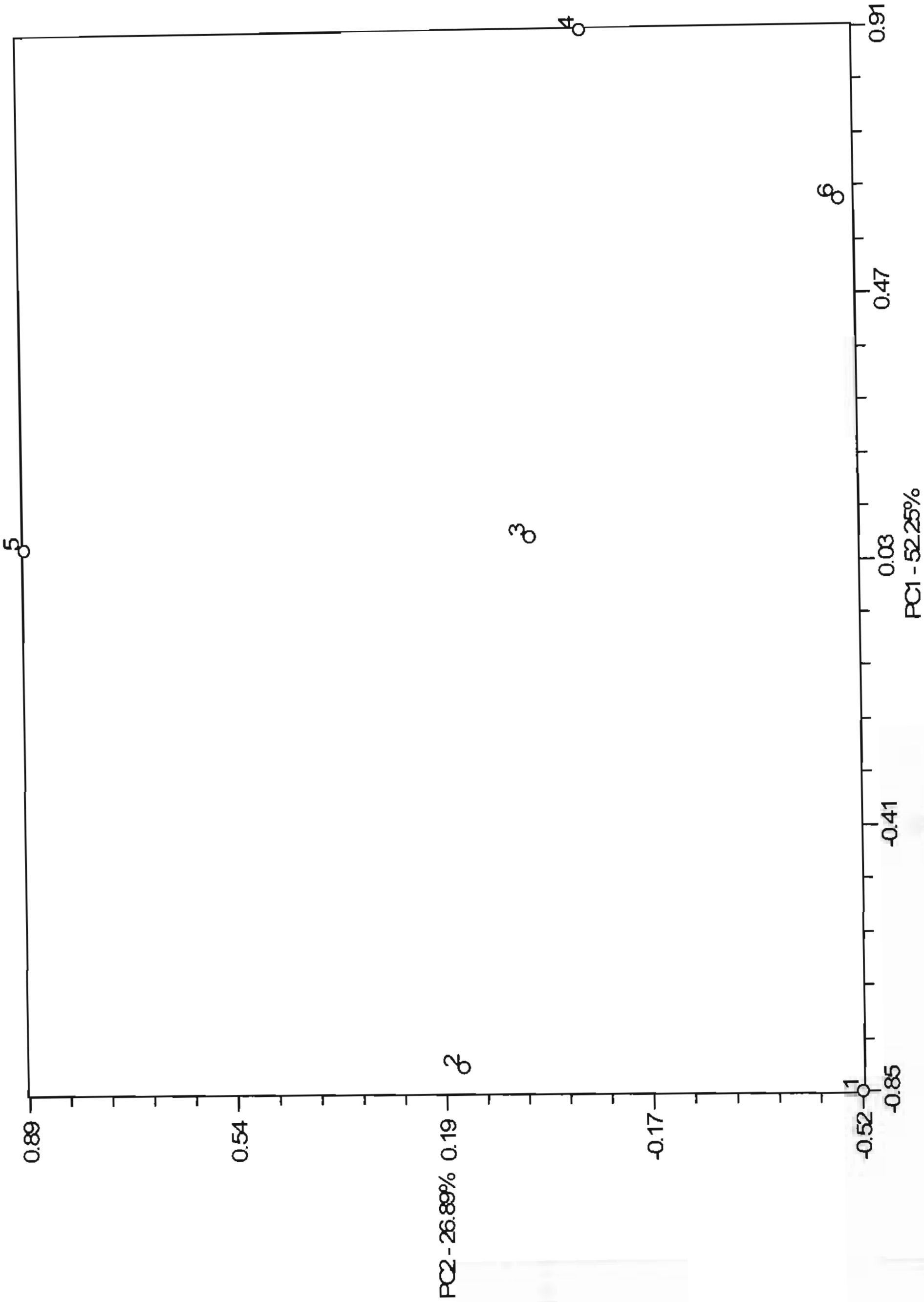


Figure 6.29 Scatterplot of the first two principal component axes based on six OTUs of *Pipistrellus hesperidus* from southern Africa. OTU numbers correspond to those in Table 6.32.

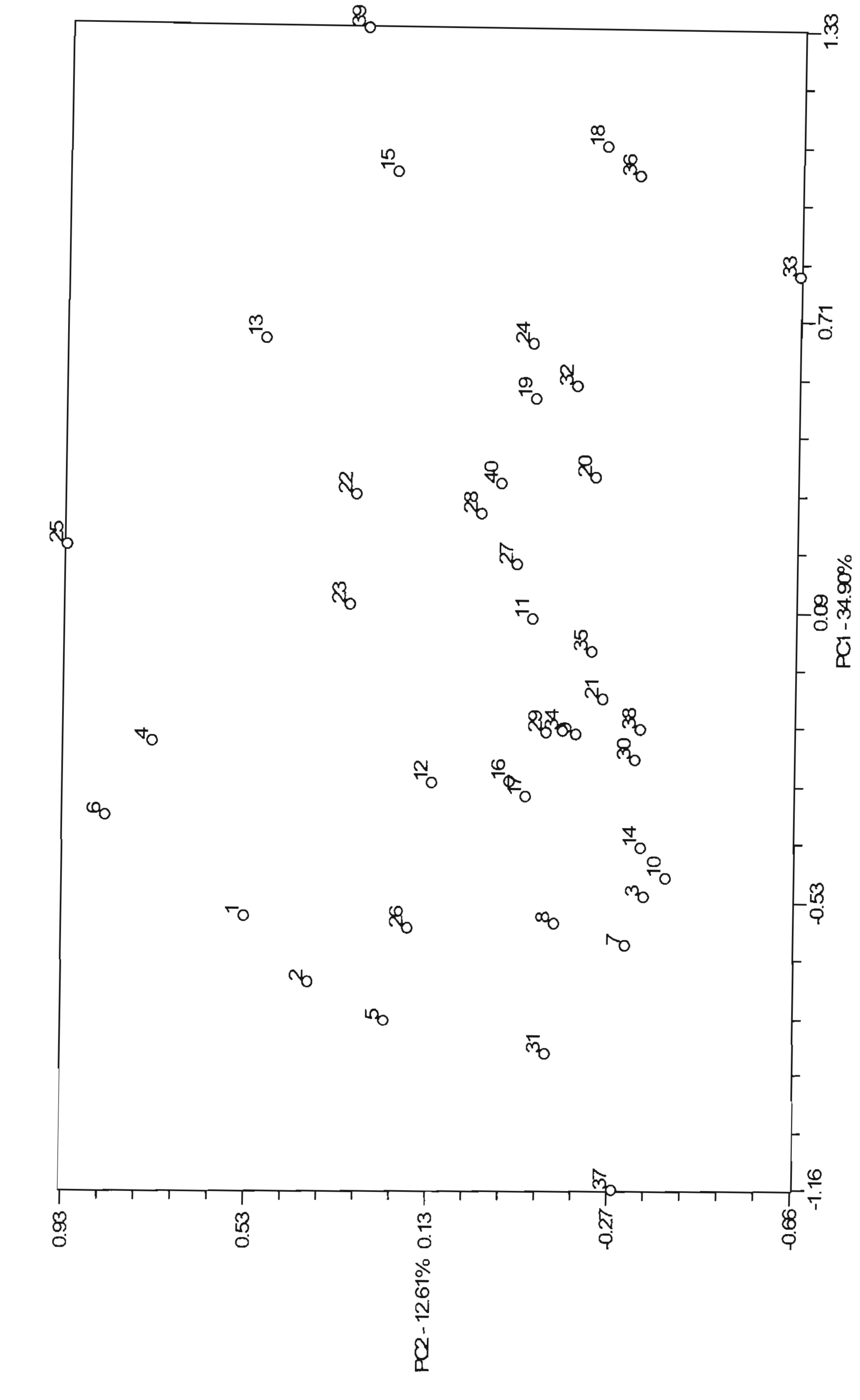


Figure 6.30 Scatterplot of the first two principal component axes based on 40 individuals of *Pipistrellus hesperidus* in southern Africa. Individual numbers correspond to those in Table 6.32.

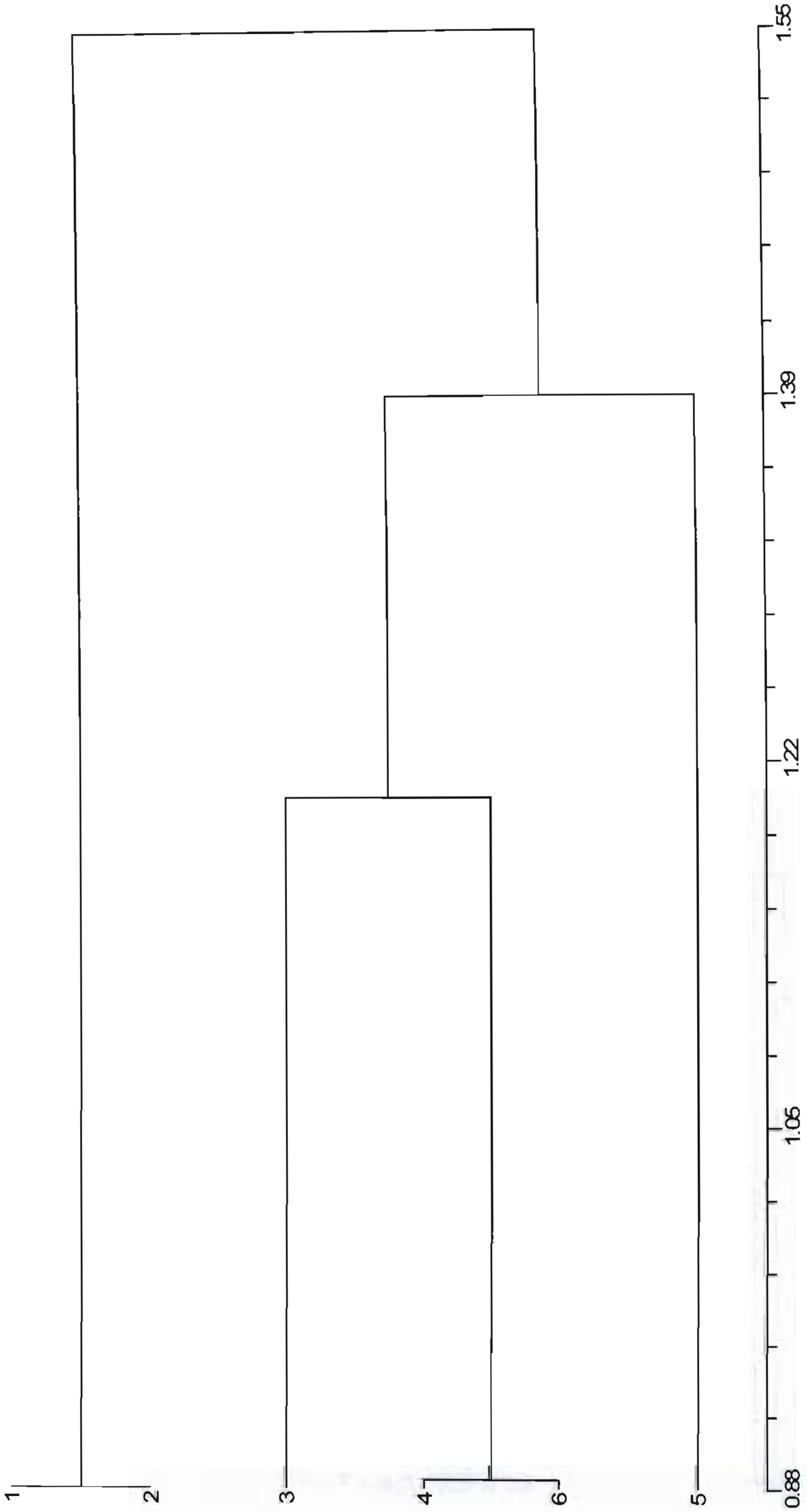


Figure 6.31 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on six OTUs of *Pipistrellus hesperidus* from southern Africa. OTU numbers correspond to those in Table 6.32. Cophenetic correlation coefficient = 0.792.

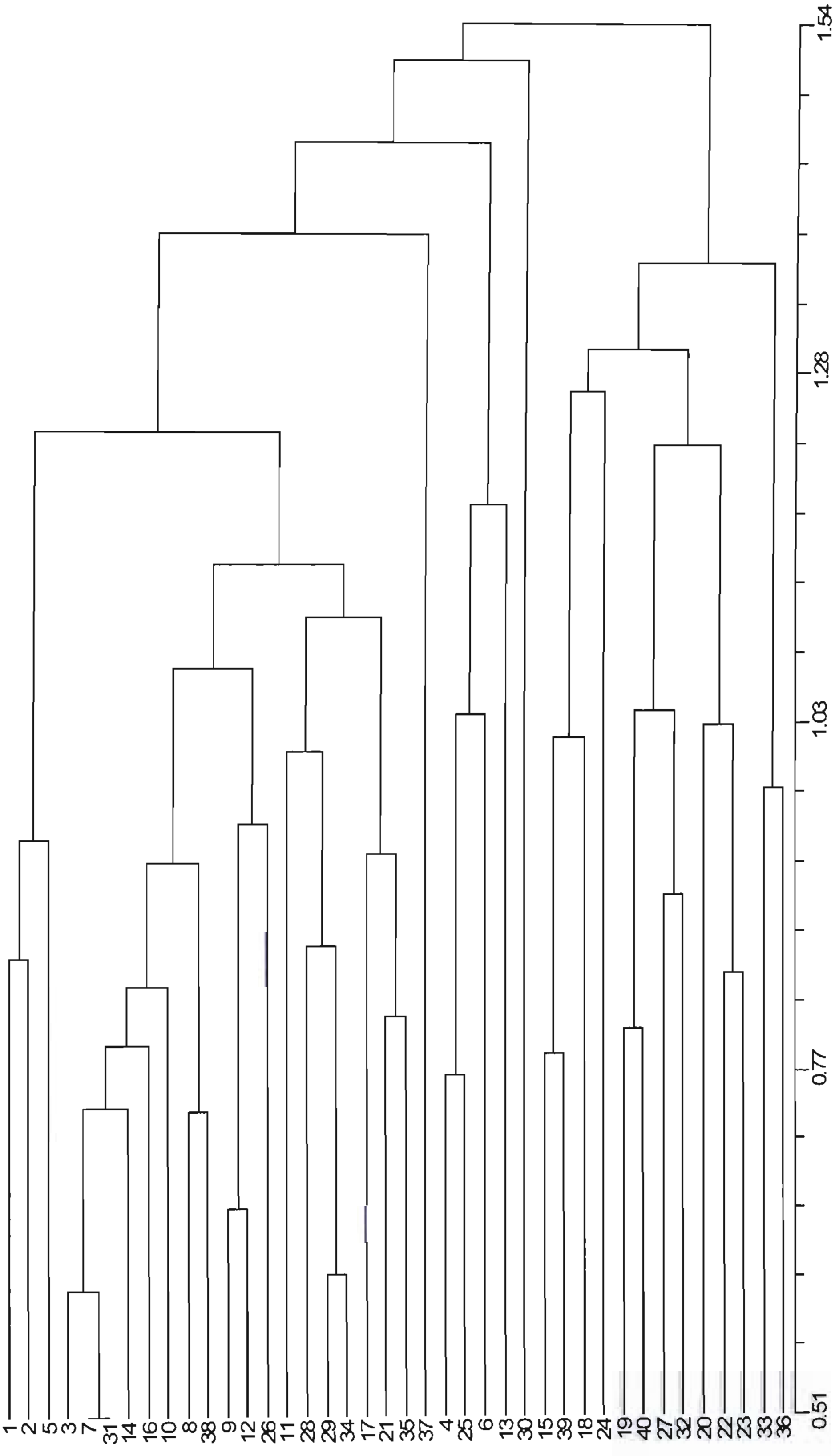


Figure 6.32 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on 40 individuals of *Pipistrellus hesperidus* from southern Africa. Individual numbers correspond to those in Table 6.32. Cophenetic correlation coefficient = 0.625.

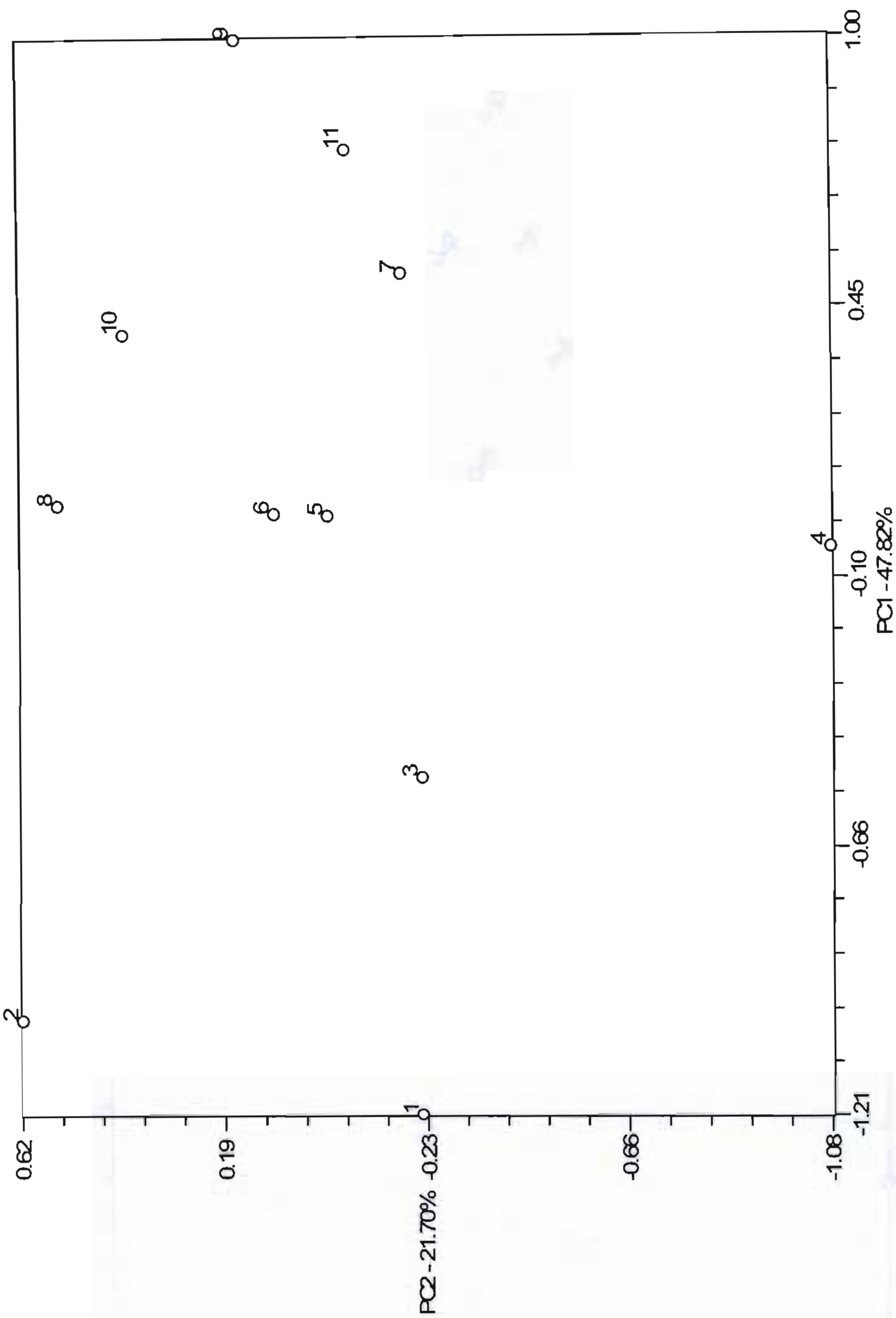


Figure 6.33 Scatterplot of the first two principal component axes based on six OTUs and five individuals of *Pipistrellus hesperidus* from southern Africa. OTU numbers correspond to those in Table 6.32.

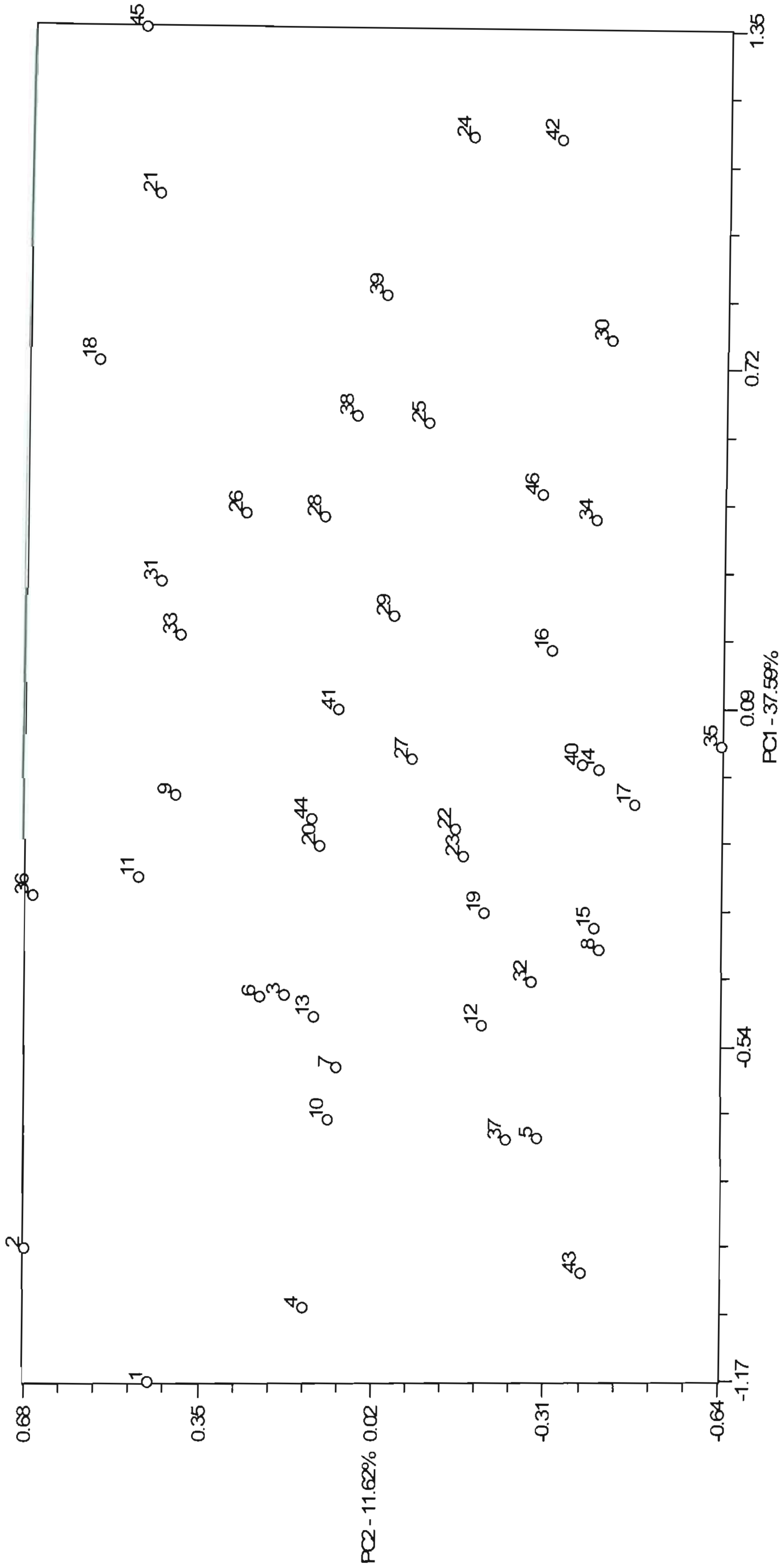


Figure 6.34 Scatterplot of the first two principal component axes based on 46 individuals of *Pipistrellus hesperidus* from southern Africa. Individual numbers correspond to those in Table 6.32.

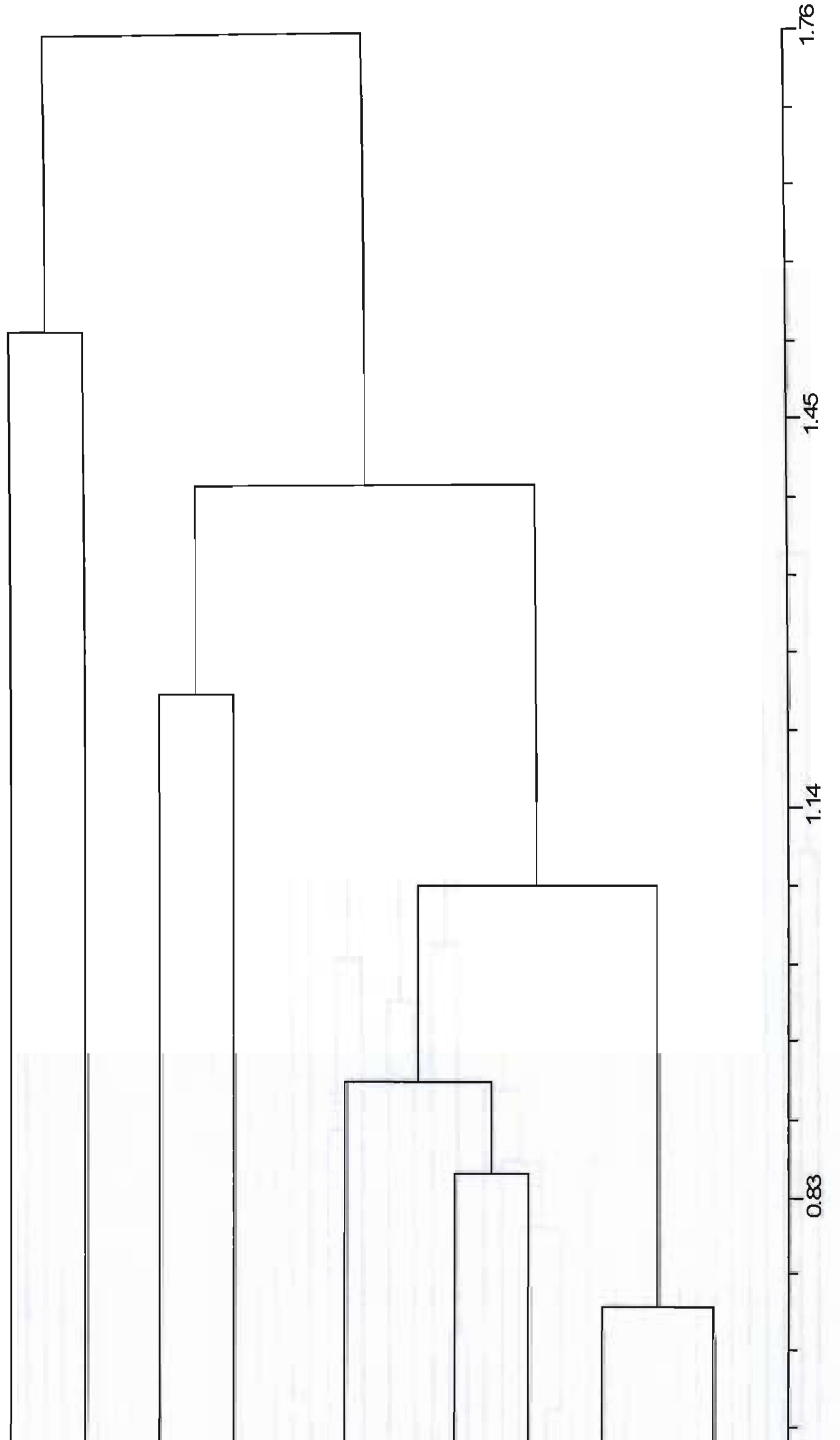


Figure 6.35 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on six OTUs and five individuals of *Pipistrellus hesperidus* from southern Africa. OTU and individual numbers correspond to those in Table 6.32. Cophenetic correlation coefficient = 0.832.

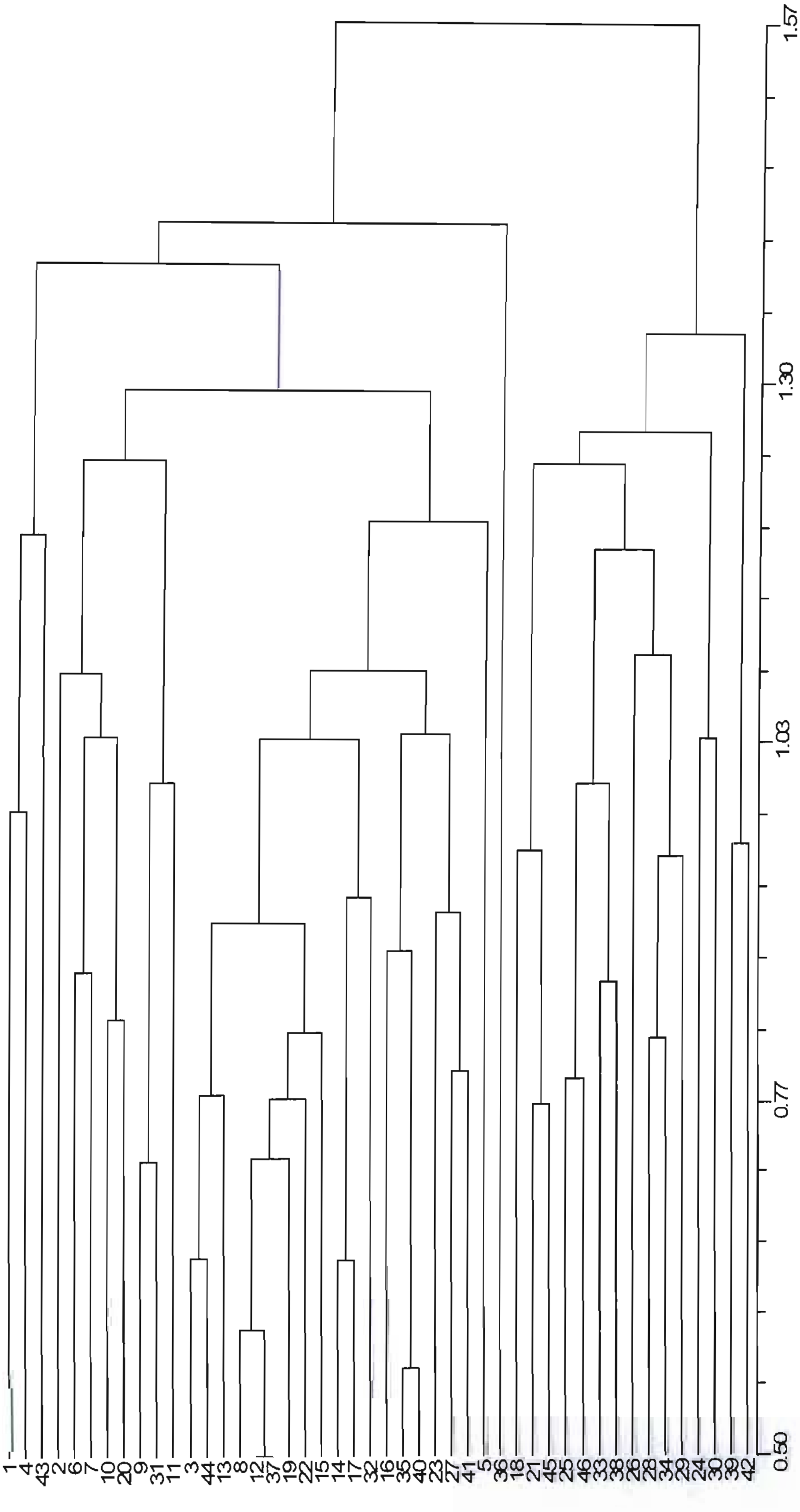


Figure 6.36 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on 46 individuals of *Pipistrellus hesperidus* from southern Africa. Individual numbers correspond to those in Table 6.32. Cophenetic correlation coefficient = 0.608.

Table 6.32 Six OTUs of single and pooled localities, and 11 localities of OTUs and single specimens (LOC) for *Pipistrellus hesperidus* from southern Africa in relation to occurrence from north to south, and east to west, with associated numbering of individuals in each OTU (IC) and locality (LOC IC), and number of specimens included in each OTU (*n*). For details on the localities and specimens used see Appendix 6.1

OTU	IC	LOC	LOC IC	Locality	*n*
-	-	1	1	Zimbabwe: Chikupo Cave	1
-	-	2	2	Zimbabwe: Banti	1
-	-	3	3-4	Zimbabwe: Rusito Forest	1
-	-	4	5	South Africa: Limpopo Province; Tzaneen Government Estate	1
1	1-3	5	6-8	South Africa: KwaZulu-Natal Province; Ndumu Game Reserve and Kosi Lake	3
2	4-7	6	9-12	South Africa: KwaZulu-Natal Province; Ngome Forest Reserve	4
3	8-14	7	13-19	South Africa: KwaZulu-Natal Province; Hluhluwe Game Reserve, Ipheva, and Dukuduku Forest	7
-	-	8	20	South Africa: KwaZulu-Natal Province; Harrismith	1
4	15-24	9	21-30	South Africa: KwaZulu-Natal Province; Dlinza Forest	10
5	25-27	10	31-33	South Africa: KwaZulu-Natal Province; Umlalazi, Twin Streams, and Harold Johnson Nature Reserve	3
6	28-40	11	34-46	South Africa: KwaZulu-Natal Province; Malvern, Yellowwood Park, Stainbank Nature Reserve	13

Table 6.33 Eigenvector scores of principal components one and two of PCAs based on 12 cranial measurements of A) six OTUs, B) 40 individuals, C) six OTUs and five individuals, and D) 54 individuals of *Pipistrellus hesperidus* from southern Africa. See the material and methods section of Chapter 5 for an explanation of the measurement codes. Highest and lowest scores are indicated in bold type.

	A)			B)			C)			D)	
Meas	**PC1**	**PC2**		**PC1**	**PC2**		**PC1**	**PC2**		**PC1**	**PC2**
CIL	0.820	0.106		**0.827**	0.158		0.891	0.335		**0.851**	0.086
BH	0.609	0.683		0.322	0.340		0.792	0.467		0.524	-0.265
ZB	**0.942**	-0.276		0.670	-0.332		0.802	-0.404		0.686	-0.320
BB	0.374	**0.918**		0.621	0.270		0.784	0.363		0.703	-0.083
POW	0.696	0.088		0.432	0.253		**0.895**	0.090		0.545	-0.179
WFM	0.330	**-0.860**		0.313	-0.251		0.816	-0.128		0.442	**-0.571**
WAS	0.885	-0.142		0.578	**-0.577**		-0.106	0.419		0.478	0.115
WOUC	0.779	0.614		**0.805**	0.021		0.590	0.499		**0.791**	0.196
WIUM1	0.849	0.174		0.687	-0.004		0.684	-0.451		0.666	0.241
WUPM4	**-0.732**	0.377		0.221	**0.845**		**-0.502**	0.645		0.082	**0.794**
LUM1	0.649	-0.690		0.651	-0.025		0.700	**-0.490**		0.672	0.138
MAOT	0.734	-0.192		0.596	-0.114		0.146	**0.819**		0.546	0.300

Table 6.34 Basic statistics and ANOVA results to test for OTU variation in six OTUs of *Pipistrellus hesperidus* in southern Africa. SD = standard deviation; CV = coefficient of variation; Min = minimum value; Max = maximum value; *n* = sample size; SS = sum of squares; df = degrees of freedom; *P* = significance of *F* values; * denotes significance at $P < 0.05$; ** denotes significance at $P < 0.01$. See Table 6.33 for a description of the OTU codes, and the material and methods section of Chapter 5 for an explanation of the measurement codes.

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
1	**Mean**	12.32	4.79	7.38	6.66	3.77	3.48	1.39	4.11	2.72	0.95	1.27	2.87
(*n* = 3)	**SD**	0.12	0.02	0.06	0.09	0.03	0.10	0.13	0.11	0.15	0.12	0.04	0.08
	CV	1.03	0.39	0.81	1.48	0.88	3.14	9.98	2.80	5.86	13.40	3.35	2.94
	Min	12.19	4.78	7.32	6.56	3.74	3.37	1.27	4.02	2.55	0.81	1.22	2.80
	Max	12.41	4.81	7.43	6.73	3.80	3.57	1.53	4.23	2.80	1.02	1.29	2.95
2	**Mean**	12.45	4.81	7.25	6.73	3.74	3.39	1.36	4.24	2.77	0.96	1.26	2.85
(*n* = 4)	**SD**	0.16	0.07	0.18	0.12	0.08	0.12	0.13	0.11	0.13	0.09	0.03	0.07
	CV	1.39	1.62	2.63	1.83	2.15	3.87	10.45	2.63	4.91	10.36	2.73	2.68
	Min	12.21	4.70	7.04	6.61	3.69	3.23	1.17	4.12	2.60	0.85	1.22	2.80
	Max	12.56	4.87	7.45	6.85	3.85	3.50	1.48	4.33	2.90	1.05	1.29	2.95
3	**Mean**	12.37	4.86	7.50	6.75	3.76	3.46	1.50	4.33	2.86	0.86	1.27	2.81
(*n* = 7)	**SD**	0.24	0.13	0.10	0.12	0.18	0.11	0.05	0.09	0.09	0.08	0.06	0.09
	CV	2.04	2.85	1.39	1.85	4.91	3.35	3.44	2.04	3.09	9.36	5.26	3.19
	Min	12.07	4.70	7.40	6.53	3.54	3.29	1.43	4.23	2.75	0.78	1.19	2.70
	Max	12.83	5.08	7.63	6.86	4.00	3.63	1.58	4.48	3.00	1.02	1.39	2.90
4	**Mean**	12.78	4.89	7.65	6.74	3.81	3.49	1.49	4.40	2.87	0.89	1.30	3.01
(*n* = 10)	**SD**	0.38	0.12	0.20	0.20	0.09	0.12	0.12	0.11	0.08	0.05	0.05	0.10
	CV	3.05	2.60	2.72	3.07	2.37	3.52	8.42	2.58	2.87	5.82	4.19	3.51
	Min	12.14	4.64	7.43	6.49	3.65	3.28	1.32	4.28	2.75	0.81	1.22	2.85
	Max	13.24	5.06	8.05	7.08	3.92	3.68	1.68	4.63	3.00	0.98	1.39	3.16

Table 6.34 continued

		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
5	Mean	12.52	4.89	7.43	6.81	3.82	3.35	1.46	4.43	2.80	0.95	1.24	2.88
(*n* = 15)	SD	0.32	0.06	0.08	0.04	0.14	0.09	0.32	0.05	0.10	0.10	0.09	0.06
	CV	2.76	1.30	1.17	0.64	3.97	2.80	24.00	1.25	3.94	11.61	7.44	2.21
	Min	12.18	4.82	7.35	6.77	3.71	3.30	1.27	4.38	2.70	0.85	1.15	2.85
	Max	12.81	4.93	7.51	6.85	3.98	3.45	1.83	4.48	2.90	1.05	1.32	2.95
6	Mean	12.58	4.81	7.62	6.71	3.83	3.47	1.55	4.33	2.82	0.87	1.32	2.94
(*n* = 4)	SD	0.31	0.13	0.19	0.18	0.13	0.17	0.13	0.18	0.11	0.06	0.05	0.14
	CV	2.50	2.70	2.50	2.77	3.51	4.99	8.60	4.24	4.08	6.84	3.77	4.68
	Min	12.21	4.58	7.21	6.28	3.57	3.15	1.32	4.07	2.60	0.78	1.22	2.75
	Max	13.15	5.00	7.90	6.97	4.00	3.87	1.78	4.63	3.00	1.02	1.39	3.16
ANOVA	SS	0.930	0.057	0.682	0.039	0.044	0.064	0.146	0.260	0.077	0.052	0.027	0.193
	df	5	5	5	5	5	5	5	5	5	5	5	5
	F	2.035	0.832	4.806	0.294	0.568	0.688	1.526	2.931	1.426	2.030	1.808	3.330
	P	0.098	0.536	0.002**	0.913	0.724	0.636	0.208	0.026*	0.240	0.099	0.138	0.015*

Table 6.35 Pearson correlation coefficients for correlation between latitude and longitude and principal component scores and A) six OTUs, and B) six OTUs and five individuals, within the 12 cranial measurements of *Pipistrellus hesperidus* from southern Africa. ** denotes significance at $P < 0.01$; *** denotes significance at $P < 0.001$.

A)	PC1	PC2	CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Latitude														
Pearson Correlation	-0.837	-0.190	-0.680	-0.434	-0.686	-0.529	-0.756	0.082	-0.824	-0.805	-0.674	0.559	-0.539	-0.536
Significance (2-tailed)	0.038*	0.719	0.137	0.390	0.132	0.280	0.082	0.877	0.044*	0.053	0.142	0.248	0.270	0.273
Longitude														
Pearson Correlation	-0.538	-0.103	-0.688	-0.100	-0.343	-0.317	-0.513	0.204	-0.414	-0.526	-0.383	0.202	-0.540	-0.565
Significance (2-tailed)	0.271	0.846	0.131	0.850	0.506	0.541	0.298	0.698	0.415	0.284	0.454	0.701	0.269	0.243
B)														
Latitude														
Pearson Correlation	-0.920	-0.190	-0.886	-0.855	-0.607	-0.933	-0.878	-0.750	0.059	-0.588	-0.410	0.314	-0.551	-0.136
Significance (2-tailed)	6.01E-05***	0.575	2.84E-04***	0.001**	0.048*	2.82E-05***	3.74E-04***	0.008**	0.863	0.057	0.210	0.348	0.079	0.690
Longitude														
Pearson Correlation	-0.239	0.093	-0.280	-0.012	-0.169	-0.466	-0.123	-0.156	-0.226	-0.156	0.000	0.341	-0.261	0.316
Significance (2-tailed)	0.478	0.785	0.404	0.972	0.618	0.148	0.718	0.648	0.504	0.646	0.999	0.305	0.438	0.343

manageable groups based on geographic proximity. One outlier, specimen (TM39886), was removed from further analyses. A PCA scatterplot of the first two principal components based on seven OTUs (Table 6.36) of *P. rusticus* (Fig.6.37), identified some separation along both the first and second principal components in relation to latitudinal distribution, with OTU score generally increasing with increasing latitude along the first principal component axis, and increasing with increasing longitude on the second principal component axis. The first principal component axis explained 51.65% of the variation and, as in *N. africanus*, the eigenvector scores were, unusually for the first principal component axis, both negative and positive (Table 6.37). The measurements scoring highest and lowest on the first principal component axis were width between the inner surfaces of the upper first molars and braincase height. The second principal component axis explained 17.69% of the variance and the measurements which loaded highest and lowest were braincase breadth and greatest width of the articular surface (Table 6.37). A PCA scatterplot of the first two principal components based on 50 individuals of *P. rusticus* used in the OTU analysis (Fig. 6.38) identified a similar pattern to that in the PCA of OTUs although the important measurements on the first two principal components were slightly different (Table 6.37). The clustering pattern in the distance phenogram based on seven OTUs was similar to the pattern of OTU distribution observed in the PCA (Fig. 6.39). The distance phenogram based on 50 individuals identified some clustering of individuals of OTUs 1, 4, and 5, although generally the clustering was not in relation to similar OTUs (Fig. 6.40).

Table 6.38 gives the basic statistics and the results of the one-way ANOVAs between OTUs for each measurement, which identified eight of the 12 measurements as significantly different between different OTUs. Post-hoc Tukey tests identified significantly different subsets for each of the measurements, although there were three patterns apparent (Appendix 6.2 G). The two subsets of braincase height separated subsets and OTUs largely in relation to longitude, the two subsets in each of width of the upper fourth premolar and length between the condylar and length of the upper first molar separated the subsets and the OTUs largely in relation to latitude, while the pattern was similar in width across the outer surfaces of the upper canines and length between the condylar and the coronoid processes of the mandible it was not discernable in relation to latitudinal or longitudinal change.

Three measurements showed significant negative correlations between OTUs and latitude (i.e. increased in size from north to south), and two measurements showed significant negative correlations with longitude (i.e. increasing in size from east to west), while two measurements showed significant positive correlations with longitude (i.e. decreasing in size from OTUs in the east to OTUs in the west) (Table 6.39). The first principal component scores of the OTUs was significantly negatively correlated with latitude, but not longitude (Table 6.39). Thus *P. rusticus* showed significant clinal latitudinal variation in the overall size of the 12 cranial measurements with increasing size in more southerly OTUs, and although some measurements showed significant positive and negative clinal longitudinal variation, there was no overall longitudinal clinal variation in the 12 cranial measurements.

6.3.2 Summary of results across the species analysed

The species analysed differed in the number and type of measurements showing significant geographic variation, and showed significant correlation between geographic variation and latitude and longitude. In tests for significant geographic variation within each of the 12 cranial measurements, four species (*H. anchietae*, *N.* cf. *melckorum*, *N. rueppellii*, and *P. hesperidus)* displayed the least variation in measurements between OTUs (between one and three significantly different measurements), one species (*N. zuluensis*) showed half the measurements (six) to have significant variations between OTUs, and four species (*E. hottentotus*, *N. capensis*, *N. africanus*, and *P. rusticus*) had the most significant variation in measurements between OTUs (between eight and 12 significantly different measurements). *Neoromicia capensis* had the greatest number of measurements showing significant differences between the OTUs. An assessment across all the analyses where measurements showed significant variation between the OTUs, identified that all 12 cranial measurements varied significantly among OTUs and the most commonly significantly different measurement was width across the outer surfaces of the upper canines, which was significant in seven of the nine analyses. Tukey post-hoc tests of the significantly different OTUs sometimes identified a pattern of change in relation to latitude and/or longitude, but in many cases there was no discernible relationship with neither latitude nor longitude.

The direction of significant correlations also varied: more (88.57%) of the significant

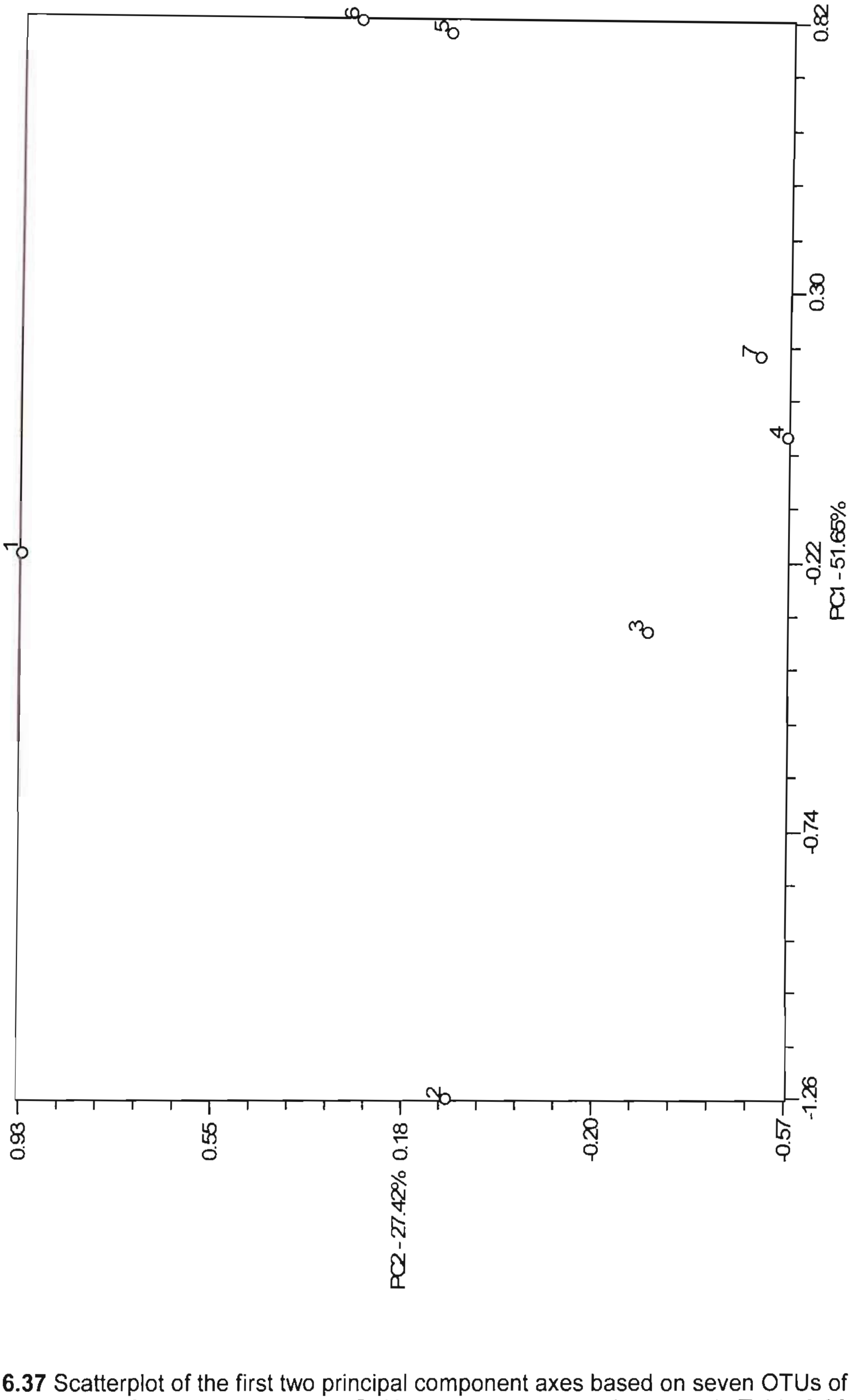


Figure 6.37 Scatterplot of the first two principal component axes based on seven OTUs of *Pipistrellus rusticus* from southern Africa. OTU numbers correspond to those in Table 6.36.

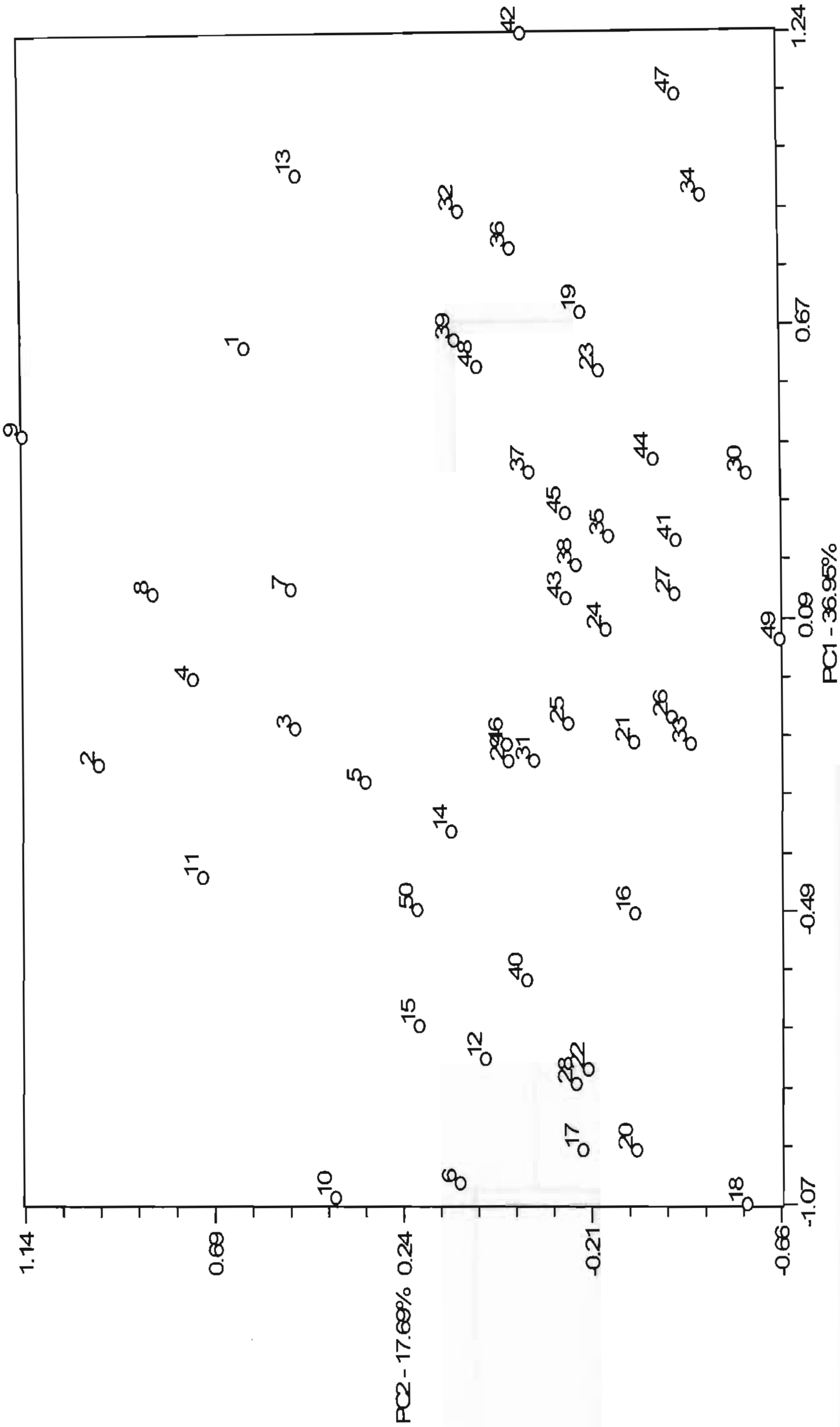


Figure 6.38 Scatterplot of the first two principal component axes based on 50 individuals of *Pipistrellus rusticus* in southern Africa. Individual numbers correspond to those in Table 6.36.

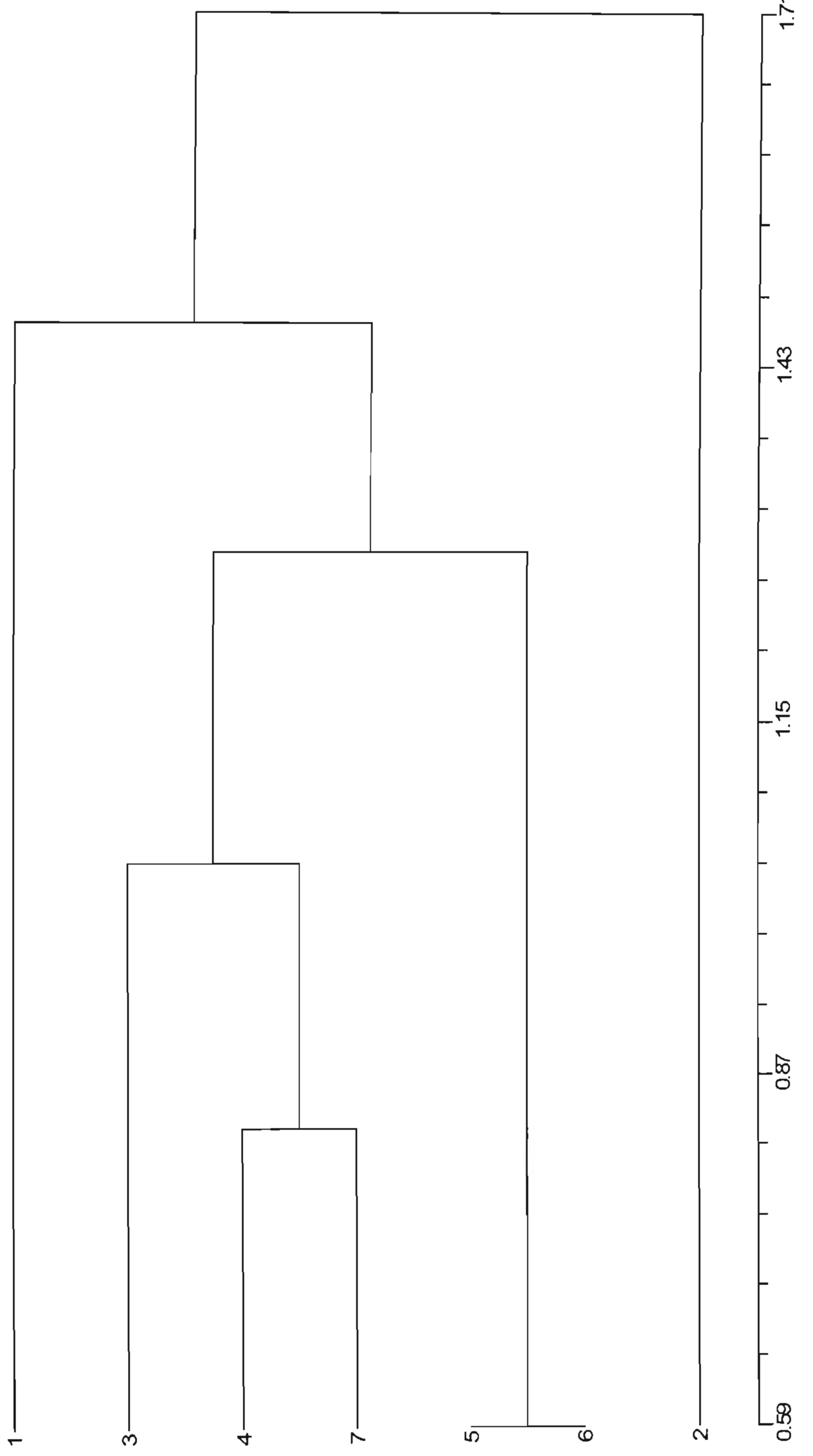


Figure 6.39 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on seven OTUs of *Pipistrellus rusticus* from southern Africa. OTU numbers correspond to those in Table 6.36. Cophenetic correlation coefficient = 0.847.

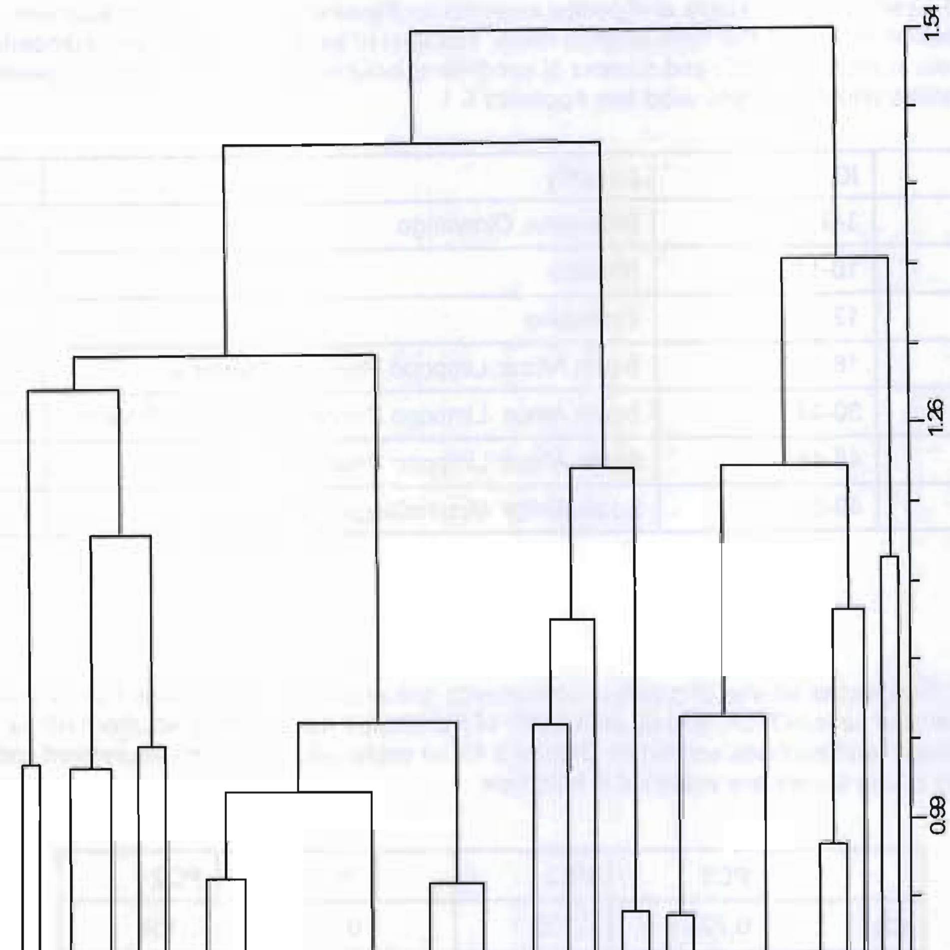


Figure 6.40 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on 50 individuals of *Pipistrellus rusticus* from southern Africa. Individual numbers correspond to those in Table 6.36. Cophenetic correlation coefficient = 0.592.

Table 6.36 Seven OTUs of single and pooled localities for *Pipistrellus rusticus* from southern Africa in relation to occurrence from north to south, and east to west, with associated numbering of individuals in each OTU (IC) and number of specimens included in each OTU (*n*). For details on the localities and specimens used see Appendix 6.1.

OTU	IC	Locality	*n*
1	1-9	Botswana: Okavango	9
2	10-11	Namibia	2
3	12-17	Zimbabwe	6
4	18-29	South Africa: Limpopo Province; Messina	12
5	30-44	South Africa: Limpopo Province; Farm Klipfontein	15
6	45-48	South Africa: Limpopo Province; Warmbaths	4
7	49-50	South Africa: Mpumalanga; Legogot	2

Table 6.37 Eigenvector scores of principal components one and two of PCAs based on 12 cranial measurements of seven OTUs, and 50 individuals of *Pipistrellus rusticus* from southern Africa. See the material and methods section of Chapter 5 for an explanation of the measurement codes. Highest and lowest scores are indicated in bold type.

	PC1	PC2		PC1	PC2
CIL	0.729	0.225		0.722	0.138
BH	**-0.424**	0.856		0.439	**0.759**
ZB	0.694	0.436		0.786	0.070
BB	-0.280	**0.937**		0.502	0.677
POW	0.090	0.927		0.399	0.470
WFM	0.832	0.379		0.465	0.173
WAS	0.768	**-0.456**		0.604	-0.425
WOUC	0.861	0.271		**0.853**	-0.239
WIUM1	**0.917**	0.045		**0.830**	-0.192
WUPM4	0.754	0.036		0.140	0.087
LUM1	0.909	-0.355		0.470	**-0.687**
MAOT	0.812	0.162		0.673	-0.245

Table 6.38 Basic statistics and ANOVA results to test for OTU variation in seven OTUs of *Pipistrellus rusticus* from southern Africa. SD = standard deviation; CV = coefficient of variation; Min = minimum value; Max = maximum value; *n* = sample size; SS = sum of squares; df = degrees of freedom; *P* = significance of *F* values; * denotes significance at $P < 0.05$. See Table 6.37 for a description of the OTU codes, and the material and methods of Chapter 5 for an explanation of the measurement codes.

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
1	**Mean**	11.48	4.59	7.02	6.41	3.59	3.25	1.24	3.86	2.60	0.90	1.09	2.65
(*n* = 9)	**SD**	0.35	0.22	0.16	0.16	0.13	0.14	0.10	0.13	0.09	0.05	0.04	0.12
	CV	3.16	4.93	2.38	2.62	3.66	4.27	8.18	3.57	3.55	6.15	3.49	4.67
	Min	10.89	4.19	6.79	6.04	3.37	3.05	1.17	3.67	2.49	0.81	1.05	2.44
	Max	11.96	4.89	7.33	6.56	3.78	3.49	1.43	4.02	2.75	0.98	1.15	2.80
2	**Mean**	11.13	4.57	6.71	6.28	3.53	3.06	1.22	3.74	2.57	0.66	1.02	2.55
(*n* = 2)	**SD**	0.16	0.03	0.11	0.19	0.13	0.08	0.07	0.11	0.04	0.07	-	-
	CV	1.57	0.70	1.78	3.42	4.29	2.86	6.63	3.25	1.58	12.24	-	-
	Min	11.02	4.55	6.63	6.14	3.43	3.00	1.17	3.67	2.55	0.61	1.02	2.55
	Max	11.24	4.59	6.78	6.41	3.62	3.11	1.27	3.82	2.60	0.71	1.02	2.55
3	**Mean**	11.60	4.35	6.95	6.19	3.50	3.07	1.25	3.82	2.59	0.87	1.17	2.48
(*n* = 6)	**SD**	0.23	0.16	0.28	0.16	0.21	0.13	0.06	0.16	0.18	0.09	0.04	0.14
	CV	2.10	3.74	4.12	2.69	6.13	4.48	5.21	4.48	7.03	10.16	3.70	5.85
	Min	11.39	4.20	6.63	5.97	3.23	2.90	1.17	3.67	2.39	0.78	1.12	2.29
	Max	11.96	4.64	7.46	6.46	3.80	3.24	1.32	4.07	2.90	1.02	1.22	2.70
4	**Mean**	11.26	4.27	6.93	6.14	3.48	3.16	1.32	3.87	2.64	0.79	1.18	2.72
(*n* = 12)	**SD**	0.33	0.11	0.32	0.18	0.11	0.09	0.10	0.15	0.13	0.05	0.04	0.13
	CV	3.00	2.51	4.73	2.99	3.08	2.83	7.67	3.94	5.13	6.28	3.27	4.85
	Min	10.75	4.07	6.40	5.85	3.34	2.97	1.17	3.56	2.39	0.71	1.12	2.49
	Max	11.89	4.42	7.47	6.46	3.67	3.28	1.48	4.07	2.85	0.88	1.22	2.95

Table 6.38 continued

OTU		CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
5	**Mean**	11.60	4.36	6.98	6.23	3.54	3.28	1.35	4.06	2.72	0.90	1.22	2.81
(*n* = 15)	**SD**	0.26	0.11	0.28	0.11	0.13	0.16	0.10	0.15	0.10	0.08	0.05	0.11
	CV	2.26	2.53	4.04	1.75	3.72	4.97	7.53	3.63	3.79	8.76	3.76	4.12
	Min	11.21	4.10	6.49	6.02	3.33	3.08	1.22	3.67	2.55	0.71	1.15	2.60
	Max	12.23	4.53	7.33	6.37	3.80	3.58	1.53	4.28	2.95	1.02	1.29	2.95
6	**Mean**	11.62	4.47	7.11	6.21	3.53	3.27	1.29	4.10	2.76	0.92	1.25	2.76
(*n* = 4)	**SD**	0.29	0.06	0.27	0.09	0.07	0.06	0.08	0.17	0.11	0.11	0.05	0.13
	CV	0.15	0.09	0.24	0.09	0.13	0.12	0.37	0.26	0.26	0.71	0.24	0.30
	Min	11.28	4.41	6.85	6.12	3.45	3.21	1.17	3.92	2.65	0.78	1.22	2.65
	Max	11.97	4.56	7.49	6.32	3.61	3.34	1.32	4.33	2.90	1.02	1.32	2.95
7	**Mean**	11.43	4.31	6.78	6.09	3.52	3.23	1.32	3.79	2.65	0.99	1.23	2.64
(*n* = 2)	**SD**	0.01	0.07	0.24	0.21	0.09	0.01	0.10	0.14	0.17	0.02	0.07	0.07
	CV	0.07	1.85	3.99	3.92	2.94	0.49	8.37	4.19	7.28	2.79	6.72	3.00
	Min	11.42	4.26	6.61	5.94	3.45	3.22	1.25	3.69	2.53	0.97	1.18	2.59
	Max	11.43	4.36	6.95	6.24	3.58	3.24	1.38	3.88	2.77	1.00	1.28	2.69
ANOVA	**SS**	1.232	0.652	0.333	0.439	0.070	0.306	0.104	0.623	0.180	0.223	0.177	0.560
	df	6	6	6	6	6	6	6	6	6	6	6	6
	F	2.403	5.749	0.771	3.271	0.672	3.162	1.979	4.774	2.067	7.675	16.606	6.317
	P	0.043*	1.85E-04***	0.597	0.010*	0.673	0.012*	0.090	0.001**	0.077	1.22E-05***	8.53E-10***	8.04E-05***

Table 6.39 Pearson correlation coefficients for correlation between latitude and longitude and principal component scores and seven OTUs within the 12 cranial measurements of *Pipistrellus rusticus* from southern Africa. ** denotes significance at $P < 0.01$; *** denotes significance at $P < 0.001$.

	PC1	PC2	CIL	BH	ZB	BB	POW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Latitude														
Pearson Correlation	-0.800	0.477	-0.480	0.659	-0.218	0.742	0.343	-0.518	-0.784	-0.547	-0.786	-0.651	-0.931	-0.543
Significance (2-tailed)	0.031*	0.279	0.276	0.108	0.639	0.056	0.451	0.234	0.037*	0.204	0.036*	0.114	0.002**	0.208
Longitude														
Pearson Correlation	0.703	-0.621	0.464	-0.892	0.313	-0.769	-0.500	0.362	0.770	0.336	0.502	0.669	0.897	0.359
Significance (2-tailed)	0.078	0.137	0.295	0.007**	0.495	0.043*	0.253	0.425	0.043*	0.462	0.251	0.100	0.006**	0.429

correlations with latitude were negative (i.e. increase in measurement size from north to south), whereas more of the significant correlations with longitude (74.07%) were negative (i.e. increase in measurement size from east to west). The analyses of *P. rueppellii* and OTUs of *N. zuluensis* found no measurements with a significant correlation between latitude and variation between OTUs. The majority of the species (*E. hottentotus*, *H. anchietae*, *N.* cf. *melckorum*, *N. africanus*, OTUs of *P. hesperidus* and *P. rusticus*) showed between one and four measurements in which variation between OTUs was significantly correlated with latitude. Of these, the significant correlations in four species (*E. hottentotus*, *N. africanus*, OTUs of *P. hesperidus*, and *P. rusticus*) were negative, hence size of the significant measurement increased from north to south, whereas in two species (*H. anchietae*, *N.* cf. *melckorum*) the significant correlations were positive and size of the significant measurement increased from south to north. Three species (*N. capensis*, OTUs with individuals of *N. zuluensis*, and OTUs with individuals of *P. hesperidus*) showed a significant negative correlation between OTU and latitude in six to nine of the 12 measurements, with size of the significant measurement increasing from north to south. *Neoromicia capensis* was the species with the greatest number of measurements displaying a significant negative correlation between OTU change and latitude.

The analyses of *P. rueppellii* and both analyses of OTUs and OTUs with individuals of *P. hesperidus,* found no measurements that showed a significant correlation between longitude and variation between OTUs. Four species (*H. anchietae*, *N. africanus*, analysis of OTUs only of *N. zuluensis*, and *P. rusticus*) had very few (between one and two) measurements with a significant negative or positive correlation between OTU change and longitude. Of these species, two (*N. africanus* and *P. rusticus*) showed measurements with mixed direction of correlation presenting a mosaic pattern of geographic variation, hence size of the significant measurements was increasing from east to west in some measurements, while decreasing in size from east to west in other measurements. One species, (*H. anchietae*) showed a positive significant correlation with longitude in which size of the significant measurement was decreasing from east to west, and one species (analysis of OTUs only of *N. zuluensis*) showed a negative significant correlation with longitude in which size of the significant measurements was increasing from east to west. Three species (*E. hottentotus*, *N.* cf. *melckorum*, and analysis of OTUs with individuals of *N. zuluensis*) showed between three and five measurements with a significant correlation between OTU change and longitude, of these species, the significant correlations in one species (*E. hottentotus*) were negative and hence, size of the significant measurements increased from OTUs in the east to OTUs in the west, while those of two species (*N.* cf. *melckorum* and the analysis of OTUs with individuals of *N. zuluensis*) were positive and size of the significant measurements decreased from east to west. *Neoromicia capensis* showed the greatest number of measurements (eight) with a significant negative correlation between OTU change and longitude, hence, size of the significant measurements increased from east to west.

Although each species showed different suites of measurements significantly correlated with latitude and/or longitude, there were also some inter-specific similarities. Comparing the results of all the tests, all 12 cranial measurements showed significant correlation with longitude, whereas 11 of the 12 showed significant correlation with latitude, with length between the condylar and the coronoid processes of the mandible not being significantly correlation with latitude in any of the tests. Across the eleven intra-specific tests, length of the upper first molar was the most common measurement to be significantly correlated with latitude (being significant in five of the tests), whereas in the correlations with longitude, three measurements were most common (occurring in four of the tests): condylo-incisor skull length, width across the outer surfaces of the upper canines, and length of the upper first molar. In only three species (*N. capensis*, *N.* cf. *melckorum*, and in the analysis of OTUs and individuals in *N. zuluensis*), there were some similarities between the measurements significantly correlated with latitude and longitude, but only in *N.* cf. *melckorum* were the same three measurements significantly correlated with both latitude and longitude.

Assessment of overall change within a species in all 12 cranial measurements (as measured by the first and second principal component scores) across OTUs, found more significant correlation between first principal component scores and latitude than with longitude. There was only one significant correlation with second principal component scores, in *N. capensis*, where overall cranial change was significantly negatively correlated with latitude. Two species (*N. capensis* and OTUs with individuals of *N. zuluensis*) showed a significant correlation between first principal component scores and both latitude and longitude, in *N. capensis* both correlations were negative, whereas in the analysis of *N. zuluensis*, the correlation with latitude was negative but that with longitude was positive. In *N. capensis,* first principal component scores increased in localities from the north-east to localities in the south-west, whereas in *N. zuluensis,* the longitudinal size variation was reversed such that first principal component scores increased in localities from the north-west to the south-east. Three species (*H. anchietae*, *P. hesperidus*, and *P. rusticus*), showed a significant negative correlation between first principal component scores and latitude in which the first principal component scores increased in localities from north to south, and one species (analysis of OTUs of *N. zuluensis*), showed a significant positive correlation between first principal component scores and longitude in which the first principal component scores increased in localities from west to east.

The measurements that were most important for the variation on the first and second principal components, varied considerably. Across the analyses of the different species, 11 of the 12 cranial measurements were important on the first principal component axis, only length of the upper first molar was never important, whereas eight of the 12 cranial measurements were important on the second principal component axis. The four measurements that were not important were condylo-incisor skull length, zygomatic breadth, width across the outer surfaces of the upper canines, and width between the inner surfaces of the upper first molars. The most commonly important measurement across the different tests on the first principal component axis (in 41.67% of the tests), was width of the upper fourth premolar, whereas width of the foramen magnum and length of the upper first molar were the most common important measurements (also in 41.67% of the tests) on the second principal component axis. In eight of 12 analyses, the signs of the first principal component eigenvalues were mixed, in most cases with just a few negative loadings suggesting variation in shape was involved in these measurements, although in two species (*N. africanus*, and the reduced areas analysis of *N. zuluensis*) the measurements of one sign relative to the other suggested complex shape differences (Dippenaar, 1995). In the other four analyses (*E. hottentotus*, *N. capensis*, *N. rendalli* and the extended area analysis of *N. zuluensis*), the eigenvector values were all positive indicating the influence of size rather than shape in this component.

6.4 DISCUSSION

Albeit for some of the species these analyses were performed on very limited numbers of specimens and limited numbers of localities, a useful first insight (with the exception of *E. hottentotus*) was, nevertheless, gained into geographic variation in size of 12 cranial morphometric measurements within the southern Africa distributions of nine vesper species. Unfortunately, the number of specimens and localities for *N. rendalli* were just too few (see description of known distribution of this species in southern Africa in the Chapter 1) to identify any pattern more than an overall size difference in the 12 cranial measurements between a Zimbabwean specimen (which was smaller) and the KwaZulu-Natal specimens. Further studies are required to confirm this size variation.

These results indicated that *N. capensis* was the most geographically variable of the species analysed over its distribution in southern Africa, although it was also the species with the widest geographic range across southern Africa. The overall cranial size of *N. capensis* showed a clinal relationship with both latitude and longitude, such that specimens increased in size from localities in the north-east to localities in the south-west. A clinal pattern of variation in overall cranial size correlated with latitude, with cranial size increasing in specimens at localities from north to south, was also found in *H. anchietae*, *P. hesperidus*, and *P. rusticus*. Over a reduced distributional area, *N. zuluensis* only showed a clinal pattern of variation in overall cranial size positively correlated with longitude, with cranial size increasing from west to east, whereas in an analysis of *N. zuluensis* from a larger distributional area, although the additional localities were represented by single individuals, a clinal pattern of variation in overall cranial size was positively correlated with longitude and negatively correlated with latitude, and hence specimens of *N. zuluensis* increased in overall cranial size from the north-west to the south-east.

These results were similar to those of the geometric morphometric shape analysis (Chapter 3) in that both found intra-specific geographic variation varied in different species, showing different intra-specific patterns of significant correlation with latitude and longitude. Both studies identified significant size variation between OTUs of *E. hottentotus*, *N. capensis*, and *P. hesperidus*, and correlations in the variation of cranial shape and size with latitude and longitude in *N. capensis*. However, there were also differences between the results of this traditional morphometric analysis and the geometric shape analysis, since traditional morphometrics identified patterns of size variation correlated with latitude and/or longitude in two species, *N.*

rendalli and *N. zuluensis* which were not found in the shape analysis. Shape analysis also identified patterns of size variation correlated with latitude in *P. hesperidus*, which were not identified by the traditional morphometric analysis. Although there were some similarities and some differences between the results of the traditional and shape analyses, the power of the shape analysis is that it describes through the splines of the skull the patterns of variation in skull shape, whereas the traditional morphometric analysis was only able to indicate which of the measurements, limited to the specific areas measured, were most involved in the variation, hence the actual variations in cranial shape and size described by each of the analyses are difficult to compare. This may also explain why the shape and traditional morphometric analyses seemed to describe different patterns of change in cranial size and shape in *N. capensis* correlated with latitude and longitude.

The contrasting direction of intra-specific geographic variation in individual characters, presenting a mosaic pattern of geographic variation, has been linked to a history of disjunct distribution in a species (Dippenaar, 1995). Whether a disjunct distributional history in *N. africanus, N. zuluensis* and *P. rusticus* could explain the mosaic pattern of geographic variation noted in two of the cranial measurements, is a possibility that would require further testing.

Although the environmental factors driving morphological change in relation to features such as latitude and longitude were not investigated in this analysis, it is useful to consider the suggested possibilities. As in the analysis of shape change (Chapter 3), whose discussion covers a number of suggested factors in more detail, the majority of the patterns of geographic change (negative correlation with latitude) observed in this study conformed to Bergmann's rule (1847). However, the causes of geographic change in *E. capensis* (negatively correlated with longitude) and *N. zuluensis* (positively correlated with longitude) were not identified and may be the possible result of a combination of environmental factors, including variation in altitude. Although difficult to account for, altitude-related size differences which are contrary to Bergman's rule (1847), i.e. where individuals get smaller at higher altitudes, may be ascribed to differences in nutrition or a condensed growth period as a result of a shorter breeding season (Rowe-Rowe and Meester, 1985).

In *E. hottentotus,* there was no similarity in the important measurements identified on the first principal component axis in this analysis and the study of *E. hottentotus* by Schlitter and Aggundey (1986) which, similarly to the present study, identified braincase height as the most important measurement on the second principal component axis. In the present investigation, the first two principal components of a PCA scatterplot based on individual specimens, did not separate specimens of the different subspecies of *E. hottentotus* in the same way as in the analysis of Schlitter and Aggundy (1986), while both analyses identified specimens of *E. h. hottentotus* as largest and those of *E. h bensoni* as smallest on the first principal component axis. The degree of overlap between specimens of *E. h. pallidior* and *E. h. hottentotus,* was less in this study which also identified an overlap between specimens of *E. h. pallidior* and *E. h. bensoni*. The latter overlap was not identified by Schlitter and Aggundy (1986), as their analysis did not include any specimens from that part of the distribution of *E. h. bensoni*. Hence, the results described in this chapter support the findings of Schlitter and Aggundy (1986) in that *E. h. pallidior* is morphometrically indistinguishable from the nominate subspecies and can thus be placed as a junior synonym of it. However, the overlap of specimens of *E. h bensoni* from Lesotho and KwaZulu-Natal with specimens of *E. h. pallidior* observed in the present study, suggests that the subspecies delineation of *E. h. bensoni* might also be in question, or that the distributions of the subspecies need to be revisited. The traditional morphometrics results were thus congruent with those of the geometric shape analysis (Chapter 3), where the pattern of variation in centroid size of *E. hottentotus* did not correspond with that of the described subspecies (Meester *et al*., 1986).

Two of the specimens of *N. capensis* (TM34185 and TM34240), identified by geometric morphometrics (Chapter 3) as potentially having been misidentified and more likely to have been *N.* cf. *melckorum* due to their larger size, were included in the original data suite of *N. capensis* specimens but were not used for further tests as DFA, PCA and cluster analysis identified these specimens as *N.* cf. *melckorum*. Hence, the traditional morphometric technique confirmed the suspicion raised by the geometric morphometric analysis. The inclusion in the traditional morphometric analysis of the type specimen and series of *E. melckorum* (Roberts, 1919), in conjunction with information from specimens whose species identification was confirmed by chromosome number or bacular morphology, indicated how the significant north-east to south-west clinal variation in cranial size of *N. capensis* contributed to the description of *E. melckorum* (Roberts, 1919).

Although *N. a. meesteri* was described by Roberts (1913) as a larger subspecies compared to *africanus* from Malvern in KwaZulu-Natal, most authors have treated *N. a. meesteri* as a synonym of the nominate subspecies *N. a. africanus*, with the exception of Peterson (1987) who claimed multivariate analysis of mensural data indicated this was a distinct subspecies. The inclusion of the type specimen of *N. a. meesteri* in the analysis of southern African *N. africanus* confirmed, on the basis of 12 cranial measurements, the position of *N. a. meesteri* as a synonym with the nominate subspecies *N. a. africanus* as indicated in Meester (*et al.*, 1986) and contrary to Peterson (1987). Although the smaller *N. africanus* specimens from Sentinel Ranch were not found, by the DFA, to have been misidentified with specimens of known identity, a possible reason for the geographic difference found by this study remains unresolved. Geographic variation has been suggested to result from stabilizing selection acting on populations of individuals with low vagility (Bronner, 1996a). Therefore, given that even as a volant species, *N. africanus* may display low vagility in relation to suitable roost sites, stabilizing selection could provide a hypothesis for a future study aimed at understanding the geographic variation of the specimens from Sentinel Ranch.

The inclusion of the type specimens of *N. zuluensis* Roberts, 1924 and *N. z. vansoni* (Roberts, 1932) in the analysis of *N. zuluensis* provided interesting results. On the basis of 12 cranial characters, both type specimens of *N. zuluensis* and *N. z. vansoni* resulted to be distinct from each other and from all other *N. zuluensis* specimens. Although more recently *N. zuluensis* has been accredited with a particular bacular morphology (Hill and Harrison, 1987) and chromosome diploid number (Rautenbach *et al.*, 1993), which were used to identify a number of the specimens in this analysis, neither of these characters are known for the type specimens. Therefore, it is worth noting that the present investigation indicates a closer association of the specimens studied with the *N. z. vansoni* type specimen than with that of *N. zuluensis*. It is possible, however, that the difference between these type specimens is the result of latitudinal clinal variation. This would be justified by the fact that the overall cranial variation of the 12 measurements was significantly correlated with latitude when the type specimens and two other specimens, which extended the range of the OTU sample both north and south, were added to the analysis of *N. zuluensis*. However, the only other specimen from KwaZulu-Natal did not plot near the type specimen of *N. zuluensis* in the UPGMA phenogram of individuals, although it was one of the closest to the type specimen in the PCA scatterplot of the first two principal component axes. Further investigations of *N. zuluensis* are required to clarify these differences.

Documenting morphological change within the distribution of a species is useful given that taxonomic confusion can occur when variations of little taxonomic significance, usually manifest as overall differences in size and observed in relation to latitude and/or longitude but probably resulting from complex combinations of interdependent environmental and climatic factors, are not identified as such (Bronner, 1996b; Chimimba *et al.* 1998). Hence the quantification of variation within a species over its southern African distributional range was important for the next section on species discrimination. Although this is the first quantification of geographic variation in the majority of the southern African species of *Eptesicus, Hypsugo, Neoromicia* and *Pipistrellus*, such variation has been documented in other species of *Eptesicus* s.l. in Australia (Kitchener *et al.*, 1987) and North America (Burnett, 1983). In *E. fuscus*, the variation in skull size across its range in North America showed a complex pattern of smaller size at lower latitudes, whereas wing size showed a strong trend toward larger size at lower latitudes (Burnett, 1983).

APPENDIX 6.1

Southern African vespertilionid specimens used in the analysis of intra-specific variation.

Acronyms: BM - The Natural History Museum, London, United Kingdom; DM - Durban Natural Science Museum, South Africa; KM - Amathole Museum, King William's Town, South Africa (formerly Kaffrarian Museum); MM - McGregor Museum, Kimberley, South Africa; TM - Transvaal Museum, Pretoria, South Africa; NMB - National Museum, Bloemfontein, South Africa; NMBZ - National Museum, Bulawayo, Zimbabwe. ZM - Iziko South African Museum, Cape Town, South Africa.

Numbering associated with *N. capensis* specimens from the Western Cape relates to Figure 6.6.

Eptesicus hottentotus: **LESOTHO:** Kofa, Qacha's Neck (syn. White Hill) (30°07'S, 28°41'E): NMB8343. Quthing, Mt. Moorosi (30°11'S, 27°52'E): NMB8176. **NAMIBIA:** Bethanie, Huns (106) (ca. 27°23'S, 17°23'E): TM32695. Omaruru District, Ombo, Eronga Mountains (syn. Eronga) (21°40'S, 15°44'E): TM9480-9482, TM9484-9486, TM9488, TM9491, TM9493. 35 km SSW Keetmanshoop, Rheinvels Farm (26°57'S, 17°56'E): TM32565-32566. 3 km W Aus, Farm Klein Aus 8 (26°39'S, 16°13'E): TM37540, TM37551-37555. 70 km W Maltahohe, Farm Zwartmodder 101 (24°54'S, 16°17'E): TM37588, TM37624. **SOUTH AFRICA:** KWAZULU-NATAL PROVINCE: 9 km NE Louwsburg, Ithala Game Reserve (syn. Ithala), Doornkraal campsite, Ngubhu River (27°30'44"S, 31°12'41"E): TM31756. Kloof, Kranskloof Nature Reserve (29°46'S, 30°49'E): TM40017. LIMPOPO PROVINCE: 67 km W of Messina, Greefswald Farm 37 (syn. Mapungubwe), Shashi-Limpopo confluence (22°13'S, 29°22'E): TM41421. Kruger National Park, 4 km W bridge, Levuvhu Hippo Pool (22°26'S, 31°11'E): TM34239. Kruger National Park, Fig Tree Camp (22°25'50"S, 31°11'50"E): TM36879, TM38167. WESTERN CAPE PROVINCE: Cederberg, Algeria State Forest Campsite (32°21'S, 19°03'E): ZM41416, ZM41418, TM35150, TM38411, TM38412, TM40630, TM40631, ZM41419. **ZIMBABWE:** Nyadiri River, near bridge (ca. 17°08'S, 32°08'E): NMBZ32580. Nyapfunde School 15, Nyashato Dam (ca. 17°08'S, 32°08'E): NMBZ32571-32574, NMBZ32577-32578.

Hypsugo anchietae: **SOUTH AFRICA:** MPUMALANGA PROVINCE: Kruger National Park, 1.5 km NW of Skukuza, dense woodland of western reservoir (24°59'S, 31°35'E): TM39768. Kruger National Park, Skukuza , Skukuza Staff Village (24°59'S, 31°35'E): TM30061, TM39767. KWAZULU-NATAL PROVINCE: Harold Johnson Nature Reserve (29°12'S, 31°25'E): DM5353, DM5357, DM5364. St. Lucia, False Bay, Lister Point (28°01'S, 32°21'E): DM2269. St. Lucia, Nibela Peninsula, Sobhengu Lodge (27°59'S, 32°24'E): DM6885. Hella-Hella, Game Valley Estates (29°54'S, 30°03'E): DM5362. Umkomaas, Empisini Nature Reserve (30°12'S, 30°48'E): DM5358, DM5377. **ZIMBABWE:** near Gwayi River, Volunteer Farms (18°49S, 27°38E): NMBZ31965.

Neoromicia capensis: **BOTSWANA:** Nekate (syn. Nekati), near Makarikari (ca. 20°00'S, 26°20'E): TM6549. Nthane (ca. 21°22'S, 26°22'E): NMBZ64072, NMBZ64079-64080, NMBZ64082-64083, NMBZ64098, NMBZ64100, NMBZ64102, NMBZ64105. **LESOTHO:** Mafeteng, Botsoela (Malealea) (29°50'S, 27°15'E): NMB8654-8655. Maseru, Marakabei (29°37'S, 28°07'E): NMB7270, NMB7354. Quthing, Mt. Moorosi (30°11'S, 27°52'E): NMB8223-8229. **NAMIBIA:** Okahandja District, Quickborn (21°09'S, 17°05'E): TM3381. Oranjemund District, Swartkop, Diamond Area No. 1 (28°33'S, 16°25'E): TM32657-32658, TM32682-32684, TM32686-32687. Outja District, Karochos (20°22'S, 14°58'E): TM9477. E of Gobabis, Sandfontein 468 (22°23'S, 19°08'E): KM2122-2123, KM2127-2128, KM2130-2131, KM2136, KM2138-2140, KM2143-2144, KM2146. Gobabis, Farm 397 (22°12'S, 18°58'E): TM6057. Rundu District (syn. Grootfontein District), Ssannakanu Village (18°06'S, 20°23'E): KM2170-2171, KM2173-2175, KM2177-2179. 35 km SSW Keetmanshoop, Rheinvels Farm (26°57'S, 17°56'E): TM32547-32548, TM32567. Rundu (syn. Grootfontein) District (ca. 19°33'S, 18°04'E): KM8083, KM8092, KM8094. Windhoek, Liebig's Ranch (22°38'S, 16°53'E): TM8308. **SOUTH AFRICA:** EASTERN CAPE PROVINCE: 9 km NW Beaufort West, Karoo National Park (ca. 32°20'S, 22°33'E): TM29512-29613. Bedford, Kaggasmoudt (ca. 32°07'S, 26°37'E): KM20188, KM2035-2036. King William's Town (32°52'S, 27°23'E): KM13280, KM18135, KM19297, KM19369, KM19374, KM1998-1999, KM2003-2007, KM24306-24308. King William's Town, Blaney Nature Reserve (32°52'S, 27°23'E): BM1925.7.9.4.

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Near Stutterheim (ca. 32°34'S, 27°25'E): KM19632. FREE STATE PROVINCE: Bethlehem, Orange River confluence (28°14'S, 28°18'E): BM1902.4.3.1. Brandfort (ca. 28°38'S, 26°23'E): TM17041-17046. Brandfort, Florisbad (686) (28°46'S, 26°05'E): NMB7751-7752, NMB7762-7777. Clocolan district, Alma (ca. 29°38'S, 25°08'E): TM11785, TM7847. Hoopstad, Farm Middelwater 750 (27°37'S, 25°22'E): NMB7802-7810. Jagersfontein Commonage, Disused Mine (ca. 29°39'S, 25°23'E): NMB7578-7579, NMB7584-7585, NMB7595, NMB7600-7601, NMB7603-7606, NMB7609, NMB7611, NMB7617-7619, NMB7625, NMB7629, NMB7633-7636, NMB7639, NMB7642-7643, NMB7646-7647, NMB7675, NMB7677, NMB7680-7683, NMB7685-7686, NMB7688-7689, NMB7692-7695, NMB7697, NMB7699. Vredefort, Farm Aasvogelrand-Oost 291 (26°52'S, 27°22'E): NMB5885-5888, NMB5891-5892, NMB5894, NMB5896-5897. Vredefort, Helena (780) (ca. 26°53'S, 27°23'E): NMB3171. Vredefort, Vredefort Road (26°52'S, 27°22'E): BM1904.3.1.3, BM1904.3.1.51. GAUTENG PROVINCE: 16 km W Heidelberg, Suikerbosrand (syn. Suikerboschrand) Nature Reserve (ca. 26°30'S, 28°13'E): DM6900. West Rand District, Mogale City (syn. Krugersdorp) (ca. 26°06'S, 27°46'E): BM1898.4.4.8, BM1898.4.4.9. KWAZULU-NATAL PROVINCE: 9 km NE Louwsburg, Ithala (syn. Itala) Game Reserve, Main Camp (27°31'S, 31°22'E): DM5368. 9 km NE Louwsburg, Ithala (syn. Itala) Game Reserve, eastern side of reserve, Square Darvel (27°32'30"S, 31°22'23"E): DM5899. 9 km NE Louwsburg, Ithala Game Reserve (syn. Itala), Doornkraal Campsite, Ngubhu River (27°30'44"S, 31°12'41"E): DM5890-5891, DM5894, DM5902-5903. Drakensberg, Loteni Nature Reserve (29°27'S, 29°32'E): DM1909-1912, DM1941-1946, DM1949. Drakensberg, Royal Natal National Park (28°41'S, 28°56'E): DM2389, DM2417-2418. Eshowe, Dlinza Forest (28°53'S, 31°27'E): DM5355. Forest Hills, Epping Crescent (29°45'S, 30°49'E): DM7017. Gloria, Subdivision of Farm Olyvekloof 184, Jamestown (ca. 31°07'S, 26°52'E): NMB4998, NMB5009, NMB5013, NMB5021, NMB5025. Hella-Hella, Game Valley Estates (29°54'S, 30°03'E): DM6894. Merrivale (29°30'S, 30°15'E): DM5387. Mkuze Game Reserve, Bube Pan (27°47'S, 32°12'E): TM35309-35314. Mkuze Game Reserve, Malibali Pan (27°47'S, 32°12'E): TM35246-35247, TM35249. Mkuze Game Reserve, Msinga Pan (27°47'S, 32°12'E): DM5380, DM5400, TM35270, TM35322-35325. Mooi River District (ca. 29°13'S, 29°59'E): NM814, NM816, NM818. New Hanover School (29°22'S, 30°37'E): DM7020. Nottingham Road, Clifton School (29°21'S, 30°00'E): DM5873. Near Upington, south bank of Orange River (28°22'S, 21°07'E): ZM17074. Weenan Game Reserve (28°51'S, 30°00'E): DM2319. Westriding, 14 Marion Road (29°47'S, 30°46'E): DM5881-5882. Westriding, 22 Ashley Road (29°47'S, 30°46'E): DM7018. LIMPOPO PROVINCE: Kruger National Park, 4 km W bridge, Levuvhu Hippo Pool (22°26'S, 31°11'E): TM30489, TM34185-34186, TM34240, TM34263. Kruger National Park, Pafuri, Culling Camp (22°25'S, 31°15'E): TM37833. Kruger National Park, Pafuri, Old Picnic Site (22°25'S, 31°18'E): TM37819, TM37823. Messina, Messina Nature Reserve (22°23'S, 30°03'E): DM5396, DM5398. NORTH WEST PROVINCE: 13 km W Ventersdorp, Farm Ratsegaai 204 (ca. 26°22'S, 26°32'E): TM27752, TM27767-27769, TM27772-27774, TM27776, TM27778-27783. Ganyesa (26°32'S, 24°07'E): MM7061. Molopo Nature Reserve, swimming tank (25°58'S, 22°55'E): MM7062-7063. 5 km NNE Christiana, Farm Welgedaan 292 (27°41'S, 25°14'E): TM20832-20833, TM20841-20848. Farm Taylors Pan, water reservoir (26°02'S, 22°40'E): SRSITE75/4/96. MPUMALANGA PROVINCE: Kruger National Park, Skukuza, Rhenosterkoppies (25°08'S, 31°37'E): TM37296-37300. Badplaas (25°57'S, 30°33'E): DM5354, DM5376. NORTHERN CAPE PROVINCE: 58 km S Kuruman, Wonderwerk Cave (27°49'S, 23°35'E): MM7065-7067. 6 km SE Nossob, Kalahari Gemsbok National Park, Marie se Gat (25°38'S, 20°38'E): TM35584-35589, TM35591-35602. Augrabies Falls National Park, Causeway (28°35'48"S, 20°19'48"E): MM7053. Farm Deelfontein (ca. 30°52'S, 23°52oE): BM1902.9.1.2, Hanover (ca. 31°07'S, 24°22'E): ZM7378, ZM7482, ZM7512. Kalahari Gemsbok National Park, Mata Mata Camp (25°45'S, 19°59'E): MM7070-7071. Kuruman (ca. 27°27'S, 23°25'E): BM1904.10.1.10. Namaqualand-Springbok, 28 km SSE Farm Narap (29°53'S, 17°45'E): TM27935, TM28002-28004. SW Williston, Farm Gouna (ca. 31°22'S, 20°37'E): KM28985-28986, KM28990-28991, KM28994-28995. WESTERN CAPE PROVINCE: 16 km N Hopefield, Kersefontein Farm (syn. Berg River) (32°54'13"S, 18°19'51"E): 1) DM7192, 2) DM7193, 3) DM7196, 4) DM7199, 5) DM7200, 6) DM7204, 7) DM7205, 8) DM7206, 9) DM7207, 10) DM7208, 11) TM2280, 12) DM2281, 13) TM2283, 14) TM2284. Cederberg, Algeria State Forest Campsite (32°21'S, 19°03'E): 20) ZM41452, 21) ZM41457, 22) TM38413. Clanwilliam, Olifants River (32°21'S, 18°57'E): 23) MM7036, 24) MM7037. NW Ladismith, Farm Buffel Rivier Poort (ca. 33°22'S, 21°37'E): KM29433, KM29437-29439, KM29448. NW Murraysburg (ca. 31°52'S, 23°37'E): KM24511-24518, KM24532, KM24534-24539, KM24663. Piketburg, SE Elandsbaai, Groote Drift farm (ca. 32°38'S, 18°38'E): KM29004, 15) KM29005, 16) KM29007, 17) KM29009,

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18) KM29010, 19) KM29011. Riversdale, Stilbaai (34°22'S, 21°25'E): TM8970-8976. SW Ladismith, Farm Zeekoegats Drift (ca. 33°37'S, 21°37'E): KM29453-29455, KM29462-29463. Vrolijkheid Nature Reserve (33°54'S, 19°53'E): DM7194-7195, DM7197-7198, DM7202-7203. **ZIMBABWE:** 25 km W Harare, Lion and Cheetah Park (17°23's, 31°17'E): TM34843, TM34845. Harare (syn. Salisbury) (ca. 17°53'S, 31°08'E): TM34844. Harare, (syn. Salisbury), Thornpark (17°38'S, 31°08'E): NMBZ58818-58819. NMBZ58822, NMBZ58826-58828. Near Gwayi River, Volunteer Farms (18°49S, 27°38E): NMBZ31989, NMBZ31991. Sengwa Wildlife Research Station (18°10'S, 28°13'E): TM34864-34865, TM34889-34890, TM34950-34951, TM34970-34971, TM34974-34975.

Neoromicia cf. *melckorum*: **SOUTH AFRICA:** LIMPOPO PROVINCE: Kruger National Park, 4 km W bridge, Levuvhu Hippo Pool (22°26'S, 31°11'E): TM34185-34186, TM34240, TM34263. Kruger National Park, Pafuri, Anthrax Camp (22°25'S, 31°12'E): TM37943-37945. Kruger National Park, Pafuri, Culling Camp (22°25'S, 31°15'E): TM37833, TM37844, TM37937. Kruger National Park, Pafuri, Fig Tree Forest (22°25'S, 31°18'E): TM38599. Kruger National Park, Pafuri, Fig Tree Forest, 4.8 km down stream of bridge (22°25'S, 31°15'E): TM37680. Kruger National Park, Pafuri, Manxeba Windmill (22°24'S, 31°14'E): TM38132. KNP, Pafuri, Mockford's Garden (22°25'S, 31°18'E): TM37852. KNP, Pafuri, New Fig Tree Forest (22°25'S, 31°18'E): TM37858, TM37906, TM38843. KNP, Pafuri, Old Picnic Site (22°25'S, 31°18'E): TM37924, TM39506. **ZIMBABWE:** Mana Pools National Park (15°43'S, 29°25'E): TM41860-41862.

Neoromicia africanus: **BOTSWANA:** Sepopa (18°50'S, 22°15'E): NMBZ64001. **MOZAMBIQUE:** 20 miles WSW Nampula, Nabaunama River (15°37'S, 38°52'E): NMBZ64000. Gorongoza Mountain (syn. Gorongosa Mountain) (18°25'S, 34°00'E): NMBZ64012, NMBZ64013, NMBZ64016. Namaacha District, Changalane (syn. Estatuane) (26°18'S, 32°12'E): NMBZ64007. **SOUTH AFRICA:** EASTERN CAPE PROVINCE: Port St. Johns (31°38'S, 29°33'E): TM1076, TM12361-12362, TM12365-12368, TM12370. KWAZULU-NATAL PROVINCE: 9 km NE Louwsburg, Ithala (syn. Itala) Game Reserve, eastern side of reserve, Square Darvel (27°32'30"S, 31°22'23"E): DM5900-5901. Durban, Yellowwood Park, Stainbank Nature Reserve (29°54'S, 30°56'E): DM5869-5871. Entumeni, Vuma farm (28°53'S, 31°23'E): DM4551-4555. Hluhluwe, Hluhluwe Game Reserve (ca. 28°05'S, 32°02'E): NM1408. Ngome, Ngome Forest Reserve (27°50'00"S, 31°24'45"E): TM39136-39199, TM39817-39818, TM39826-39828. Pongola, Jozini, Jozini Dam wall (27°25'S, 32°04'E): DM5367. Queensburgh, Malvern, 1 Rindle Rd. (ca. 29°53'S, 30°53'E): DM7019. Renishaw (30°16'S, 30°44'E): DM5365, DM5402, DM5404, DM7012. Umkomaas (ca. 30°12'S, 30°48'E): BM1917.10.3.10, BM1917.10.3.5, BM1917.10.3.6. Umkomaas, Empisini Nature Reserve (30°12'S, 30°48'E): DM5373. LIMPOPO PROVINCE: Kruger National Park, 8 km E Satara, old bridge over Nwanedzi River (24°24'S, 31°50'E): TM39621. Kruger National Park, Satara Rest Camp (24°24'S, 31°46'E): TM39642-39643. Kruger National Park, Shingwedzi Camp (23°06'S, 31°27'E): TM38317-38320, TM38322. Kruger National Park, Fig Tree Camp (22°25'50"S, 31°11'50"E): TM36120, TM36709, TM39463. Kruger National Park, Pafuri, Anthrax Camp (22°25'S, 31°12'E): TM36647. Kruger National Park, Pafuri, Culling Camp (22°25'S, 31°15'E): TM37841-37842. Kruger National Park, Pafuri, Fig Tree Forest (22°25'S, 31°18'E): TM38604. Kruger National Park, Pafuri, Mockford's Garden (22°25'S, 31°18'E): TM37849, TM38523, TM38607-38612, TM39465-39467. Kruger National Park, Pafuri, New Fig Tree Forest (22°25'S, 31°18'E): TM37856-37857, TM37907. Kruger National Park, Pafuri, Old Picnic Site (22°25'S, 31°18'E): TM37816-37820, TM37822, TM37919, TM43863. Kruger National Park, Pafuri, Picnic Site (22°25'S, 31°15'E): TM41731. MPUMALANGA PROVINCE: Kruger National Park, Skukuza, Skukuza Staff Village (24°59'S, 31°35'E): TM42126-42127, TM42129. Nelspruit, Logogotu (syn. Legogot) (25°13'S, 31°15'E): 1906.8.2.36. **SWAZILAND:** 10 km N Simunye (26°07'S, 31°57'E): DM5880. **ZIMBABWE:** Eastern Highlands, 15 km SE Juliesdale, Chingamwe Estates, ZTA Cottage (18°27'S, 32°45'E): DM5366. Mount Selinda, Chirinda Forest (20°24'S, 32°42'E): TM34607, TM34609. Rusito Forest, on Rusito River (20°02'S, 32°59'E): TM34769, TM34783. Sentinel Ranch (22°10S, 29°30E): NMBZ29585, NMBZ29588, NMBZ29600- 29602, NMBZ29607-29609, TM41618, TM41621-41622. Sengwa Wildlife Research Station (18°10'S, 28°13'E): TM34973.

Neoromicia rendalli: **SOUTH AFRICA:** KWAZULU-NATAL PROVINCE: Bonamanzi Game Reserve (28°06'S, 32°18'E): DM5361, DM5370, DM5877-5878. **ZIMBABWE:** Mana Pools

APPENDIX 6.1 continued

National Park (15°43'S, 29°25'E): TM41858.

Neoromicia rueppellii: **BOTSWANA:** Maun (ca. 19°53'S, 23°23'E): TM6546. **SOUTH AFRICA:** LIMPOPO PROVINCE: Kruger National Park, 4 km W bridge, Levuvhu Hippo Pool (22°26'S, 31°11'E): TM36122. Kruger National Park, Fig Tree Camp (22°25'50"S, 31°11'50"E): TM36934. Kruger National Park, Pafuri, Anthrax Camp (22°25'S, 31°12'E): TM38279. Kruger National Park, Pafuri, Fig Tree Forest, 4.8 km down stream of bridge (22°25'S, 31°15'E): TM36791. Kruger National Park, Pafuri, New Fig Tree Forest (22°25'S, 31°18'E): TM37908. NORTHERN CAPE PROVINCE: Augrabies Falls National Park (28°35'S, 20°20'E): MM7047. **ZIMBABWE:** Volunteer Farms, near Gwayi River (18°49S, 27°38E): NMBZ31995.

Neoromicia zuluensis: **BOTSWANA:** Chobe, N Tsotsoroga, Zweizwi River Waterhole (18°36'S, 24°22'E): TM6553. **NAMIBIA:** Rundu (syn. Grootfontein) District (ca. 19°33'S, 18°04'E): KM8083, KM8092, KM8094. Gobabeb, Namibia Desert Research Station (syn. DERU) (23°33'S, 15°03'E): NMBZ64058, NMBZ64060-64065, NMBZ64067, NMBZ64069-64071, TM27593. **SOUTH AFRICA:** KWAZULU-NATAL PROVINCE: Mkuze Game Reserve, Malibali Pan (27°47'S, 32°12'E): TM35248. Umfolosi Game Reserve (ca. 28°19'S, 31°50'E): TM3024. LIMPOPO PROVINCE: 67 km W of Messina, Greefswald Farm 37 (syn. Mapungubwe), Shashi-Limpopo Confluence (22°13'S, 29°22'E):TM41408. Kruger National Park, 12 km E of Phalaborwa Gate, Erfplaas Windmill (23°57'S, 31°07'E): TM36572, TM36574. Kruger National Park, 2 km E Letaba Olifants Confluence, Lebombo Ironwood Forest (23°59'S, 31°50'E): TM39697. Kruger National Park, 2 km SE Roodewal Private Camp (24°08'S, 31°36'E): TM39684. Kruger National Park, Shashanga Windmill (22°40'S, 30°59'E): TM30672-30673. Kruger National Park, 4 km W bridge, Levuvhu Hippo Pool (22°26'S, 31°11'E): TM30534, TM34213. Kruger National Park, Fig Tree Camp (22°25'50"S, 31°11'50"E): TM36118, TM36705, TM36759, TM36778, TM37001, TM37017, TM37436, TM38169. Kruger National Park, Pafuri, Anthrax Camp (22°25'S, 31°12'E): TM36846, TM37863. Kruger National Park, Pafuri, Culling Camp (22°25'S, 31°15'E): TM37938. Kruger National Park, Pafuri, Fig Tree Forest, 4.8 km down stream of bridge (22°25'S, 31°15'E): TM37678. KNP, Pafuri, New Fig Tree Forest (22°25'S, 31°18'E): TM37905. Kruger National Park, Pafuri, Old Picnic Site (22°25'S, 31°18'E): TM36631. Messina, Messina Nature Reserve (22°23'S, 30°03'E): DM5359, DM5375. Soutpansberg, 13 km W Vivo, Farm Urk 10, Blouberg Private Nature Reserve (23°02'S, 29°07'E): TM24087. Waterberg, 30 km NE Vaalwater, Farm Klipfontein (24°08'S, 28°08'E): TM19372, TM24752, TM39794. Waterberg, 65 km N Vaalwater, Lapalala Wilderness Area (23°51'S, 28°09'E): TM39792, TM39795. MPUMALANGA PROVINCE: 11 km N of Newington, Acornhoek (24°45'E, 31°25'E): TM17293. Kruger National Park, 1.5 km NW of Skukuza, dense woodland of western reservoir (24°59'S, 31°35'E): TM39760-3976. Leydsdorp, Sheila No. 10 (24°04'S, 31°09'E): TM6457-6458. **ZIMBABWE:** Mavhuradonha District, Sohwe River (16°37'S, 30°52'E): NMBZ82881. Umfuli River, Frog Mine (17°53'S, 29°52'E): NMBZ58889.

Pipistrellus hesperidus: **SOUTH AFRICA:** LIMPOPO PROVINCE: Tzaneen Government Estate (23°50'S, 30°10'E): TM1085, TM1087. EASTERN CAPE PROVINCE: Ngqeleni (31°46'S, 29°02'E): TM1073. KWAZULU-NATAL PROVINCE: 6 km NNE Mtubatuba, Dukuduku Forest (28°23'S, 32°21'E): TM40406, TM40410. Durban, 108 Bowen Avenue (ca. 29°53'S, 30°53'E): DM6893. Durban, Cowies Hill (29°50'S, 30°53'E): DM7201. Durban, Glenwood, Pigeon Valley Park (29°51'S, 30°59'E): DM5384-5385. Durban, Malvern (ca. 29°53'S, 30°56'E): TM1085. Durban, Queensburgh, North Park Nature Reserve (29°52'S, 30°45'E): DM5382, DM5403, TM35184. Durban, Yellowwood Park, 18 Dove Crescent (ca. 29°54'S, 30°52'E): DM5388. Durban, Yellowwood Park, Stainbank Nature Reserve (29°54'S, 30°56'E):DM5868. Kloof, Kranskloof Nature Reserve (29°46'S, 30°49'E): DM5876, TM40014-40015. Eshowe, Dlinza Forest (28°53'S, 31°27'E): DM5352, DM5356, DM5360, DM5363, DM5372, DM5374, DM5386, DM5393, DM5397, DM5406. Harold Johnson Nature Reserve (29°12'S, 31°25'E): DM5369. Harrismith, Rockcliff Farm (28°37'S, 29°01'E): TM38493. Hillcrest, Wishart Road, 26 Hathaway (29°47'S, 30°46'E): DM7016. Hluhluwe, Hluhluwe Game Reserve, Research Camp (28°04'S, 32°02'E): TM44399. Kosi Lake, Department of Health Camp (26°57'30"S, 32°49'30"E): TM40455, TM40457. Mount Edgecombe, SASEX (29°42'S, 31°04'E): DM7143. Mtunzini, Twin Streams Farm (28°57'S, 31°30'E): DM5872. Mtunzini, Umlalazi Nature Reserve (28°58'S, 31°48'E): TM30126. Ndumu Game Reserve (26°53'S, 32°15'E): TM35207, TM35232. Ngome, Ngome Forest Reserve (27°50'00"S, 31°24'45"E): TM39134-39135, TM39840, TM39854. St. Lucia, 2 km N of St Lucia

APPENDIX 6.1 continued

Village, Ipheva Camp Site (28°21'S, 32°25'E): DM1063-1064, DM6895-6896. **ZIMBABWE:** 10 km SSW Bindura, Chikupo Cave (17°23'S, 31°17'E): TM34839. Banti, Shinda Estates (ca. 19°18'S, 32°48'E): NMBZ60472. Eastern Highland District, Rhodes Inyanga National Park (ca. 18°17'S, 32°46'E): TM11403, TM34757. Eastern Highlands, 15 km SE Juliesdale, Chingamwe Estates, ZTA Cottage (18°27'S, 32°45'E): DM4692. Mount Selinda, Chirinda Forest (20°24'S, 32°42'E): TM34634. Rusito Forest, on Rusito River (20°02'S, 32°59'E): TM34767-34768, TM34778.

Pipistrellus rusticus: **BOTSWANA:** 20 km N Francis Town (21°07'S, 27°37'E): NMBZ63995. Four Rivers Camp, Okavango River (19°03'S, 23°10'E): NMBZ54104, NMBZ54106-54109, NMBZ54218, NMBZ63997-63999. **NAMIBIA:** Otjozondjupa, Tsumkwe (syn. Grootfontein) District, Kano Vlei (19°22'S, 19°07'E): KM1891, KM1894. **SOUTH AFRICA:** LIMPOPO PROVINCE: 8 km E Warmbaths, Rissik Private Nature Reserve (24°53'S, 28°27'E):TM20649, TM20651, TM20654-20655. Kruger National Park, 4 km W bridge, Levuvhu Hippo Pool (22°26'S, 31°11'E): TM36440. Messina, Messina Nature Reserve (22°23'S, 30°03'E): DM5318, DM5379, DM5389-5391, DM5394-5395, DM5399, DM5407, DM5865-5866. Waterberg, 30 km NE Vaalwater, Farm Klipfontein (24°08'S, 28°08'E): TM39813-39815, TM39879-39884, TM39886-39887, TM39890-39891, TM39894, TM40287, TM40291. MPUMALANGA PROVINCE: Nelspruit, Logogotu (syn. Legogot) (25°13'S, 31°15'E): BM1906.8.2.34, BM1906.8.2.37. **ZIMBABWE:** Sentinel Ranch (22°10S, 29°30E): NMBZ9896, NMBZ9901, NMBZB9891-9893. Near Gwayi River, Volunteer Farms (18°49S, 27°38E): NMBZ31992.

APPENDIX 6.2

Post-hoc Tukey test results

Non-significant subsets identified among OTUs by post-hoc Tukey tests in 12 cranial measurements of vespertilionid bats from southern Africa. Mean values are indicated for each OTU in the homogenous subsets. *n* = sample size.

A) *Eptesicus hottentotus*

CIL		Subset	
OTU	*n*	1	2
4	4	17.72	
1	7	18.14	
5	5		19.12
2	5		19.28
7	4		19.29
6	5		19.50
8	8		19.60
3	4		19.66
Significance		0.788	0.532

BH		Subset			
OTU	*n*	1	2	3	4
4	4	6.25			
1	7	6.28	6.28		
5	5	6.33	6.33	6.33	
7	4	6.56	6.56	6.56	6.56
8	8	6.62	6.62	6.62	6.62
3	4		6.69	6.69	6.69
2	5			6.76	6.76
6	5				6.83
Significance		0.129	0.062	0.052	0.472

ZB		Subset		
OTU	*n*	1	2	3
4	4	10.50		
5	5	10.71	10.71	
6	5	11.05	11.05	11.05
1	7	11.06	11.06	11.06
2	5	11.18	11.18	11.18
7	4		11.35	11.35
3	4		11.39	11.39
8	8			11.69
Significance		0.098	0.111	0.153

APPENDIX 6.2 A) continued

Eptesicus hottentotus

BB		Subset				
OTU	*n*	1	2	3	4	5
4	4	8.61				
5	5	8.73	8.73			
1	7	8.89	8.89	8.89		
6	5	8.91	8.91	8.91		
2	5		9.03	9.03	9.03	
7	4			9.20	9.20	9.20
3	4				9.36	9.36
8	8					9.48
Significance		0.163	0.171	0.152	0.091	0.226

POW		Subset	
OTU	*n*	1	2
6	5	4.15	
5	5	4.15	
4	4	4.18	
2	5	4.26	
3	4	4.37	
7	4	4.38	4.38
1	7	4.40	4.40
8	8		4.66
Significance		0.122	0.054

WAS		Subset	
OTU	*n*	1	2
4	4	2.33	
1	7	2.49	2.49
5	5	2.51	2.51
7	4	2.58	2.58
2	5		2.71
3	4		2.72
6	5		2.77
8	8		2.77
Significance		0.101	0.053

WOUC		Subset		
OTU	*n*	1	2	3
1	7	5.66		
4	4	5.88	5.88	
6	5		6.21	6.21
5	5		6.23	6.23
3	4			6.34
7	4			6.36
2	5			6.41
8	8			6.54
Significance		0.704	0.174	0.231

APPENDIX 6.2 A) continued

Eptesicus hottentotus

WIUM1		Subset		
OTU	*n*	1	2	3
4	4	3.30		
1	7	3.37	3.37	
6	5	3.55	3.55	3.55
5	5	3.55	3.55	3.55
2	5	3.59	3.59	3.59
7	4	3.60	3.60	3.60
3	4		3.64	3.64
8	8			3.70
Significance		0.057	0.140	0.805

WUPM4		Subset	
OTU	*n*	1	2
4	4	1.29	
1	7	1.37	1.37
6	5	1.40	1.40
2	5	1.44	1.44
5	5	1.44	1.44
3	4	1.46	1.46
7	4	1.48	1.48
8	8		1.60
Significance		0.291	0.127

LUM1		Subset	
OTU	*n*	1	2
1	7	1.82	
3	4	1.94	1.94
4	4	1.94	1.94
6	5	1.95	1.95
5	5	1.99	1.99
2	5		2.04
8	8		2.05
7	4		2.093
Significance		0.181	0.265

MAOT		Subset	
OTU	*n*	1	2
1	7	4.32	
4	4	4.37	4.37
5	5	4.46	4.46
7	4	4.59	4.59
2	5	4.61	4.61
6	5	4.65	4.65
3	4	4.76	4.76
8	8		4.82
Significance		0.116	0.091

APPENDIX 6.2 B)

Neoromicia capensis

BB		Subset												
OTU	***n***	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
1	8	6.49												
2	12	6.58	6.58											
6	4	6.64	6.64	6.64										
3	10	6.64	6.64	6.64										
8	18	6.69	6.69	6.69	6.69									
22	11	6.76	6.76	6.76	6.76	6.76								
7	5	6.85	6.85	6.85	6.85	6.85	6.85							
30	7	6.85	6.85	6.85	6.85	6.85	6.85							
5	14	6.86	6.86	6.86	6.86	6.86	6.86							
19	3	6.86	6.86	6.86	6.86	6.86	6.86							
21	6		6.87	6.87	6.87	6.87	6.87							
27	11		6.88	6.88	6.88	6.88	6.88	6.88						
13	7		6.89	6.89	6.89	6.89	6.89	6.89						
16	13		6.89	6.89	6.89	6.89	6.89	6.89						
25	4		6.93	6.93	6.93	6.93	6.93	6.93	6.93					
4	3		6.96	6.96	6.96	6.96	6.96	6.96	6.96	6.96				
34	15		6.96	6.96	6.96	6.96	6.96	6.96	6.96	6.96				
23	7			6.97	6.97	6.97	6.97	6.97	6.97	6.97	6.97			
10	13			7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00		
24	32			7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00		
28	3			7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00	7.00		
12	5			7.01	7.01	7.01	7.01	7.01	7.01	7.01	7.01	7.01	7.01	
29	6			7.02	7.02	7.02	7.02	7.02	7.02	7.02	7.02	7.02	7.02	
14	8				7.05	7.05	7.05	7.05	7.05	7.05	7.05	7.05	7.05	7.05
11	11					7.08	7.08	7.08	7.08	7.08	7.08	7.08	7.08	7.08
15	10					7.09	7.09	7.09	7.09	7.09	7.09	7.09	7.09	7.09
20	18					7.11	7.11	7.11	7.11	7.11	7.11	7.11	7.11	7.11
18	5					7.13	7.13	7.13	7.13	7.13	7.13	7.13	7.13	7.13
31	18						7.15	7.15	7.15	7.15	7.15	7.15	7.15	7.15
36	4						7.19	7.19	7.19	7.19	7.19	7.19	7.19	7.19
9	3						7.19	7.19	7.19	7.19	7.19	7.19	7.19	7.19
38	6						7.23	7.23	7.23	7.23	7.23	7.23	7.23	7.23
26	4							7.26	7.26	7.26	7.26	7.26	7.26	7.26
35	14								7.29	7.29	7.29	7.29	7.29	7.29
39	5									7.32	7.32	7.32	7.32	7.32
32	5										7.34	7.34	7.34	7.34
37	5											7.37	7.37	7.37
17	7												7.38	7.38
33	5													7.40
Significance		0.076	0.052	0.058	0.083	0.071	0.055	0.060	0.092	0.103	0.073	0.061	0.060	0.162

APPENDIX 6.2 B) continued

Neoromicia capensis

BH		Subset											
OTU	*n*	1	2	3	4	5	6	7	8	9	10	11	12
3	10	4.52											
1	8	4.54	4.54										
2	12	4.59	4.59	4.59									
22	11	4.61	4.61	4.61	4.61								
8	18	4.66	4.66	4.66	4.66	4.66							
6	4	4.70	4.70	4.70	4.70	4.70	4.70						
25	4	4.72	4.72	4.72	4.72	4.72	4.72	4.72					
21	6	4.74	4.74	4.74	4.74	4.74	4.74	4.74	4.74				
12	5	4.74	4.74	4.74	4.74	4.74	4.74	4.74	4.74				
13	7	4.75	4.75	4.75	4.75	4.75	4.75	4.75	4.75				
16	13	4.77	4.77	4.77	4.77	4.77	4.77	4.77	4.77	4.77			
30	7	4.77	4.77	4.77	4.77	4.77	4.77	4.77	4.77	4.77			
23	7	4.80	4.80	4.80	4.80	4.80	4.80	4.80	4.80	4.80			
34	15	4.82	4.82	4.82	4.82	4.82	4.82	4.82	4.82	4.82	4.82		
24	32	4.82	4.82	4.82	4.82	4.82	4.82	4.82	4.82	4.82	4.82		
15	10	4.82	4.82	4.82	4.82	4.82	4.82	4.82	4.82	4.82	4.82		
4	3	4.83	4.83	4.83	4.83	4.83	4.83	4.83	4.83	4.83	4.83		
7	5	4.83	4.83	4.83	4.83	4.83	4.83	4.83	4.83	4.83	4.83		
19	3	4.84	4.84	4.84	4.84	4.84	4.84	4.84	4.84	4.84	4.84	4.84	
5	14		4.84	4.84	4.84	4.84	4.84	4.84	4.84	4.84	4.84	4.84	
14	8			4.87	4.87	4.87	4.87	4.87	4.87	4.87	4.87	4.87	
10	13			4.87	4.87	4.87	4.87	4.87	4.87	4.87	4.87	4.87	
18	5			4.89	4.89	4.89	4.89	4.89	4.89	4.89	4.89	4.89	4.89
9	3			4.89	4.89	4.89	4.89	4.89	4.89	4.89	4.89	4.89	4.89
31	18			4.89	4.89	4.89	4.89	4.89	4.89	4.89	4.89	4.89	4.89
36	4			4.89	4.89	4.89	4.89	4.89	4.89	4.89	4.89	4.89	4.89
27	11				4.92	4.92	4.92	4.92	4.92	4.92	4.92	4.92	4.92
29	6					4.96	4.96	4.96	4.96	4.96	4.96	4.96	4.96
11	11					4.96	4.96	4.96	4.96	4.96	4.96	4.96	4.96
20	18					4.96	4.96	4.96	4.96	4.96	4.96	4.96	4.96
28	3					4.97	4.97	4.97	4.97	4.97	4.97	4.97	4.97
32	5						5.01	5.01	5.01	5.01	5.01	5.01	5.01
37	5							5.03	5.03	5.03	5.03	5.03	5.03
38	6								5.05	5.05	5.05	5.05	5.05
33	5									5.08	5.08	5.08	5.08
35	14										5.12	5.12	5.12
26	4										5.13	5.13	5.13
17	7											5.15	5.15
39	5												5.20
Significance		0.062	0.093	0.085	0.063	0.076	0.087	0.059	0.083	0.067	0.054	0.053	0.052

APPENDIX 6.2 B) continued

Neoromicia capensis

CIL		Subset												
OTU	***n***	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
1	8	12.79												
3	10	12.97	12.97											
2	12	12.98	12.98											
25	4	13.00	13.00											
22	11	13.00	13.00											
21	6	13.20	13.20	13.20										
16	13	13.30	13.30	13.30	13.30									
6	4	13.32	13.32	13.32	13.32	13.32								
13	7	13.35	13.35	13.35	13.35	13.35								
8	18	13.40	13.40	13.40	13.40	13.40								
34	15	13.43	13.43	13.43	13.43	13.43								
19	3		13.52	13.52	13.52	13.52	13.52							
10	13		13.60	13.60	13.60	13.60	13.60	13.60						
30	7		13.63	13.63	13.63	13.63	13.63	13.63	13.63					
5	14			13.68	13.68	13.68	13.68	13.68	13.68					
12	5			13.69	13.69	13.69	13.69	13.69	13.69					
24	32			13.71	13.71	13.71	13.71	13.71	13.71	13.71				
9	3			13.73	13.73	13.73	13.73	13.73	13.73	13.73				
28	3			13.75	13.75	13.75	13.75	13.75	13.75	13.75				
27	11			13.75	13.75	13.75	13.75	13.75	13.75	13.75				
7	5			13.79	13.79	13.79	13.79	13.79	13.79	13.79				
4	3			13.80	13.80	13.80	13.80	13.80	13.80	13.80				
14	8			13.81	13.81	13.81	13.81	13.81	13.81	13.81				
15	10			13.85	13.85	13.85	13.85	13.85	13.85	13.85	13.85			
23	7				13.89	13.89	13.89	13.89	13.89	13.89	13.89			
20	18					13.99	13.99	13.99	13.99	13.99	13.99			
31	18						14.11	14.11	14.11	14.11	14.11	14.11		
11	11						14.13	14.13	14.13	14.13	14.13	14.13		
37	5						14.17	14.17	14.17	14.17	14.17	14.17	14.17	
18	5							14.21	14.21	14.21	14.21	14.21	14.21	
38	6							14.26	14.26	14.26	14.26	14.26	14.26	14.26
36	4							14.27	14.27	14.27	14.27	14.27	14.27	14.27
29	6								14.31	14.31	14.31	14.31	14.31	14.31
39	5									14.39	14.39	14.39	14.39	14.39
32	5										14.52	14.52	14.52	14.52
35	14										14.53	14.53	14.53	14.53
33	5											14.74	14.74	14.74
17	7												14.82	14.82
26	4													14.89
Significance		0.100	0.062	0.073	0.230	0.054	0.084	0.055	0.051	0.055	0.053	0.128	0.077	0.117

APPENDIX 6.2 B) continued

Neoromicia capensis

LUM1		Subset			
OTU	*n*	1	2	3	4
1	8	1.22			
7	5	1.29	1.29		
2	12	1.32	1.32	1.32	
16	13	1.33	1.33	1.33	
14	8	1.33	1.33	1.33	
6	4	1.34	1.34	1.34	1.34
28	3	1.34	1.34	1.34	1.34
5	14	1.34	1.34	1.34	1.34
25	4	1.35	1.35	1.35	1.35
34	15	1.35	1.35	1.35	1.35
3	10	1.35	1.35	1.35	1.35
8	18	1.35	1.35	1.35	1.35
10	13	1.35	1.35	1.35	1.35
15	10	1.35	1.35	1.35	1.35
13	7	1.36	1.36	1.36	1.36
21	6	1.36	1.36	1.36	1.36
22	11	1.37	1.37	1.37	1.37
12	5	1.37	1.37	1.37	1.37
31	18	1.37	1.37	1.37	1.37
19	3		1.38	1.38	1.38
4	3		1.38	1.38	1.38
30	7		1.38	1.38	1.38
23	7		1.40	1.40	1.40
11	11		1.40	1.40	1.40
9	3		1.40	1.40	1.40
24	32		1.40	1.40	1.40
27	11		1.42	1.42	1.42
36	4		1.43	1.43	1.43
26	4		1.44	1.44	1.44
20	18		1.44	1.44	1.44
17	7		1.44	1.44	1.44
39	5		1.44	1.44	1.44
29	6		1.45	1.45	1.45
18	5			1.45	1.45
33	5			1.46	1.46
32	5			1.47	1.47
37	5			1.48	1.48
35	14			1.48	1.48
38	6				1.49
Significance		0.077	0.059	0.051	0.093

APPENDIX 6.2 B) continued

Neoromicia capensis

MAOT		Subset								
OTU	*n*	1	2	3	4	5	6	7	8	9
34	15	2.85								
1	8	2.95	2.95							
29	6	2.97	2.97	2.97						
25	4	3.00	3.00	3.00	3.00					
31	18	3.03	3.03	3.03	3.03	3.03				
37	5	3.05	3.05	3.05	3.05	3.05	3.05			
36	4	3.06	3.06	3.06	3.06	3.06	3.06	3.06		
6	4	3.12	3.12	3.12	3.12	3.12	3.12	3.12	3.12	
33	5	3.13	3.13	3.13	3.13	3.13	3.13	3.13	3.13	
2	12	3.13	3.13	3.13	3.13	3.13	3.13	3.13	3.13	
22	11	3.14	3.14	3.14	3.14	3.14	3.14	3.14	3.14	3.14
30	7	3.15	3.15	3.15	3.15	3.15	3.15	3.15	3.15	3.15
3	10	3.16	3.16	3.16	3.16	3.16	3.16	3.16	3.16	3.16
21	6	3.18	3.18	3.18	3.18	3.18	3.18	3.18	3.18	3.18
12	5	3.18	3.18	3.18	3.18	3.18	3.18	3.18	3.18	3.18
5	14		3.1	3.1	3.1	3.1	3.1	3.1	3.1	3.1
13	7		3.21	3.21	3.21	3.21	3.21	3.21	3.21	3.21
19	3		3.21	3.21	3.21	3.21	3.21	3.21	3.21	3.21
8	18		3.23	3.23	3.23	3.23	3.23	3.23	3.23	3.23
16	13		3.23	3.23	3.23	3.23	3.23	3.23	3.23	3.23
27	11		3.29	3.29	3.29	3.29	3.29	3.29	3.29	3.29
24	32			3.29	3.29	3.29	3.29	3.29	3.29	3.29
38	6			3.30	3.30	3.30	3.30	3.30	3.30	3.30
4	3				3.33	3.33	3.33	3.33	3.33	3.33
9	3				3.33	3.33	3.33	3.33	3.33	3.33
39	5				3.33	3.33	3.33	3.33	3.33	3.33
10	13					3.34	3.34	3.34	3.34	3.34
28	3					3.35	3.35	3.35	3.35	3.35
18	5					3.36	3.36	3.36	3.36	3.36
32	5						3.37	3.37	3.37	3.37
14	8						3.38	3.38	3.38	3.38
15	10						3.38	3.38	3.38	3.38
23	7							3.39	3.39	3.39
20	18								3.41	3.41
35	14								3.42	3.42
7	5								3.44	3.44
26	4								3.45	3.45
11	11								3.45	3.45
17	7									3.48
Significance		0.055	0.058	0.069	0.077	0.072	0.061	0.077	0.056	0.056

APPENDIX 6.2 B) continued

Neoromicia capensis

POW		Subset					
OTU	*n*	1	2	3	4	5	6
1	8	3.44					
8	18	3.45					
2	12	3.47	3.47				
5	14	3.48	3.48				
3	10	3.50	3.50	3.50			
6	4	3.51	3.51	3.51	3.51		
7	5	3.56	3.56	3.56	3.56	3.56	
28	3	3.57	3.57	3.57	3.57	3.57	
12	5	3.59	3.59	3.59	3.59	3.59	3.59
21	6	3.59	3.59	3.59	3.59	3.59	3.59
16	13	3.61	3.61	3.61	3.61	3.61	3.61
23	7	3.63	3.63	3.63	3.63	3.63	3.63
22	11	3.63	3.63	3.63	3.63	3.63	3.63
24	32	3.63	3.63	3.63	3.63	3.63	3.63
30	7	3.64	3.64	3.64	3.64	3.64	3.64
11	11	3.64	3.64	3.64	3.64	3.64	3.64
10	13	3.66	3.66	3.66	3.66	3.66	3.66
29	6	3.66	3.66	3.66	3.66	3.66	3.66
27	11	3.67	3.67	3.67	3.67	3.67	3.67
13	7	3.67	3.67	3.67	3.67	3.67	3.67
19	3	3.67	3.67	3.67	3.67	3.67	3.67
15	10	3.67	3.67	3.67	3.67	3.67	3.67
20	18	3.69	3.69	3.69	3.69	3.69	3.69
4	3	3.70	3.70	3.70	3.70	3.70	3.70
34	15	3.70	3.70	3.70	3.70	3.70	3.70
14	8	3.70	3.70	3.70	3.70	3.70	3.70
26	4	3.70	3.70	3.70	3.70	3.70	3.70
18	5	3.72	3.72	3.72	3.72	3.72	3.72
31	18	3.72	3.72	3.72	3.72	3.72	3.72
9	3		3.75	3.75	3.75	3.75	3.75
17	7			3.79	3.79	3.79	3.79
35	14				3.79	3.79	3.79
36	4				3.79	3.79	3.79
37	5					3.82	3.82
25	4					3.82	3.82
38	6					3.83	3.83
33	5					3.83	3.83
39	5					3.84	3.84
32	5						3.86
Significance		0.060	0.068	0.052	0.063	0.071	0.092

APPENDIX 6.2 B) continued

Neoromicia capensis

WAS		Subset				
OTU	*n*	1	2	3	4	5
34	15	1.46				
36	4	1.48	1.48			
29	6	1.48	1.48	1.48		
1	8	1.48	1.48	1.48		
3	10	1.51	1.51	1.51	1.51	
31	18	1.52	1.52	1.52	1.52	
37	5	1.52	1.52	1.52	1.52	
25	4	1.54	1.54	1.54	1.54	
28	3	1.55	1.55	1.55	1.55	
8	18	1.55	1.55	1.55	1.55	
30	7	1.56	1.56	1.56	1.56	
33	5	1.56	1.56	1.56	1.56	
2	12	1.56	1.56	1.56	1.56	
13	7	1.56	1.56	1.56	1.56	
10	13	1.58	1.58	1.58	1.58	
6	4	1.58	1.58	1.58	1.58	
5	14	1.60	1.60	1.60	1.60	1.60
38	6	1.60	1.60	1.60	1.60	1.60
7	5	1.61	1.61	1.61	1.61	1.61
4	3	1.61	1.61	1.61	1.61	1.61
22	11	1.62	1.62	1.62	1.62	1.62
27	11	1.63	1.63	1.63	1.63	1.63
21	6	1.64	1.64	1.64	1.64	1.64
19	3	1.65	1.65	1.65	1.65	1.65
12	5	1.65	1.65	1.65	1.65	1.65
18	5	1.66	1.66	1.66	1.66	1.66
32	5	1.66	1.66	1.66	1.66	1.66
24	32	1.66	1.66	1.66	1.66	1.66
14	8	1.67	1.67	1.67	1.67	1.67
35	14	1.68	1.68	1.68	1.68	1.68
16	13		1.69	1.69	1.69	1.69
20	18		1.70	1.70	1.70	1.70
15	10		1.70	1.70	1.70	1.70
26	4			1.71	1.71	1.71
17	7				1.72	1.72
23	7				1.72	1.72
9	3				1.72	1.72
11	11				1.73	1.73
39	5					1.82
Significance		0.074	0.061	0.063	0.069	0.059

APPENDIX 6.2 B) continued

Neoromicia capensis

WFM		Subset					
OTU	*n*	1	2	3	4	5	6
3	10	3.36					
34	15	3.37					
1	8	3.38					
22	11	3.38					
2	12	3.39	3.39				
4	3	3.41	3.41	3.41			
19	3	3.41	3.41	3.41			
25	4	3.42	3.42	3.42	3.42		
16	13	3.43	3.43	3.43	3.43		
23	7	3.46	3.46	3.46	3.46	3.46	
14	8	3.47	3.47	3.47	3.47	3.47	3.47
6	4	3.49	3.49	3.49	3.49	3.49	3.49
12	5	3.49	3.49	3.49	3.49	3.49	3.49
30	7	3.50	3.50	3.50	3.50	3.50	3.50
8	18	3.51	3.51	3.51	3.51	3.51	3.51
5	14	3.52	3.52	3.52	3.52	3.52	3.52
28	3	3.52	3.52	3.52	3.52	3.52	3.52
24	32	3.52	3.52	3.52	3.52	3.52	3.52
13	7	3.53	3.53	3.53	3.53	3.53	3.53
27	11	3.53	3.53	3.53	3.53	3.53	3.53
36	4	3.54	3.54	3.54	3.54	3.54	3.54
37	5	3.55	3.55	3.55	3.55	3.55	3.55
7	5	3.56	3.56	3.56	3.56	3.56	3.56
20	18	3.57	3.57	3.57	3.57	3.57	3.57
29	6	3.58	3.58	3.58	3.58	3.58	3.58
15	10	3.59	3.59	3.59	3.59	3.59	3.59
31	18	3.60	3.60	3.60	3.60	3.60	3.60
21	6	3.60	3.60	3.60	3.60	3.60	3.60
10	13	3.61	3.61	3.61	3.61	3.61	3.61
11	11	3.62	3.62	3.62	3.62	3.62	3.62
39	5	3.63	3.63	3.63	3.63	3.63	3.63
17	7	3.67	3.67	3.67	3.67	3.67	3.67
33	5		3.70	3.70	3.70	3.70	3.70
38	6			3.71	3.71	3.71	3.71
18	5			3.71	3.71	3.71	3.71
32	5			3.72	3.72	3.72	3.72
9	3				3.74	3.74	3.74
35	14					3.76	3.76
26	4						3.79
Significance		0.070	0.069	0.074	0.054	0.134	0.052

APPENDIX 6.2 B) continued

Neoromicia capensis

WIUM1		Subset				
OTU	*n*	**1**	**2**	**3**	**4**	**5**
1	8	2.53				
34	15	2.54				
13	7	2.55				
25	4	2.56	2.56			
2	12	2.56	2.56			
8	18	2.58	2.58	2.58		
12	5	2.61	2.61	2.61	2.61	
3	10	2.62	2.62	2.62	2.62	
22	11	2.63	2.63	2.63	2.63	
21	6	2.63	2.63	2.63	2.63	
36	4	2.63	2.63	2.63	2.63	
5	14	2.64	2.64	2.64	2.64	
30	7	2.66	2.66	2.66	2.66	
19	3	2.66	2.66	2.66	2.66	
16	13	2.67	2.67	2.67	2.67	
29	6	2.67	2.67	2.67	2.67	
28	3	2.68	2.68	2.68	2.68	
6	4	2.69	2.69	2.69	2.69	
24	32	2.70	2.70	2.70	2.70	
10	13	2.71	2.71	2.71	2.71	2.71
4	3	2.72	2.72	2.72	2.72	2.72
31	18	2.72	2.72	2.72	2.72	2.72
37	5	2.72	2.72	2.72	2.72	2.72
18	5	2.72	2.72	2.72	2.72	2.72
27	11	2.73	2.73	2.73	2.73	2.73
38	6	2.73	2.73	2.73	2.73	2.73
7	5	2.74	2.74	2.74	2.74	2.74
15	10	2.74	2.74	2.74	2.74	2.74
20	18	2.75	2.75	2.75	2.75	2.75
11	11	2.75	2.75	2.75	2.75	2.75
23	7	2.76	2.76	2.76	2.76	2.76
35	14	2.80	2.80	2.80	2.80	2.80
14	8		2.83	2.83	2.83	2.83
33	5			2.85	2.85	2.85
17	7				2.86	2.86
26	4				2.86	2.86
9	3				2.87	2.87
32	5				2.88	2.88
39	5					2.97
Significance		0.068	0.061	0.068	0.058	0.117

APPENDIX 6.2 B) continued

Neoromicia capensis

WOUC		Subset									
OTU	*n*	1	2	3	4	5	6	7	8	9	10
1	8	4.24									
3	10	4.27	4.27								
34	15	4.28	4.28	4.28							
2	12	4.32	4.32	4.32	4.32						
21	6	4.33	4.33	4.33	4.33	4.33					
25	4	4.37	4.37	4.37	4.37	4.37	4.37				
9	3	4.40	4.40	4.40	4.40	4.40	4.40	4.40			
8	18	4.40	4.40	4.40	4.40	4.40	4.40	4.40			
28	3	4.43	4.43	4.43	4.43	4.43	4.43	4.43	4.43		
22	11	4.43	4.43	4.43	4.43	4.43	4.43	4.43	4.43		
5	14	4.45	4.45	4.45	4.45	4.45	4.45	4.45	4.45		
19	3	4.46	4.46	4.46	4.46	4.46	4.46	4.46	4.46		
12	5	4.47	4.47	4.47	4.47	4.47	4.47	4.47	4.47		
13	7	4.47	4.47	4.47	4.47	4.47	4.47	4.47	4.47		
31	18	4.48	4.48	4.48	4.48	4.48	4.48	4.48	4.48		
29	6	4.49	4.49	4.49	4.49	4.49	4.49	4.49	4.49	4.49	
36	4	4.51	4.51	4.51	4.51	4.51	4.51	4.51	4.51	4.51	
16	13	4.51	4.51	4.51	4.51	4.51	4.51	4.51	4.51	4.51	
30	7	4.51	4.51	4.51	4.51	4.51	4.51	4.51	4.51	4.51	
7	5	4.55	4.55	4.55	4.55	4.55	4.55	4.55	4.55	4.55	4.55
24	32	4.58	4.58	4.58	4.58	4.58	4.58	4.58	4.58	4.58	4.58
6	4		4.59	4.59	4.59	4.59	4.59	4.59	4.59	4.59	4.59
4	3			4.62	4.62	4.62	4.62	4.62	4.62	4.62	4.62
10	13				4.63	4.63	4.63	4.63	4.63	4.63	4.63
27	11				4.64	4.64	4.64	4.64	4.64	4.64	4.64
18	5				4.65	4.65	4.65	4.65	4.65	4.65	4.65
23	7				4.65	4.65	4.65	4.65	4.65	4.65	4.65
38	6				4.67	4.67	4.67	4.67	4.67	4.67	4.67
15	10					4.67	4.67	4.67	4.67	4.67	4.67
37	5						4.67	4.67	4.67	4.67	4.67
33	5						4.68	4.68	4.68	4.68	4.68
26	4						4.70	4.70	4.70	4.70	4.70
20	18						4.70	4.70	4.70	4.70	4.70
11	11						4.70	4.70	4.70	4.70	4.70
14	8							4.74	4.74	4.74	4.74
35	14								4.77	4.77	4.77
39	5								4.77	4.77	4.77
32	5									4.83	4.83
17	7										4.87
Significance		0.073	0.105	0.073	0.052	0.059	0.071	0.058	0.051	0.068	0.153

APPENDIX 6.2 B) continued

Neoromicia capensis

WUPM4		Subset				
OTU	*n*	**1**	**2**	**3**	**4**	**5**
26	4	0.90				
8	18	0.91	0.91			
19	3	0.93	0.93	0.93		
1	8	0.93	0.93	0.93		
7	5	0.94	0.94	0.94		
22	11	0.94	0.94	0.94		
6	4	0.95	0.95	0.95	0.95	
14	8	0.96	0.96	0.96	0.96	
13	7	0.96	0.96	0.96	0.96	
24	32	0.96	0.96	0.96	0.96	
21	6	0.97	0.97	0.97	0.97	0.97
17	7	0.97	0.97	0.97	0.97	0.97
18	5	0.98	0.98	0.98	0.98	0.98
39	5	0.98	0.98	0.98	0.98	0.98
15	10	0.99	0.99	0.99	0.99	0.99
27	11	0.99	0.99	0.99	0.99	0.99
30	7	0.99	0.99	0.99	0.99	0.99
5	14	1.00	1.00	1.00	1.00	1.00
32	5	1.00	1.00	1.00	1.00	1.00
10	13	1.00	1.00	1.00	1.00	1.00
12	5	1.00	1.00	1.00	1.00	1.00
16	13	1.01	1.01	1.01	1.01	1.01
20	18	1.01	1.01	1.01	1.01	1.01
2	12	1.01	1.01	1.01	1.01	1.01
4	3	1.02	1.02	1.02	1.02	1.02
38	6	1.02	1.02	1.02	1.02	1.02
35	14	1.02	1.02	1.02	1.02	1.02
23	7	1.03	1.03	1.03	1.03	1.03
25	4	1.03	1.03	1.03	1.03	1.03
33	5	1.04	1.04	1.04	1.04	1.04
31	18	1.05	1.05	1.05	1.05	1.05
11	11	1.05	1.05	1.05	1.05	1.05
34	15	1.05	1.05	1.05	1.05	1.05
37	5	1.06	1.06	1.06	1.06	1.06
36	4		1.09	1.09	1.09	1.09
3	10			1.10	1.10	1.10
29	6			1.10	1.10	1.10
28	3				1.13	1.13
9	3					1.15
Significance		0.140	0.055	0.077	0.062	0.053

APPENDIX 6.2 B) continued

Neoromicia capensis

WUPM4		Subset				
OTU	*n*	1	2	3	4	5
26	4	0.90				
8	18	0.91	0.91			
19	3	0.93	0.93	0.93		
1	8	0.93	0.93	0.93		
7	5	0.94	0.94	0.94		
22	11	0.94	0.94	0.94		
6	4	0.95	0.95	0.95	0.95	
14	8	0.96	0.96	0.96	0.96	
13	7	0.96	0.96	0.96	0.96	
24	32	0.96	0.96	0.96	0.96	
21	6	0.97	0.97	0.97	0.97	0.97
17	7	0.97	0.97	0.97	0.97	0.97
18	5	0.98	0.98	0.98	0.98	0.98
39	5	0.98	0.98	0.98	0.98	0.98
15	10	0.99	0.99	0.99	0.99	0.99
27	11	0.99	0.99	0.99	0.99	0.99
30	7	0.99	0.99	0.99	0.99	0.99
5	14	1.00	1.00	1.00	1.00	1.00
32	5	1.00	1.00	1.00	1.00	1.00
10	13	1.00	1.00	1.00	1.00	1.00
12	5	1.00	1.00	1.00	1.00	1.00
16	13	1.01	1.01	1.01	1.01	1.01
20	18	1.01	1.01	1.01	1.01	1.01
2	12	1.01	1.01	1.01	1.01	1.01
4	3	1.02	1.02	1.02	1.02	1.02
38	6	1.02	1.02	1.02	1.02	1.02
35	14	1.02	1.02	1.02	1.02	1.02
23	7	1.03	1.03	1.03	1.03	1.03
25	4	1.03	1.03	1.03	1.03	1.03
33	5	1.04	1.04	1.04	1.04	1.04
31	18	1.05	1.05	1.05	1.05	1.05
11	11	1.05	1.05	1.05	1.05	1.05
34	15	1.05	1.05	1.05	1.05	1.05
37	5	1.06	1.06	1.06	1.06	1.06
36	4		1.09	1.09	1.09	1.09
3	10			1.10	1.10	1.10
29	6			1.10	1.10	1.10
28	3				1.13	1.13
9	3					1.15
Significance		0.140	0.055	0.077	0.062	0.053

APPENDIX 6.2 C)

Neoromicia cf. *melckorum*

WOUC		Subset	
OTU	*n*	**1**	**2**
4	7	4.69	
3	4	4.72	
2	4	4.75	
5	4	4.81	
1	3		5.04
Significance		0.337	1

APPENDIX 6.2 D)

Neoromicia africanus

CIL		Subset			
OTU	*n*	1	2	3	4
3	9	10.9			
9	4	10.92	10.92		
2	4	10.95	10.95	10.95	
4	28	11.01	11.01	11.01	
10	8	11.15	11.15	11.15	11.15
1	5	11.19	11.19	11.19	11.19
7	7	11.21	11.21	11.21	11.21
11	8	11.25	11.25	11.25	11.25
8	4		11.33	11.33	11.33
6	4			11.35	11.35
5	8				11.44
Significance		0.169	0.053	0.05	0.43

BH		Subset		
OTU	*n*	1	2	3
4	28	4.17		
3	9	4.21	4.21	
2	4	4.35	4.35	4.35
5	8	4.37	4.37	4.37
1	5	4.39	4.39	4.39
11	8		4.44	4.44
10	8		4.46	4.46
6	4			4.48
7	7			4.50
8	4			4.51
9	4			4.52
Significance		0.188	0.087	0.571

BB		Subset		
OTU	*n*	1	2	3
2	4	5.89		
6	4	5.97	5.97	
9	4	5.99	5.99	5.99
8	4	6.00	6.00	6.00
10	8	6.01	6.01	6.01
11	8	6.02	6.02	6.02
5	8	6.05	6.05	6.05
1	5	6.10	6.10	6.10
7	7		6.13	6.13
4	28		6.17	6.17
3	9			6.22
Significance		0.122	0.18	0.081

APPENDIX 6.2 D) continued

Neoromicia africanus

WOUC		Subset		
OTU	*n*	1	2	3
3	9	3.30		
1	5	3.41	3.41	
4	28	3.43	3.43	
2	4	3.52	3.52	3.52
10	8		3.60	3.60
9	4		3.61	3.61
5	8		3.64	3.64
6	4		3.65	3.65
11	8		3.67	3.67
8	4			3.69
7	7			3.78
Significance		0.164	0.053	0.056

WIUM1		Subset	
OTU	*n*	1	2
3	9	2.22	
9	4	2.32	2.32
4	28	2.33	2.33
6	4	2.38	2.38
11	8		2.40
2	4		2.41
10	8		2.41
5	8		2.42
8	4		2.44
1	5		2.45
7	7		2.48
Significance		0.088	0.063

WUPM4		Subset	
OTU	*n*	1	2
6	4	0.68	
4	28	0.70	0.70
2	4	0.72	0.72
8	4	0.75	0.75
9	4	0.75	0.75
5	8	0.75	0.75
11	8	0.79	0.79
7	7	0.79	0.79
3	9	0.81	0.81
1	5	0.83	0.83
10	8		0.85
Significance		0.063	0.098

LUM1		Subset	
OTU	*n*	1	2
9	4	1.02	
3	9	1.03	
7	7	1.05	1.05
6	4	1.05	1.05
8	4	1.05	1.05
4	28	1.05	1.05
10	8	1.06	1.06
11	8	1.06	1.06
5	8	1.07	1.07
1	5	1.10	1.10
2	4		1.12
Significance		0.128	0.214

MAOT		Subset	
OTU	*n*	1	2
3	9	2.25	
9	4	2.32	2.32
1	5	2.35	2.35
6	4	2.41	2.41
10	8	2.42	2.42
11	8		2.44
4	28		2.44
2	4		2.44
5	8		2.45
8	4		2.46
7	7		2.47
Significance		0.067	0.142

APPENDIX 6.2 E)

Neoromicia zuluensis

POW		Subset		
OTU	*n*	1	2	3
3	11	3.26		
4	3	3.37	3.37	
2	15	3.40	3.40	3.40
1	4	3.47	3.47	3.47
6	3		3.49	3.49
5	3			3.62
Significance		0.079	0.563	0.066

WOUC		Subset	
OTU	*n*	1	2
3	11	3.66	
4	3	3.68	
5	3	3.73	3.73
1	4	3.75	3.75
2	15	3.79	3.79
6	3		3.95
Significance		0.596	0.113

WUPM4		Subset	
OTU	*n*	1	2
5	3	0.78	
6	3	0.79	
1	4	0.80	
4	3	0.80	
2	15	0.82	
3	11		1.02
Significance		0.981	1

LUM1		Subset	
OTU	*n*	1	2
4	3	1.15	
5	3	1.16	1.16
2	15	1.18	1.18
6	3	1.22	1.22
1	4	1.24	1.24
3	11		1.32
Significance		0.594	0.059

APPENDIX 6.2 F)

Pipistrellus hesperidus

ZB		Subset	
OTU	*n*	1	2
2	4	7.25	
1	3	7.38	7.38
5	3	7.43	7.43
3	7	7.50	7.50
6	13		7.62
4	10		7.65
Significance		0.224	0.134

WOUC		Subset	
OTU	*n*	1	2
1	3	4.11	
2	4	4.24	4.24
6	13	4.33	4.33
3	7	4.33	4.33
4	10		4.40
5	3		4.43
Significance		0.109	0.25

APPENDIX 6.2 G)

Pipistrellus rusticus

BH		Subset	
OTU	*n*	1	2
4	12	4.27	
7	2	4.31	4.31
3	6	4.35	4.35
5	15	4.36	4.36
6	4	4.47	4.47
2	2		4.57
1	9		4.59
Significance		0.375	0.078

WOUC		Subset	
OTU	*n*	1	2
2	2	3.74	
7	2	3.79	3.79
3	6	3.82	3.82
1	9	3.86	3.86
4	12	3.87	3.87
5	15	4.06	4.06
6	4		4.10
Significance		0.052	0.054

WUPM4		Subset		
OTU	*n*	1	2	3
2	2	0.66		
4	12	0.79	0.79	
3	6		0.87	0.87
1	9		0.90	0.90
5	15		0.90	0.90
6	4		0.93	0.93
7	2			0.99
Significance		0.124	0.11	0.221

MAOT		Subset		
OTU	*n*	1	2	3
3	6	2.48		
2	2	2.55	2.55	
7	2	2.64	2.64	2.64
1	9	2.66	2.66	2.66
4	12	2.72	2.72	2.72
6	4		2.76	2.76
5	15			2.81
Significance		0.094	0.161	0.44

LUM1		Subset		
OTU	*n*	1	2	3
2	2	1.02		
1	9	1.09	1.09	
3	6		1.17	1.17
4	12		1.18	1.18
5	15			1.22
7	2			1.23
6	4			1.25
Significance		0.156	0.057	0.078

CHAPTER 7

INTER-SPECIFIC VARIATION OF TRADITIONAL CRANIAL MORPHOMETRIC MEASUREMENTS

7.1 INTRODUCTION

Many of the current keys to the vespertilionid species (as with most mammal species) relate to variations in cranial and dental characters (Meester *et al.*, 1986), which for the 10 vespertilionid species central to this study are not always very discernible (Kearney and Taylor, 1997; Kearney and Seamark, 2004 - see Appendix I). Furthermore, analyses with more recent molecular techniques have shown that cranial morphology in vespertilionids is not always related to phylogeny (Hoofer and Van Den Bussche, 2003; Ruedi and Mayer, 2001).

The aim of this chapter was to establish whether traditional morphometric methods applied to 12 cranial measurements, could discern patterns of cranial shape and size change which would allow separation between ten vespertilionid species and, if so, whether any cranial difference between species would be phylogenetically informative. Further, it was also investigated whether the traditional morphometric results would concur with those of the shape morphometric analysis (Chapter 3), which showed a high degree of homoplasy in skull morphology of the taxa in question (as captured by the landmarks used in the analysis) that hindered species separation. Presumably, such homoplasy occurs as a result of allometry (Singleton, 2002) and ecological constraints (Jacobs, 1996; Freeman 1998; Pedersen 1998; Sanchez-Villagra and Williams, 1998; Stadelmann *et al.* 2004). Hence relationships based on skull shape of the different species lacked concordance with currently recognised phylogenetic relationships of the species (Hoofer and Van Den Bussche, 2003; Volleth *et al.* 2001; Kearney *et al.*, 2002).

7.2 MATERIAL AND METHODS

The following statistical analyses were performed to assess variation between the 10 vespertilionid species: PCA based on correlation matrices from standardized variables, UPGMA cluster analysis based on standardized average taxonomic distance matrices, and DFA of OTUs and individuals of each species. The same OTUs and individuals identified in Chapter 6 were used in this analysis (see Appendix 6.1 for specimen details). However, the coding was modified as shown in Table 7.1 to incorporate analyses across the different species. A minimum spanning tree based on a distance matrix was added to one of the PCA scatterplots to help detect local distortions, i.e. pairs of points which seem close together in a plot but actually are far apart if other dimensions are taken into account (Rohlf, 1997).

An assessment was made as to whether there was an association between cranial morphology and size between species, i.e. if the crania of the different species are allometrically scaled (Milne and O'Higgens, 2002). Principal component scores were tested for significant linear relationships with size. A measure of overall skull length, condylo-incisor length, was also chosen to represent size. Principal component scores were plotted against the log of the condylo-incisor lengths and regression statistics were calculated for the relationship between the axes. Additionally, multivariate allometric coefficients (Jolicoeur, 1963) were calculated from the morphometric data using JACKIE – JACKknife Interactive Eigenanalysis (Calvalcanti, 1997-2001) available as freeware from the State University of New York, Stony Brook web MORPHOMETRICS page: http://life.bio.sunysb.edu/morph/ . JACKIE calculates multivariate allometric coefficients following a PCA of a log transformed variance-covariance matrix. Multivariate allometric coefficient values and regression slope values (allometric coefficients) which are above 1.0 indicate positive allometry, whereas values below 1.0 indicate negative allometry, and the special case when these values are equal to 1.0 indicates isometry (Huxley and Teissier, 1936).

Unfortunately, many of the type specimens measured for this analysis by Dr Peter Taylor, were missing data from the 12 measurement suite chosen. However, given the importance of these specimens, additional PCA and cluster analyses were performed on data suites of fewer measurements. To accommodate the different suite of measurements available for each of the type specimens, four additional analyses were run on the maximum number of measurements available. Table 7.2 gives the details of which type specimens and measurements were included in each analysis. See Appendix 7.1 for details of the additional specimens included.

DFA of all 12 measurements entered together and stepwise were computed for pairs of species to provide a means of species identification using cranial characters following Dippenaar *et al.* (1993), Robinson and Dippenaar (1987) and Taylor *et al.* (1993). In discriminant analysis, the discriminating variables are weighted according to their discriminating power and are linearly

Table 7.1 Coding for OTUs and individuals of each vespertilionid species used in the inter-specific analyses (Inter), with the equivalent number code used in the intra-specific analyses (Intra).

Species	Inter	Intra
Neoromicia capensis	1c	1
	2c	2
	3c	3
	4c	4
	5c	5
	6c	6
	7c	7
	8c	8
	9c	9
	10c	10
	11c	11
	12c	12
	13c	13
	14c	14
	15c	15
	16c	16
	17c	17
	18c	18
	19c	19
	20c	20
	21c	21
	22c	22
	23c	23
	24c	24
	25c	25
	26c	26
	27c	27
	28c	28
	29c	29
	30c	30
	31c	31
	32c	32
	33c	33
	34c	34
	35c	35
	36c	36
	37c	37
	38c	38
	39c	39
Eptesicus hottentotus	40h	1
	41h	2
	42h	3
	43h	4
	44h	5
	45h	6
	46h	7
	47h	8
Hypsugo anchietae	48a	1
	49a	2
	50a	3
	51a	4
	52a	5

Species	Inter	Intra
Neoromicia cf. *melckorum*	53m	1
	54m	2
	55m	3
	56m	4
	57m	5
Neoromicia africanus	58n	1
	59n	2
	60n	3
	61n	4
	62n	5
	63n	6
	64n	7
	65n	8
	66n	9
	67n	10
	68n	11
Neoromicia rendalli	69re	2
	70re	1
Neoromicia rueppellii	71ru	1
	72ru	2
	73ru	3
	74ru	4
Neoromicia zuluensis	75z	1
	76z	2
	77z	3
	78z	4
	79z	5
	80z	6
	81z	7
	82z	8
	83z	9
	84z	10
Pipistrellus hesperidus	85k	1
	86k	2
	87k	3
	88k	4
	89k	5
	90k	6
	91k	7
	92k	8
	93k	9
	94k	10
	95k	11
Pipistrellus rusticus	96rs	1
	97rs	2
	98rs	3
	99rs	4
	100rs	5
	101rs	6
	102rs	7

Table 7.2 Details of four different analyses run with additional type and other vespertilionid specimens, with details of the additional specimens (Species), the numbers used to identify them (Code), the number (*n*) and type of measurements used in each analysis.

Analysis	**Species**	**Code**	**Measurements used**	*n*
1	*Neoromicia rendalli* (PM89.12.12.1-paratype; BM89.3.2.3 - holotype); *Pipistrellus hesperidus fuscatus* (BM1.8.9.96 - holotype); *Neoromicia africanus fouriei* (BM25.12.4.20 - holotype); *Neoromicia capensis gracilior* (BM4.8.31.3 - holotype); *Neoromicia somalicus* (BM98.6.9.1 - holotype)	103-108	CIL, BH, ZB, BB, POW, WFM, WIUM1, LUM1, MAOT	9
2	*Neoromicia africanus fouriei* (BM25.12.4.20 - holotype); *Neoromicia africanus nanus* (BM7.1.1.422 - syntype)	103-104	CIL, BH, ZB, BB, POW, WFM, LUM1, MAOT	8
3	*Pipistrellus rusticus* (PM35.9.1.101; PM35.9.1.102 - not type specimens); *Pipistrellus rusticus* (BM7.1.1.419 - lectotype).	103-105	CIL, BH, ZB, BB, POW, WIUM1, LUM1, MAOT	8
4	*Hypsugo anchietae* (PM69.1248; PM70.2632; PM70.2633 – not type specimens). *Hypsugo anchietae* (BM6.1.3.1 - syntype).	103-106	CIL, BH, ZB, BB, POW, WIUM1, MAOT	7

combined so that the taxonomic groups are made as statistically distinct from each other as possible. Given a set of variables, discriminant analysis selects those that together give the greatest possible separation. Variables that do not significantly add to the separating power of the derived linear functions are not included in the analysis (Tidemann *et al.*, 1981). For the DFA, *a priori* classifications were based on previous PCA, CA and DFA with individuals of known identity, and excluded OTUs or individuals that were mis-identified or outliers to the rest of the taxa.

Basic statistics were calculated for the southern African distribution of each species (mean, standard deviation, coefficient of variation, range, and total number of specimens). The statistical analyses were run using the statistical packages of SPSS 9.0.1 (SPSS Inc., 1999) and NTSYS-pc, version 2.01h (Rohlf, 1997).

7.3 RESULTS

7.3.1 Inter-specific variation between 10 vespertilionid species

A scatterplot of the first two principal components (Fig. 7.1 A) of a PCA of all ten vespertilionid species based on OTUs and individuals identified in the intra-specific analysis (Chapter 6), clearly separated the larger *E. hottentotus* from the other species on the first principal component axis, and *Neoromicia rueppellii* was separated from all species on the second principal component axis. Accounting for the large size component in this axis, the eigenvector loadings were all high and positive on the first principal component axis which accounted for 90.93% the variation (Table 7.3). Although all the measurements loaded highly on the first axis, those that loaded highest were the overall measures of skull length and breadth: condylo-incisor skull length, zygomatic breadth, and braincase breadth. The measurements that were most important in the separation of *N. rueppellii* from the other species on the second principal component axis were length between the condylar and the coronoid processes and post-orbital width. Although the distinct separations of *E. hottentotus* and *N. rueppellii* rather dominated the overall pattern in the PCA scatterplot, the OTUs and individuals of *N.* cf. *melckorum*, *N. capensis* and *N. africanus* largely separate into clusters of similar taxa. On the other hand, there were overlaps between the OTUs of *N. zuluensis* and *P. rusticus*, and between *H. anchietae* and *P. hesperidus*, as well as a few outlier OTUs and individuals of *N. capensis*, *N. zuluensis* and *P. hesperidus*.

Removing the dominant size component of the first principal component axis and plotting the second and third principal component axes (Fig. 7.1 B), clearly distinguished *N. rueppellii* from the other taxa on the second principal component axis. *Neoromicia rendalli* also partially separated partially from the other taxa along the second principal component axis, although it was closer to the main cluster of OTUs and individuals. The remaining taxa, with the exception of *P. hesperidus,* which almost separated along the second principal component axis, overlapped with each other. Length between the condylar and the coronoid processes and post-orbital width were important measurements on the second principal axis in the distinction of *P. rueppellii* and *N. rendalli.* The important characters on the third principal component axis, greatest width of the articular surface and width of the upper fourth premolar and which explained 1.33% of the variation, did not separate taxa.

The average taxonomic distance phenogram (Fig. 7.2) based on OTUs and individuals of all 10 vespertilionid species, also identified the clear distinction of *E. hottentotus* from the rest of the species, but the separation of *N. rueppellii* was less distinct. Of the four OTUs of *N. rueppellii,* three formed a relatively distinct cluster together with the OTU of *N. rendalli* from KwaZulu-Natal, while the other OTU of *N. rueppellii* formed a neighbouring group to one which included *H. anchietae*, *P. rusticus*, *N. africanus* and *N. zuluensis.* Although the clustering in the distance phenogram was not unlike the pattern of distribution seen in the PCA scatterplot, there were a few distinctions, e.g., the clustering of *N.* cf. *melckorum* together with specimens of *N. capensis* (with the exception of OTU 9 from Gauteng) with OTUs from the eastern and western Cape, and the clustering of several *N. capensis* OTUs with *P. hesperidus.*

The separation along the first PC, with the largest and the smallest species at either ends of the axes and the species of intermediate-size arranged in between, indicated an allometric relationship between the species. A plot of PC1 scores based on a PCA of 12 cranial measurements of 10 taxa OTUs and individuals against log CIL (Fig. 7.3) confirmed the presence of an allometric relationship between the species, since the slope of the regression line showed significant negative allometry (standardised Beta coefficient = 0.985; P = 0.00E-17). Neither regression analyses of the second (standardised Beta coefficient = -0.116; P = 0.245) or the third principal components (standardised Beta coefficient = -0.316; P = 0.753) with log CIL showed

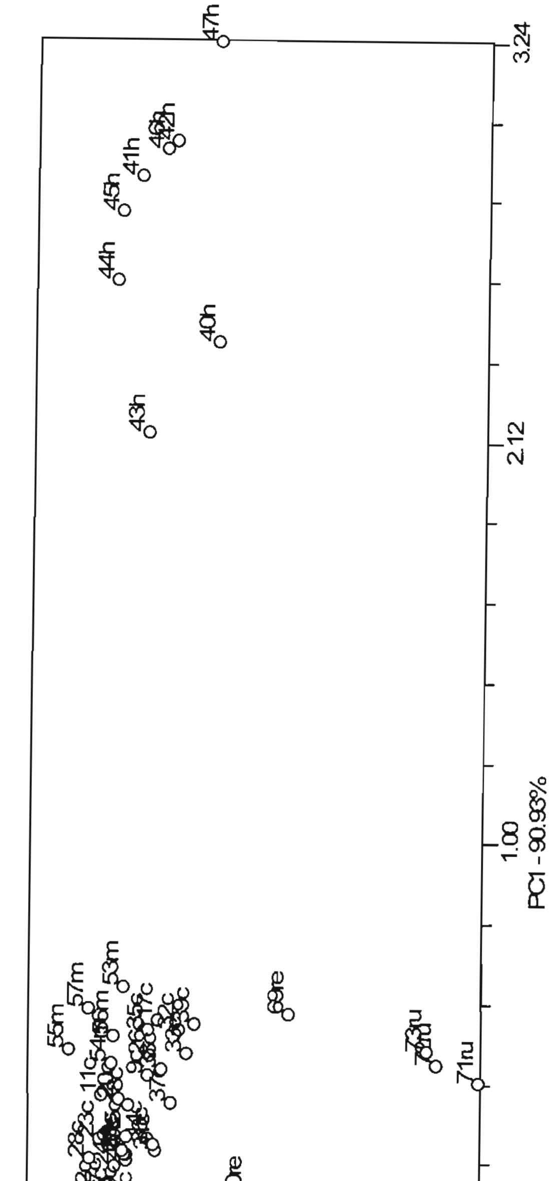


Figure 7.1 A) Scatterplot of the first two principal components of a PCA of 10 different vespertilionid species, based on 12 cranial measurements. OTU and individual numbers and subspecies codes correspond to those in Table 7.1.

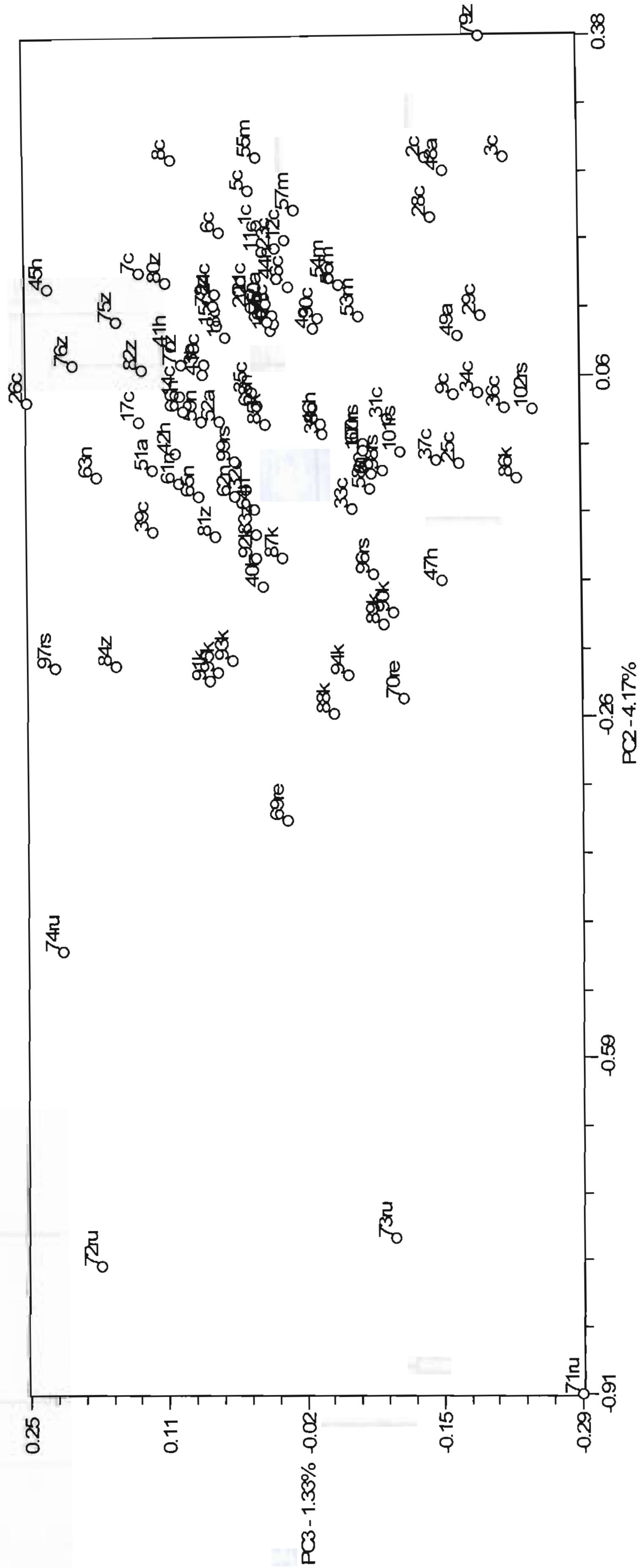


Figure 7.1 B) Scatterplot of the second and third principal components of a PCA of 10 different vespertilionid species, based on 12 cranial measurements. OTU and individual numbers and subspecies codes correspond to those in Table 7.1.

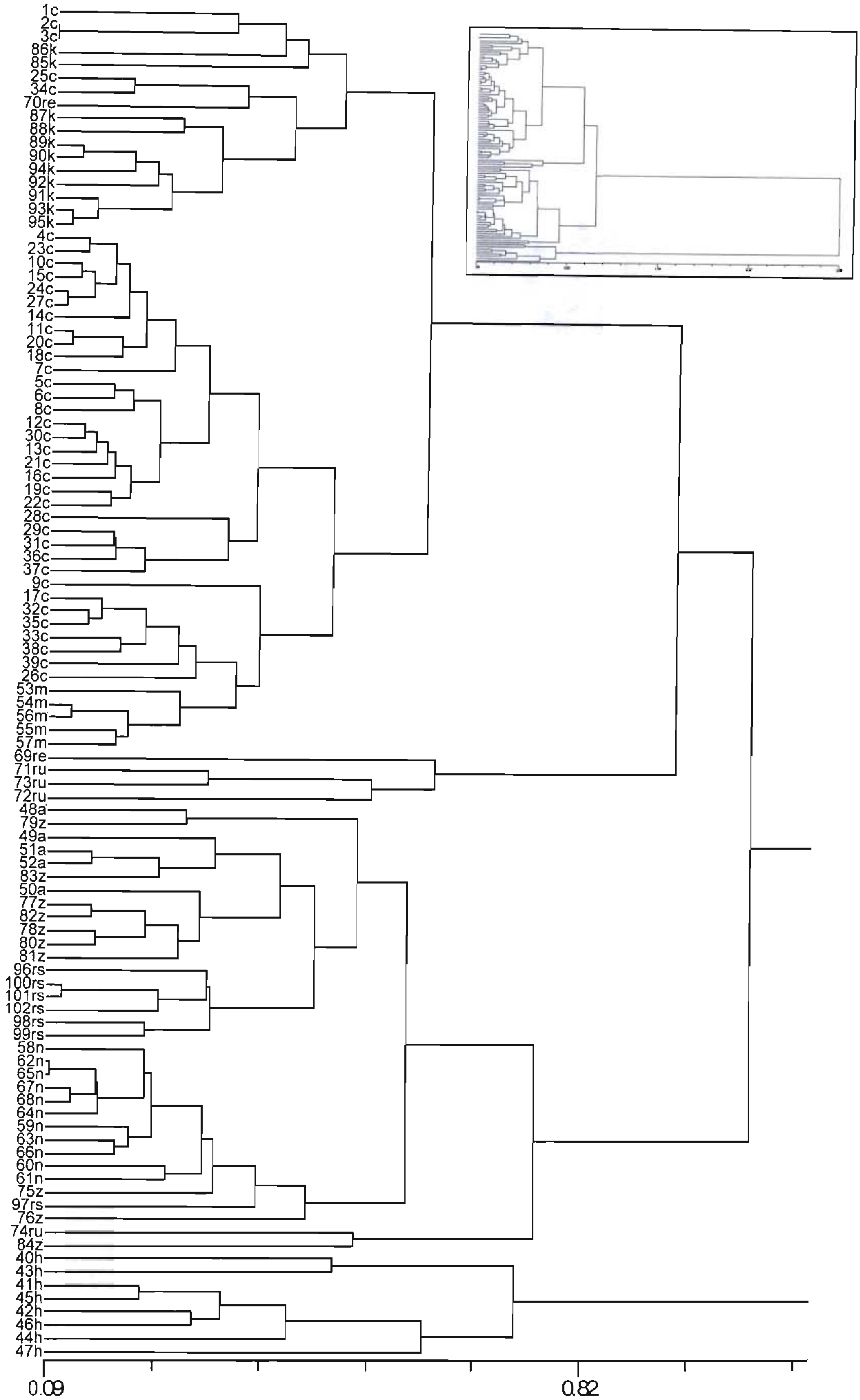


Figure 7.2 Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on 12 cranial measurements of 10 different vespertilionid species. OTU and individual numbers and subspecies codes correspond to those in Table 7.1. Cophenetic correlation coefficient = 0.929. Inset shows entire phenogram.

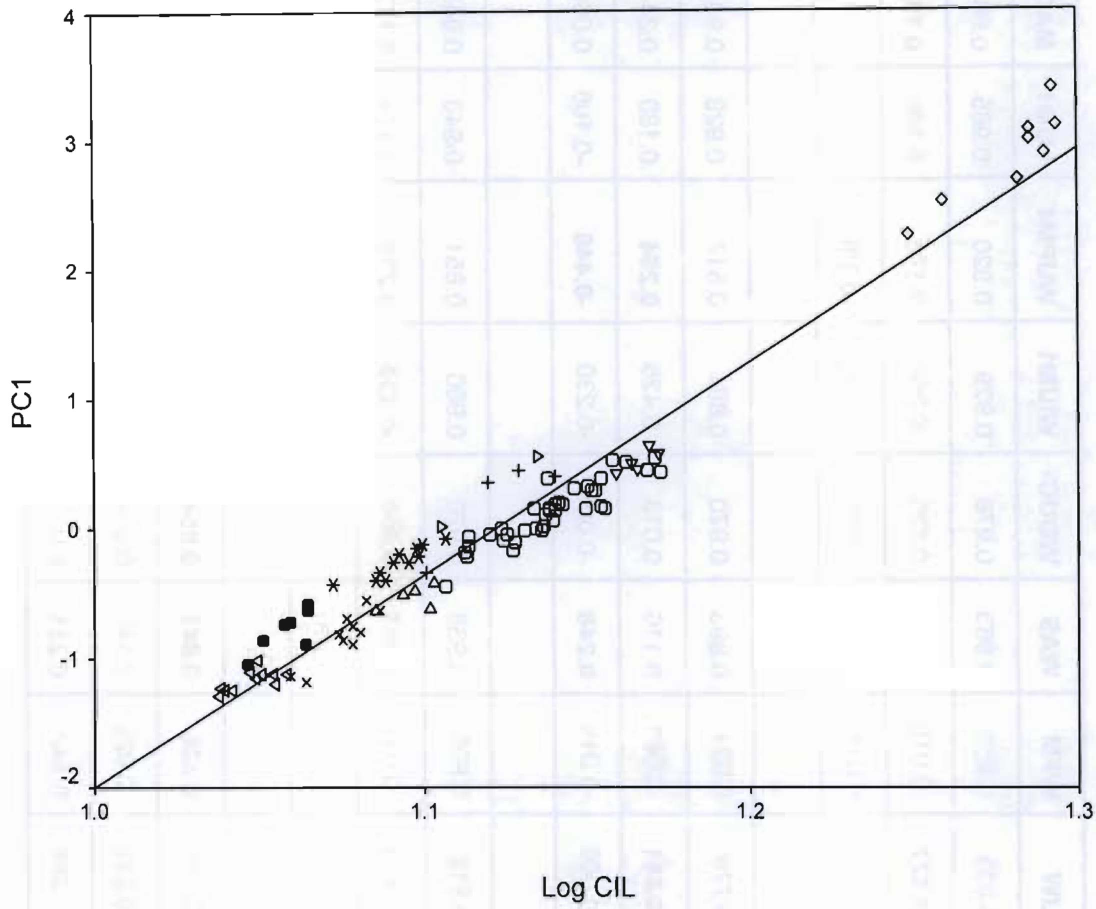


Figure 7.3 Scatterplot of log condylo-incisor length against first principal component scores of a PCA of 10 vespertilionid species based on 12 cranial measurements. $r^2 = 0.956$. Species symbols: *Neoromicia capensis* = ○, *Eptesicus hottentotus* = ◇, *Hypsugo anchietae* = △, *Neoromicia* cf. *melckorum* = ▽, *Neoromicia africanus* = ◁, *Neoromicia rendalli* = ▷, *Neoromicia rueppellii* = +, *Neoromicia zuluensis* = ×, *Pipistrellus hesperidus* = ∗, *Pipistrellus rusticus* = ●

Table 7.3 Eigenvalues of principal component analyses of vespertilionid bats assessed. Figures in bold type are the most important measurements on that axis.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
10 species	**PC1**	**0.985**	0.960	**0.990**	**0.985**	0.833	0.959	0.963	0.976	0.929	0.920	0.965	0.966
OTUs	**PC2**	0.109	-0.125	0.050	-0.089	**-0.527**	-0.010	0.106	0.125	-0.250	0.176	0.165	**0.194**
	PC3	0.047	0.085	0.042	0.019	-0.092	0.028	**0.126**	0.026	0.018	**-0.336**	-0.064	0.072
8 species	**PC1**	**0.961**	0.890	**0.977**	**0.972**	0.779	0.921	0.893	0.970	0.801	0.817	0.928	0.931
OTUs	**PC2**	0.184	-0.170	0.036	-0.007	**-0.551**	-0.001	0.116	0.013	-0.426	**0.254**	0.180	0.244
	PC3	0.092	0.199	0.044	0.088	-0.009	-0.019	**0.246**	-0.008	-0.230	**-0.446**	-0.106	0.069
10 species	**PC1**	**0.978**	0.944	**0.980**	0.972	0.818	0.905	0.938	0.970	0.900	0.851	0.940	0.945
Individuals	**PC2**	0.098	-0.098	0.024	-0.072	-0.521	-0.014	0.107	0.068	**-0.230**	**0.232**	0.174	0.172
	PC3	0.042	0.010	0.043	-3.67E-04	-0.156	**0.173**	0.106	0.069	0.030	**-0.453**	-0.056	0.130
8 species	**PC1**	0.953	0.851	**0.954**	0.934	0.671	0.828	0.841	**0.954**	0.758	0.698	0.879	0.899
Individuals	**PC2**	0.141	-0.151	0.019	-0.062	**-0.618**	-0.029	0.148	0.006	-0.390	**0.375**	0.224	0.198
	PC3	0.038	-0.023	0.058	-0.029	-0.268	0.142	**0.251**	0.083	0.037	**-0.575**	-0.091	0.201

significant allometry. The plot, however, also indicates slightly different scaling patterns for the different species. The multivariate allometric coefficients (Table 7.4) identified significant allometric scaling in the following five of the 12 measurements: braincase height (BH), braincase breadth (BB), least inter-orbital width (LIW), width of the foramen magnum (WFM), and width between the inner surfaces of the upper first molars (WIUM1). These measurements were also the only measurements that showed negative allometry (multivariate allometric coefficients of less than 1.0), since the other measurements which did not show significant allometry had positive multivariate allometric coefficients (values of above 1.0). Although condylo-incisor length (CIL) did not have a significant multivariate allometric coefficient, the coefficient was the closest to isometry (a value of equal to 1.0), of the multivariate allometric coefficients of all 12 measurements.

7.3.2 Inter-specific variation between eight vespertilionid species

An analysis was carried out on eight species excluding *E. hottentotus* and *N. rueppellii*, with the rationale that removing the source of variation provided by these two species would provide a clearer indication of the relationship among the remaining species. A scatterplot of the first two principal component axes and a distance phenogram based on the eight species, showed similar patterns of variation to those observed in the analyses which included *E. hottentotus* and *N. rueppellii*. The PCA scatterplot (Fig. 7.4 A) separated *N.* cf. *melckorum*, *N. capensis*, *H. anchietae*, *P. hesperidus* and *N. africanus*. However, the OTU distributions of *H. anchietae* and *P. hesperidus* almost overlapped, as they were separated more on the second than the first principal component axes (i.e. very similar in size but of slightly different cranial configuration), while the OTU distributions of *N. zuluensis* and *P. rusticus* did overlap. The distribution patterns of OTUs and individuals showed an ellipsoid pattern, on the diagonal between the first and second principal component axes, and the area of separation between each species occurred on the diagonal between the first and second principal component axes. The scatter within each of the species of OTUs along the diagonal of the first and second principal component, which also encompassed a large range of principal component scores on both axes, mostly reflected the latitudinal distribution of the OTUs and individuals analysed within each species. This pattern of distribution was also identified within many of the species in the intra-specific analysis (Chapter 6). With the exception of *N.* cf. *melckorum*, the latitudinal distribution occurred from south to north with a combination of decreasing principal component score on first principal component axis and increasing principal component score on the second principal component axis. In *N.* cf. *melckorum*, however, the pattern was visa-versa.

As was also identified in the PCA scatterplot of the analysis with *E. hottentotus* and *N. rueppellii*, there were several OTUs and individuals that appeared as outliers to the general pattern of distribution for their species. These outlying OTUs and individuals included: OTU 1 of *N. capensis* specimens from Ssannakanu Village in Namibia, which plotted between the other *N. capensis* and the *H. anchietae*; OTU 79 of *N. zuluensis* from Gobabeb in Namibia, which plotted at the positive extreme of the second principal component axis albeit above the other *N. zuluensis* OTUs on the first principal component axis; OTU 75 of the holotype specimen of *N. z. vansoni* from northern Botswana which plots closer to *N. africanus* on the first principal component analysis; OTU 76 of a single specimen (KM8092) of *N. zuluensis* from Grootfontein in the Okavango region of Namibia which plotted closer to *N. africanus* on both the first and second principal component axes; and OTU 97 of *P. rusticus* from Namibia which plotted lower on the second principal component axis than the other *P. rusticus* OTUs and closer to *N. africanus* on the first principal component axis.

As in the PCA that included *E. hottentotus*, the major separation between the species on the first principal component axis was in relation to overall size, separating at either extremes of the first principal component axis the largest (*N.* cf. *melckorum*) and smallest (*N. africanus*) of the species in this analysis. The important measurements on the first principal component axis, which explained 82.03% of the variation, were the same three as in the analysis with *E. hottentotus* and *N. rueppellii*: condylo-incisor skull length, zygomatic breadth, and braincase breadth (Table 7.3). The second principal component axis, although only explaining 5.99% of the variation, appeared to influence both the separation between the species and the geographic distribution within the species. The important measurements on the second principal component axis were width of the upper fourth premolar and post-orbital width (Table 7.3). Post-orbital width was also an important measurement in the analysis with *E. hottentotus* and *N. rueppellii*. In that analysis, however, width of the upper fourth premolar had the second highest positive eigenvalue scores, whereas in the analysis without *E. hottentotus* and *N. rueppellii*, the rankings of these measurements were

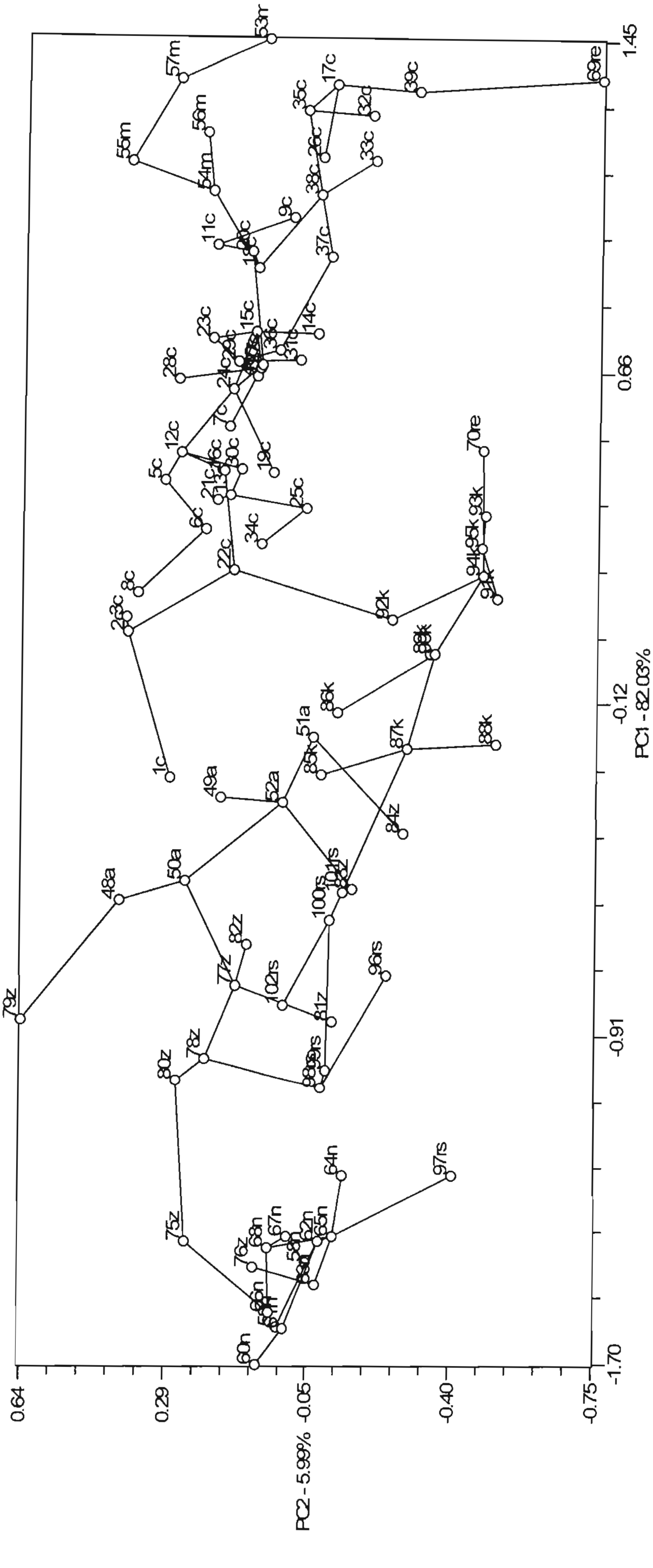


Figure 7.4 A) Scatterplot of the first two principal components (with a minimum spanning tree) of a PCA of eight different vespertilionid species, based on 12 cranial measurements. OTU and individual numbers and subspecies codes correspond to those in Table 7.1.

Table 7.4 Multivariate allometric coefficients (MAC) for 12 cranial measurements in analyses of A) 10 and B) eight vespertilionid taxa. SE = standard error; *P* = probability; * = significant allometry at *P* < 0.001.

	A)			B)		
	MAC	SE	P	MAC	SE	P
CIL	1.040	0.003	1.000	1.036	0.005	1.000
BH	0.726	0.004	0.000*	0.486	0.008	0.000*
ZB	1.016	0.004	1.000	0.960	0.009	0.000*
BB	0.764	0.005	0.000*	0.717	0.010	0.000*
POW	0.443	0.005	0.000*	0.386	0.010	0.000*
WFM	0.678	0.005	0.000*	0.713	0.010	0.000*
WAS	1.450	0.005	1.000	1.392	0.011	1.000
WOUC	1.081	0.006	1.000	1.169	0.011	1.000
WIUM1	0.728	0.006	0.000*	0.611	0.012	0.000*
WUPM4	1.213	0.011	1.000	1.297	0.020	1.000
LUM1	1.174	0.011	1.000	1.223	0.020	1.000
MAOT	1.216	0.011	1.000	1.330	0.020	1.000

inverted.

Similarly, the large size component of the first principal component axis was removed and the second and third axes plotted (Fig. 7.4 B). However, as was observed in the plot including *E. hottentotus*, size was the major distinguishing factor, and hence removing size and the most distinct species on the second axis, *N. rueppellii,* there was no separation between the remaining eight taxa. Nevertheless, there were subtle and small differences in cranial shape between the taxa, since *P. hesperidus* almost separated from the other taxa along the second principal component axis. *Pipistrellus rusticus* separated from all but *P. hesperidus* along a diagonal to the second principal component axis and *N. zuluensis*, also showed some separation on the third principal component axis from the main cluster of overlapping taxa. A scatterplot of the first three principal components together (Fig. 7.5) further visually confirms the small, subtle variations in cranial morphology between the species introduced in the third principal component axes, due to the smaller height on the third principal component axis of both *Pipistrellus* species (*P. hesperidus* and *P. rusticus*) relative to the other taxa. As in the analysis with 10 species, the important measurements on the third principal component axis, which contributed 3.22% of the variation, were greatest width of the articular surface and width of the upper fourth premolar. Figure 7.6 shows, as in the analysis with 10 species, the presence of an allometric scaling effect, since the slope of the regression line also showed significant negative allometry (standardised Beta coefficient = 0.964; P = 0.00E17). Neither regression analyses of the second (standardised Beta coefficient = -0.183; P = 0.084) or the third principal components (standardised Beta coefficient = -0.089; P = 0.403) with log condylo-incisor length showed significant allometry. The multivariate allometric coefficients (Table 7.4) identified negative, allometric scaling in six of the 12 measurements. The allometrically significant measurements were the same as in the analysis with 10 species, albeit with one more measurement, given the significance of zygomatic breadth (ZB).

The distance phenogram (Fig. 7.7 A) showed the relationships between OTUs and individuals slightly differently to the pattern in the PCA. The major distinction in the distance phenogram separated the smaller *N. africanus*, *N. zuluensis*, *H. anchietae* and *P. rusticus* from the larger *N. capensis*, *N.* cf. *melckorum* and *P. hesperidus*. Within the cluster of smaller taxa, the OTUs of *N. africanus* formed a cluster, which also included the two individuals and the OTU that were most similar to *N. africanus* on the first principal component axis in the PCA scatterplot. Most *P. rusticus* OTUs, with the exception of OTU 97 which clustered with *N. africanus*, formed a distinct cluster. There was also a cluster mixing OTUs of *H. anchietae* and *N. zuluensis* together. The holotype specimen of *N. zuluensis* from Umfolosi Game Reserve in KwaZulu-Natal, was an outlier to this cluster of smaller taxa. OTU 48, of a single individual (NMBZ31965) of *H. anchietae* from Zimbabwe, and OTU 79, of *N. zuluensis* from Gobabeb in Namibia (which was also an outlier in the PCA on the most positive side of the first principal component analysis), were outliers to the cluster which included *P. rusticus* and *N. zuluensis* and *H. anchietae*.

In the cluster of larger taxa, the OTUs were split into two major groups the first of which contained *N.* cf. *melckorum* OTUs with the majority of *N. capensis* OTUs. The other cluster contained *P. hesperidus* OTUs, together with a number of outlying OTUs of *N. capensis*, *P. hesperidus* and *N. rendalli*. In the cluster with *N.* cf. *melckorum*, all the *N.* cf. *melckorum* OTUs clustered together with OTUs of *N. capensis* from the Western and Eastern Cape and an OTU of *N. capensis* from Gauteng, the remaining OTUs of *N. capensis* clustered together as a neighbouring cluster to the one containing *N.* cf. *melckorum*. The outlier OTUs and individuals clustered alongside the cluster of *P. hesperidus* OTUs included: OTU 1-3 of *N. capensis* from Namibia, Botswana and Zimbabwe; OTU 85, of a single individual of *P. hesperidus* (TM34839) from Zimbabwe; OTU 25 of *N. capensis* from Durban in KwaZulu-Natal; OTU 34 of *N. capensis* from King William's Town in the Eastern Cape; and OTU 70 of *N. rendalli* from Zimbabwe. Hence, the distance phenogram sometimes placed as outliers specimens, which were from the geographic extremes of a species and were plotting at the extremes of the range for the species in the PCA scatterplot.

An alternative dissimilarity coefficient to average taxonomic distance, but also commonly used in numerical taxonomy, the average Manhattan distance coefficient (Rohlf, 1997), was used in another cluster analysis. The UPGMA phenogram based on the average Manhattan distance matrix (Fig. 7.7 B) clustered the OTUs and individuals of the eight species with fewer outlying OTUs and individuals. This cluster analysis also clustered more OTUs of *N. capensis* from the southern and south-western Cape with OTUs of *N.* cf. *melckorum*.

A DFA was run excluding *E. hottentotus* and *N. rueppellii* since it has been shown that

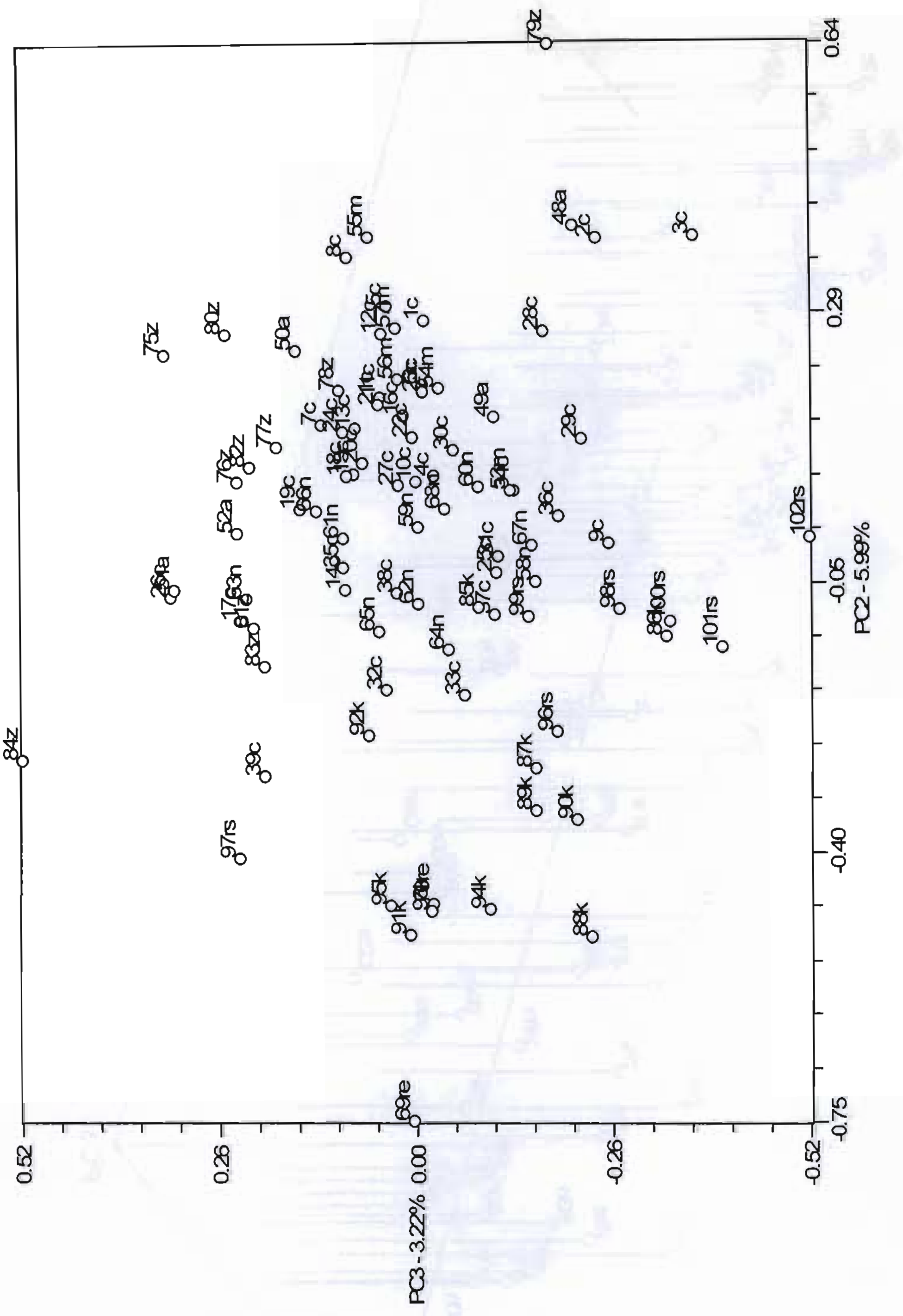


Figure 7.4 B) Scatterplot of the second and third principal components of a PCA of eight different vespertilionid species, based on 12 cranial measurements. OTU and individual numbers and subspecies codes correspond to those in Table 7.1.

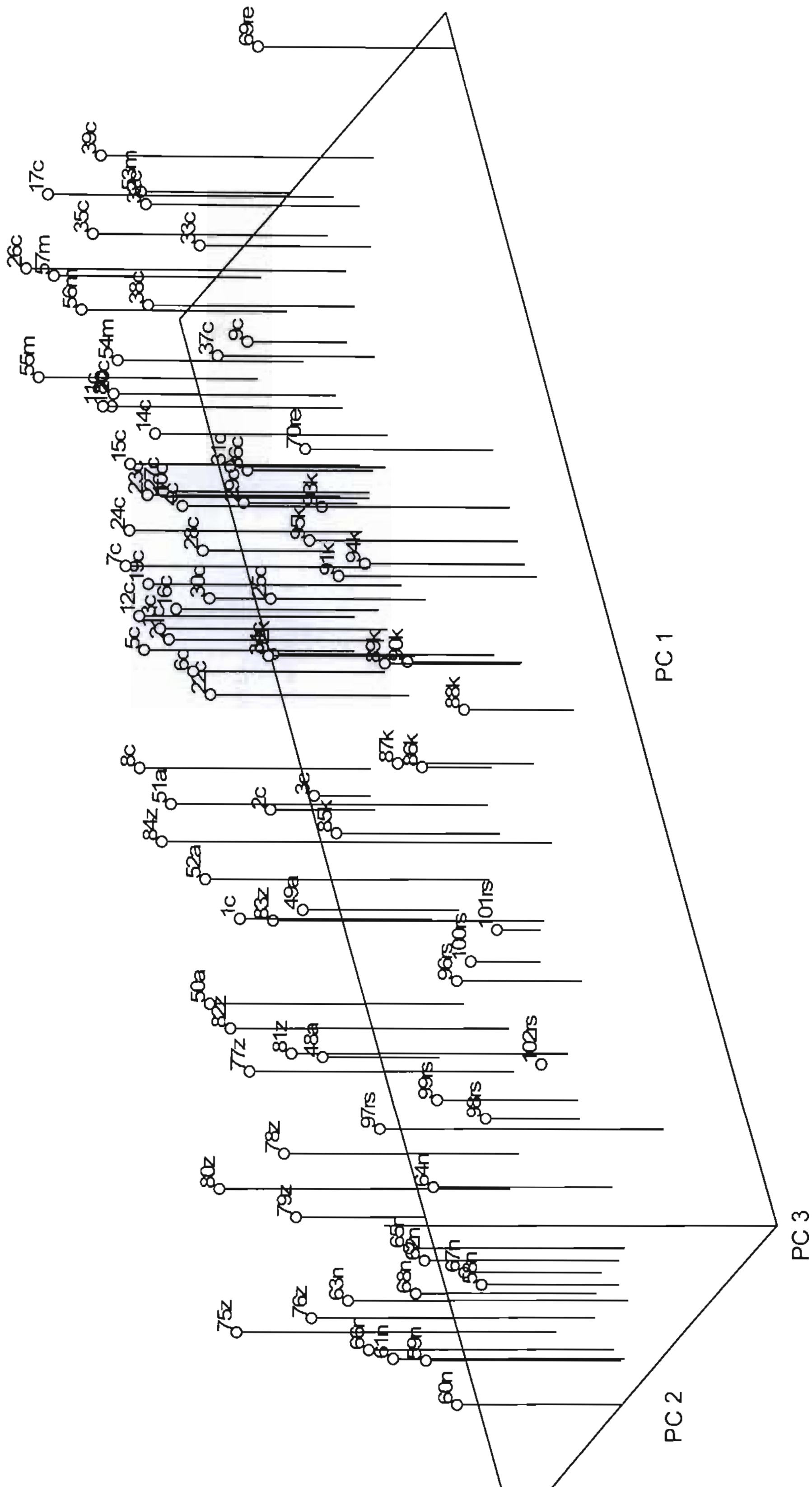


Figure 7.5 Scatterplot of the first three principal components of a PCA of eight different vespertilionid species, based on 12 cranial measurements. OTU and individual numbers and subspecies codes correspond to those in Table 7.1.

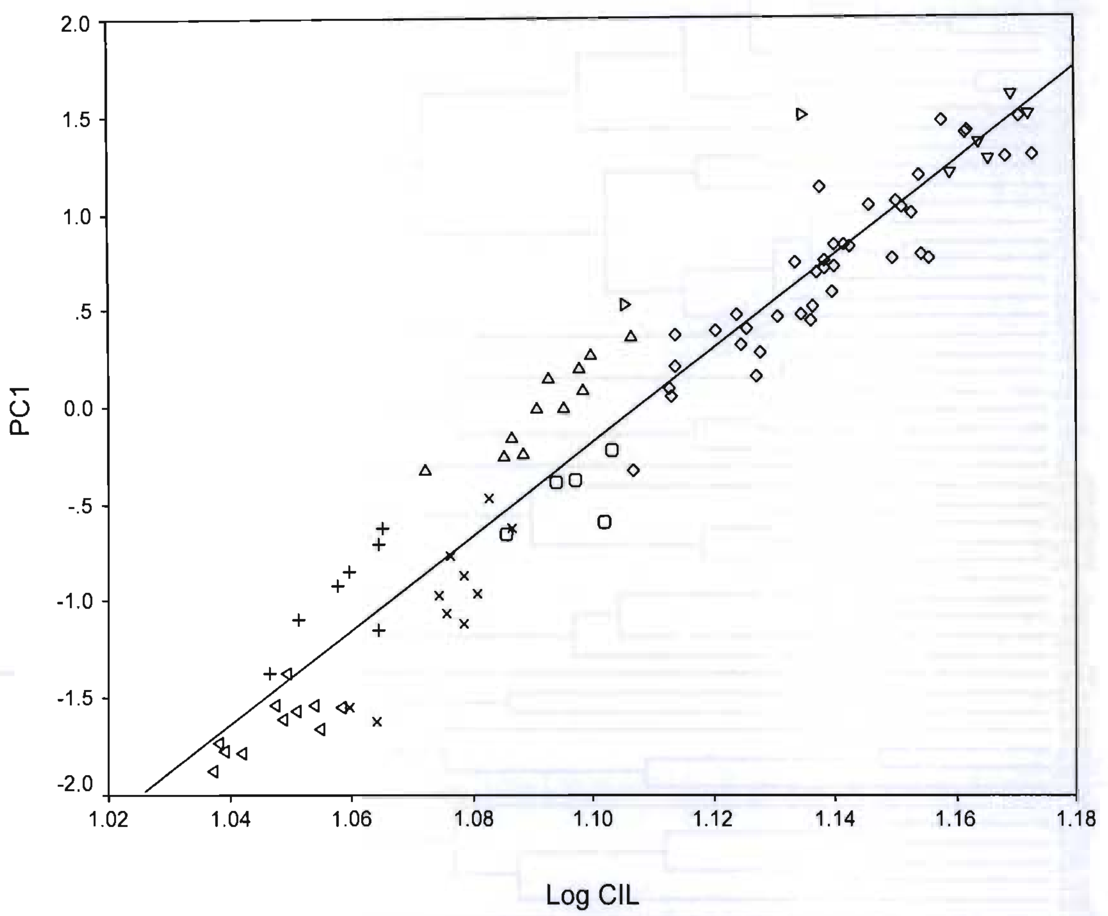


Figure 7.6 Scatterplot of log condylo-incisor length against first principal component scores of a PCA of eight species based on 12 cranial measurements. r^2 = 0.930. Species symbols: *Neoromicia capensis* = ○, *Hypsugo anchietae* = ◇, *Neoromicia* cf. *melckorum* =△, *Neoromicia africanus* = ▽, *Neoromicia rendalli* = ◁, *Neoromicia zuluensis* = ▷, *Pipistrellus hesperidus* = +, *Pipisrtellus rusticus* = ×.

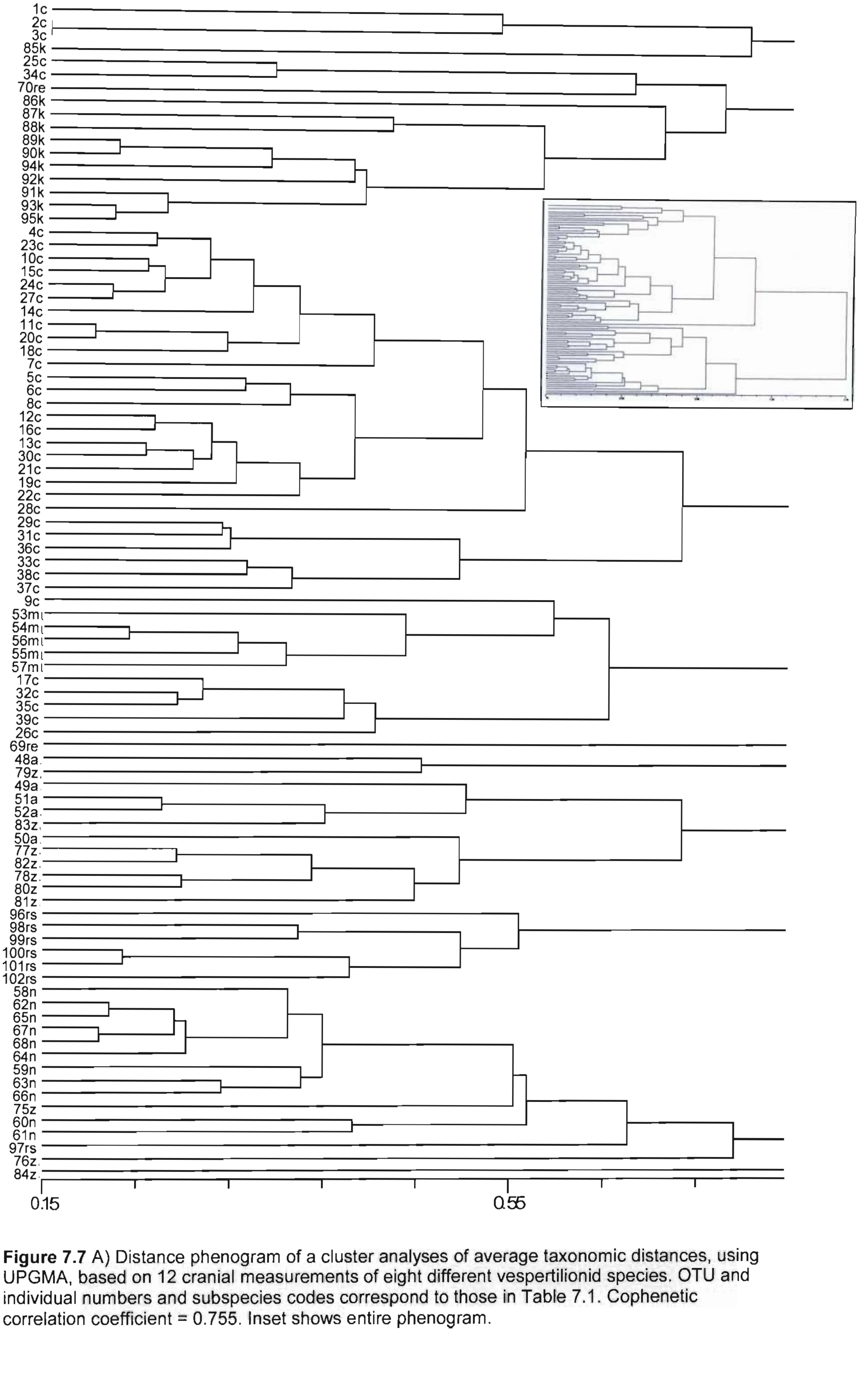


Figure 7.7 A) Distance phenogram of a cluster analyses of average taxonomic distances, using UPGMA, based on 12 cranial measurements of eight different vespertilionid species. OTU and individual numbers and subspecies codes correspond to those in Table 7.1. Cophenetic correlation coefficient = 0.755. Inset shows entire phenogram.

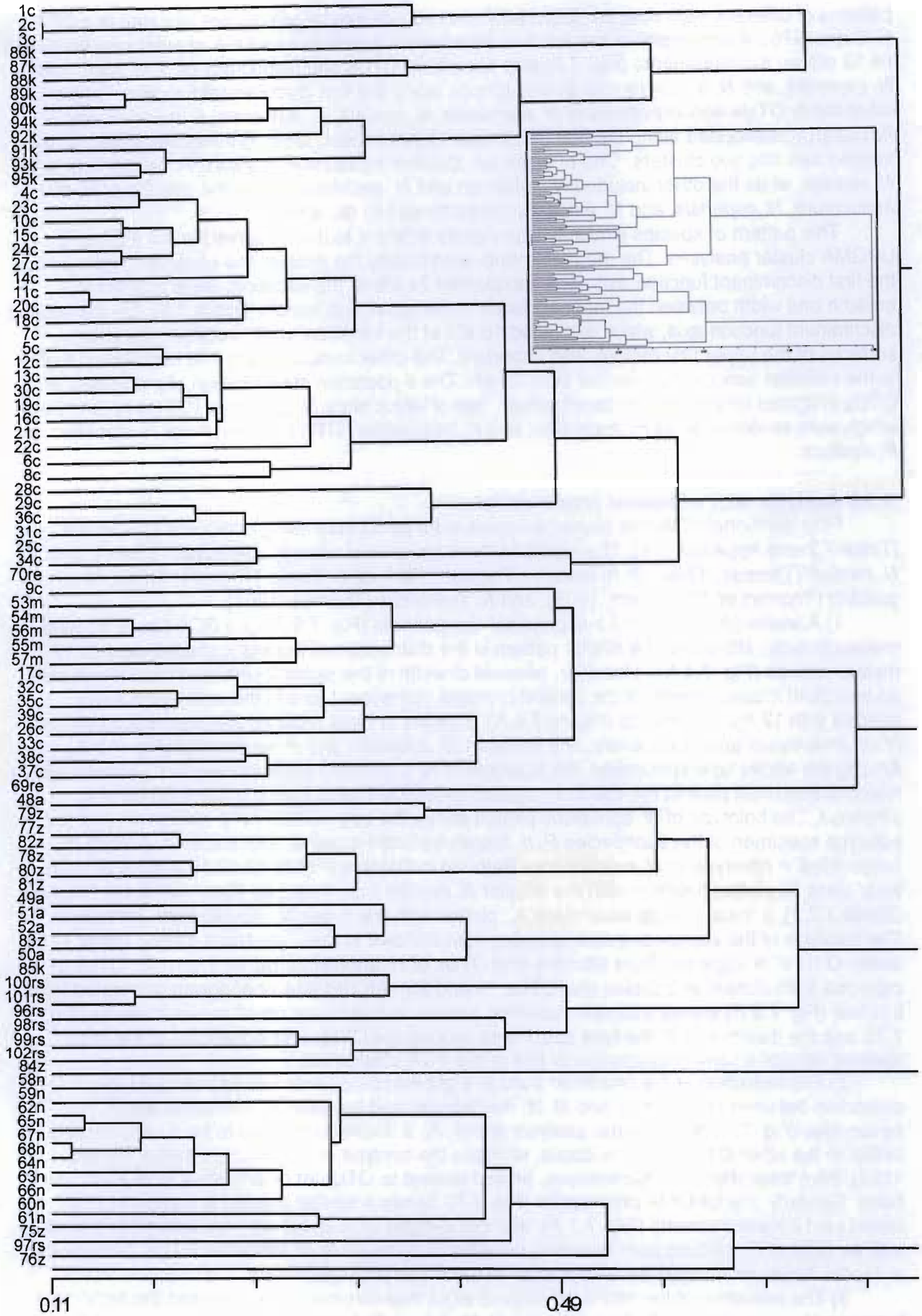


Figure 7.7 B) Distance phenogram of a cluster analyses of average Manhattan distance, using UPGMA, based on 12 cranial measurements of eight different vespertilionid species. OTU and individual numbers and subspecies codes correspond to those in Table 7.1. Cophenetic correlation coefficient = 0.743. Inset shows entire phenogram.

patterns of differentiation may be obscured if markedly dissimilar groups are included in a DFA (Thorpe,1976). A scatterplot of the first two discriminant functions of a DFA of eight species based on 12 cranial measurements (Fig. 7.8) also separated OTUs and individuals of *N.* cf. *melckorum*, *N. capensis*, and *N. africanus* into distinct groups along the first discriminant function. On the other hand, OTUs and individuals of *H. anchietae*, *N. rendalli*, *N. zuluensis*, *P. rusticus*, and *P. hesperidus* overlapped along the first discriminant function axis, although they separated on the second axis into two clusters. One of these two clusters included *P. rusticus*, *P. hesperidus*, and *N. rendalli,* while the other included *N. zuluensis* and *H. anchietae*, albeit the overlap of *N.* cf. *melckorum*, *N. capensis*, and *N. africanus* linked these two clusters.

This pattern of species similarity was slightly different to that observed in the PCA and UPGMA cluster analyses. The measurements contributing the most to the observed variation on the first discriminant function axis, which explained 74.0% of the variation, were zygomatic breadth and width between the inner surfaces of the upper first molars (Table 7.5). On the second discriminant function axis, which explained 16.8% of the variation, width between the inner surfaces of the upper first molars, was important. The other measurement that contributed highly to the variation was condylo-incisor skull length. The *a posteriori* classification of individuals and OTUs indicated only three misidentifications: two of which were *N. zuluensis* (OTUs 83 and 79) which were re-identified as *H. anchietae*, and *P. hesperidus* (OTU 88) which was re-identified as *P. rusticus.*

7.3.3 Analysis with additional type material

Four additional PCA and cluster analyses were performed using additional specimens (Table 7.2 and Appendix 7.1). The additional type specimens were *H. anchietae* (Seabra, 1900), *N. rendalli* (Thomas, 1889), *P. h. fuscatus* Thomas, 1901, *N. a. fouriei* (Thomas, 1926), *N. c. gracilior* (Thomas and Schwann, 1905), and *N. somalicus* (Thomas, 1901).

1) A scatterplot of the first two principal components (Fig. 7.9 A) of a PCA based on nine measurements, still showed a similar pattern in the distribution of the eight species as with 12 measurements (Fig. 7.4 A). However, removal of width of the upper fourth premolar, which was an important measurement on the second principal component axis in the analysis of eight species with 12 measurements (Figure 7.4 A), appears to have reduced the separation between *N.* cf. *melckorum* and *N. capensis*, and between *N. zuluensis* and *P. hesperidus* (Fig. 7.9 A). Among the added type specimens, the holotype of *N. a. fouriei* from north-western Ovamboland in Namibia was most distinct (on the first principal component axis) from the other OTUs of *N. africanus*. The holotype of *N. somalicus* plotted above the other OTUs of *N. zuluensis*, and the holotype specimen of the subspecies *P. h. fuscatus* plotted together with southern African *P. hesperidus*. A paratype of *N. rendalli* from Bathurst in Gambia (PM89.12.12.1), a male of tooth wear class C, plotted together with the smaller *N. rendalli* from KwaZulu-Natal, while the holotype (BM89.3.2.3), a male of tooth wear class A, plotted with the larger *N. rendalli* from Zimbabwe. The holotype of the subspecies *N. c. gracilior* from Eshowe in KwaZulu-Natal plotted closer to the outlier OTU of *N. capensis* from Namibia and OTUs of *H. anchietae,* rather than near OTUs of *N. capensis* from closest to Eshowe (i.e. OTUs 16 and 25). An UPGMA phenogram generated from this test (Fig. 7.9 B) shows a similar clustering pattern to that based on 12 measurements (Fig. 7.7), and the distribution of the type specimens among the OTUs and individuals of the eight species reflects a similar distribution to that in the PCA scatterplot.

2) The reduction of the character suite to eight measurements further obscured the distinction between *N. capensis* and *N.* cf. *melckorum*, and between *H. anchietae* and *P. hesperidus* (Fig. 7.10 A). As in the analysis above, *N. a. fouriei* continued to be a considerable outlier to the other OTUs of *N. africanus*, whereas the syntype of *N. africanus nanus* (Peters, 1852), from Inhambane in Mozambique, plotted closest to OTUs of *N. africanus* from KwaZulu-Natal. Similarly, the UPGMA phenogram (Fig. 7.10 B) has a similar clustering pattern to that based on 12 measurements (Fig. 7.7 A), and the syntype of *N. a. nanus* from Inhambane clusters with an OTU of *P. rusticus* from Namibia, neighbouring the other *N. africanus* OTUs. *Neoromicia a. fouriei*, however, clusters as an outlier to all the OTUs and specimens.

3) The reduction of the character suite to eight measurements, suppressed the distinction between *N. capensis* and *N.* cf. *melckorum* and between *P. hesperidus, N. zuluensis* and *P. rusticus*, but improved the separation between *H. anchietae* and *P. hesperidus* (Fig. 7.11 A). Although not type specimens, the two specimens from Kano Vlei in Namibia were added in an attempt to resolve the distinction of OTU 97, also from Kano Vlei, from other OTUs of *P. rusticus*. Both a PCA scatterplot of the first two principal component axes of a PCA (Fig. 7.11 A), as well as

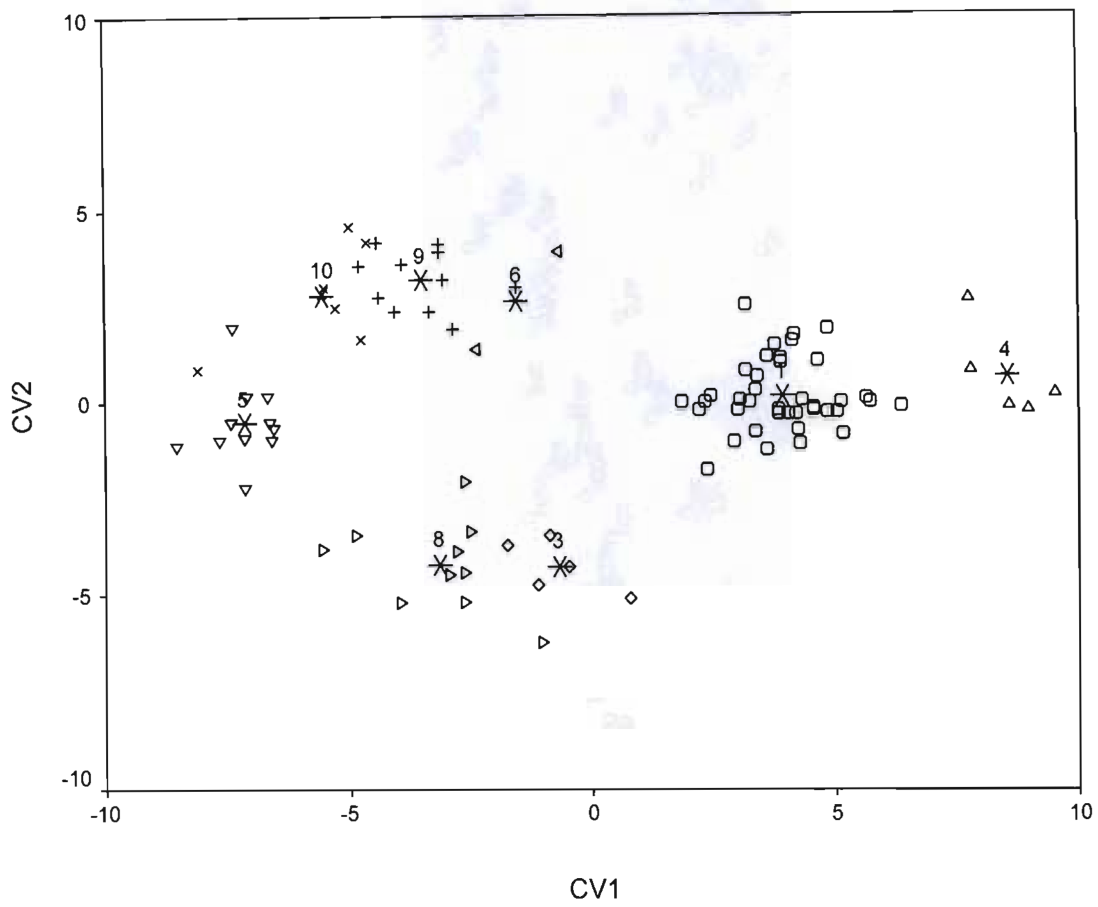


Figure 7.8 Plot of the first two discriminant function axes of a discriminant function analysis of eight vespertilionid species based on 12 cranial measurements. Species symbols: 1= *Neoromicia capensis* = ○, 3 = *Hypsugo anchietae* = ◇, 4 = *Neoromicia* cf. *melckorum* = △, 5 = *Neoromicia africanus* = ▽, 6 = *Neoromicia rendalli* = ◁, 8 = *Neoromicia zuluensis* = ▷, 9 = *Pipistrellus. hesperidus* = +, 10 = *Pipistrellus rusticus* = ×.

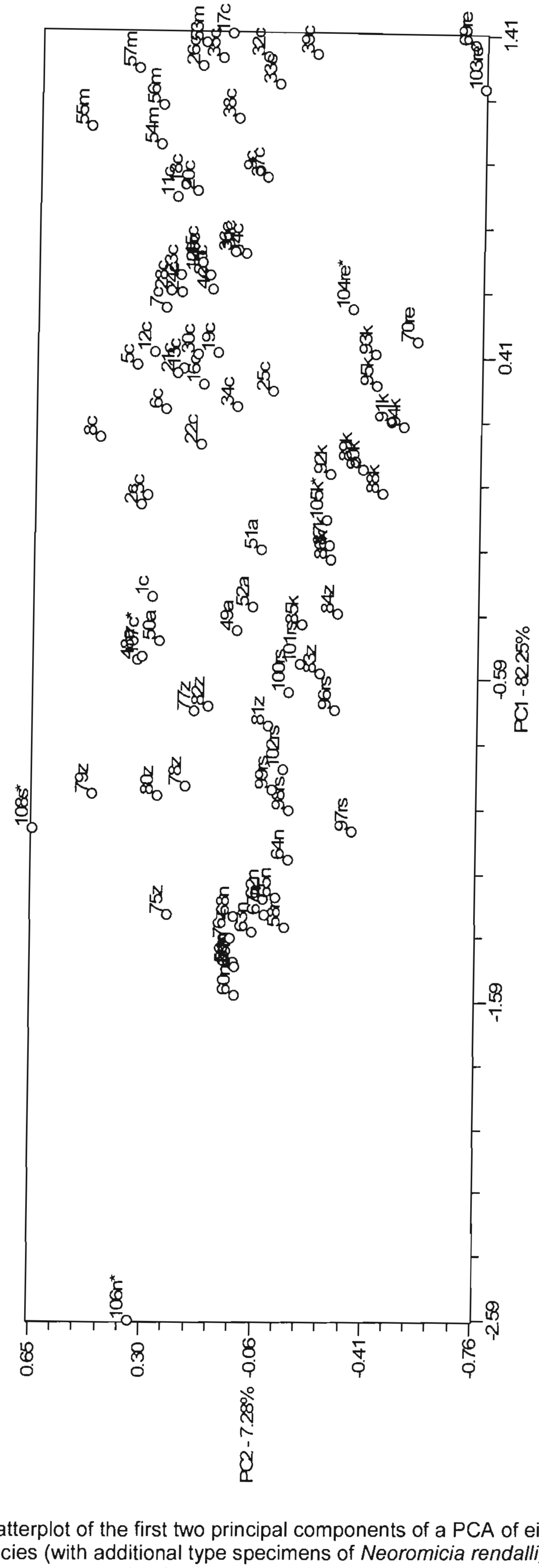


Figure 7.9 A) Scatterplot of the first two principal components of a PCA of eight different vespertilionid species (with additional type specimens of *Neoromicia rendalli, Pipistrellus. hesperidus fuscatus, Neoromicia africanus fouriei, Neoromicia capensis gracilior,* and *Neoromicia somalicus*) based on nine cranial measurements. OTU and individual numbers and subspecies codes correspond to those in Tables 7.1 and 7.2. * = additional type specimens.

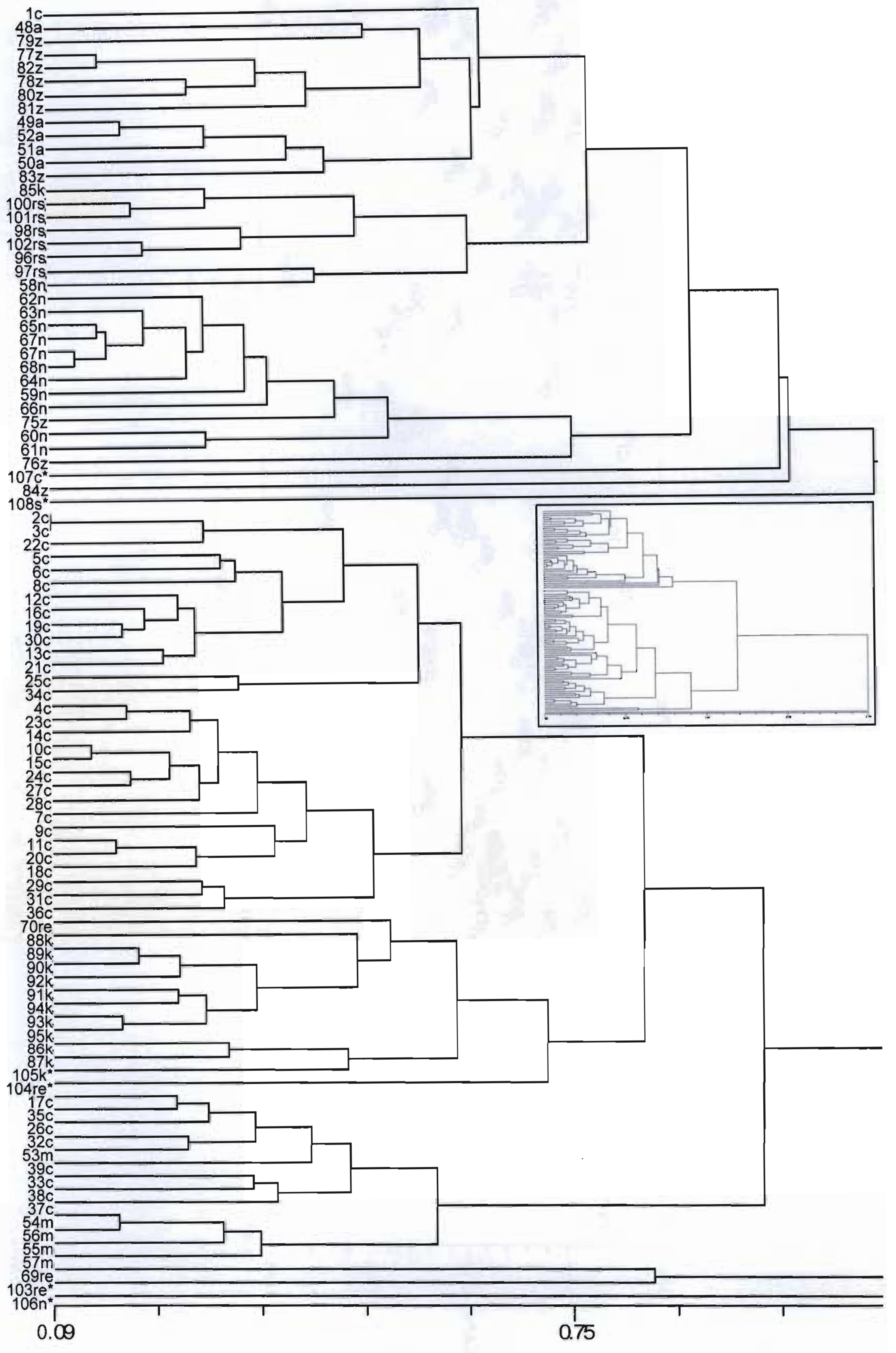


Figure 7.9 B) Distance phenogram of a cluster analyses of average taxonomic distance, using UPGMA, based on nine cranial measurements of eight different vespertilionid species (with additional type specimens of *Neoromicia rendalli, Pipistrellus hesperidus fuscatus, Neoromicia africanus fouriei, Neoromicia capensis gracilior,* and *Neoromicia somalicus*). OTU and individual numbers and subspecies codes correspond to those in Tables 7.1 and 7.2. * = additional type specimens. Cophenetic correlation coefficient = 0.767. Inset shows entire phenogram.

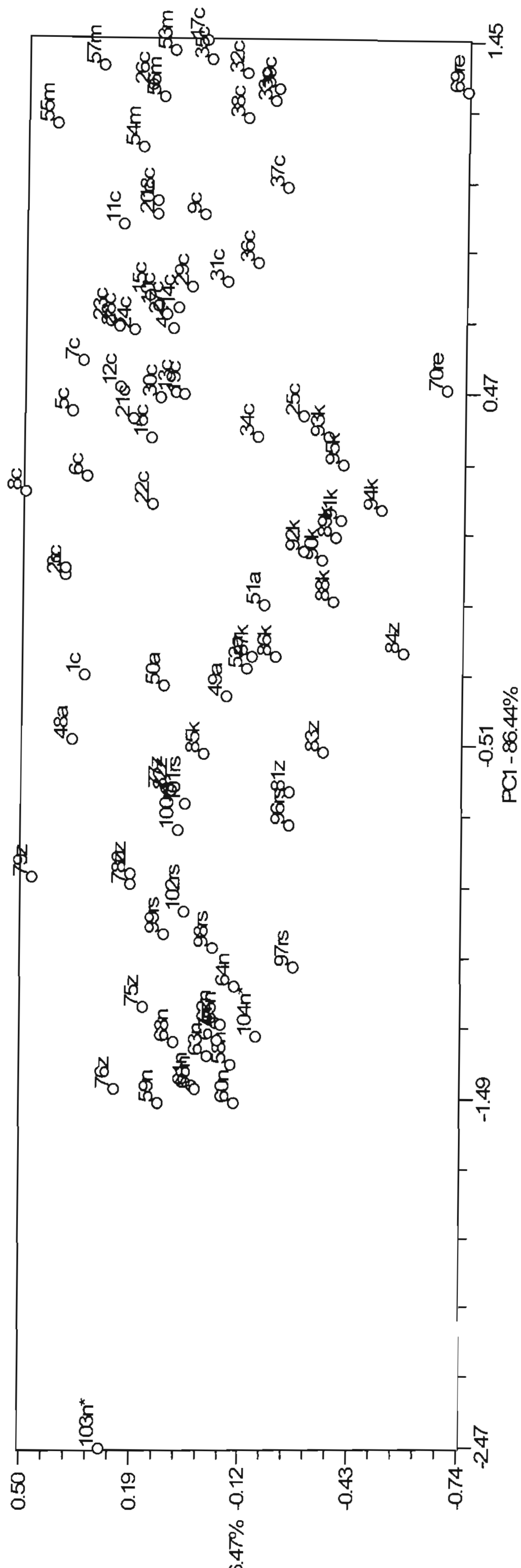


Figure 7.10 A) Scatterplot of the first two principal components of a PCA of eight different vespertilionid species (with additional type specimens of *Neoromicia africanus*) based on eight cranial measurements. OTU and individual numbers and subspecies codes correspond to those in Tables 7.1 and 7.2. * = additional specimens.

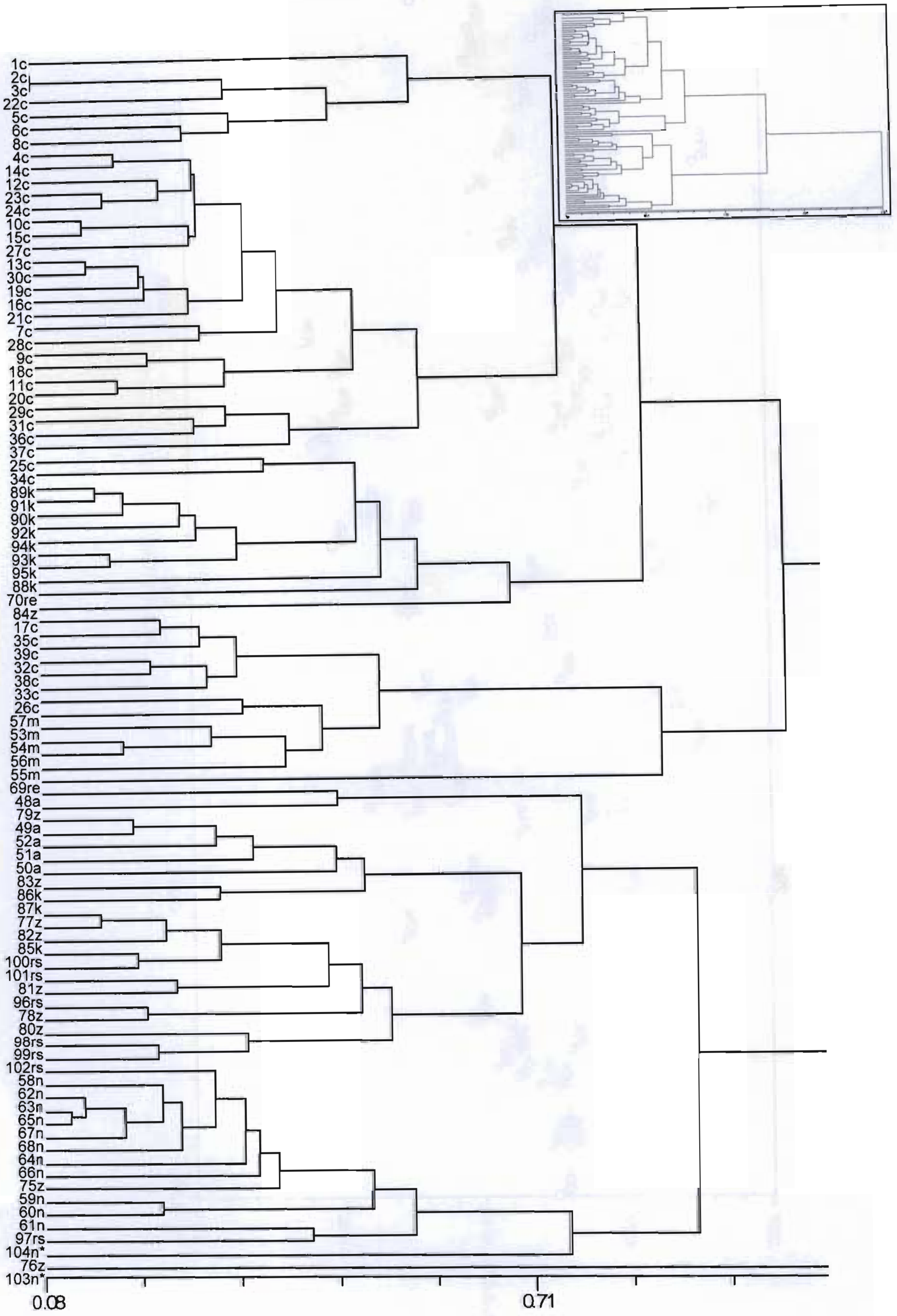


Figure 7.10 B) Distance phenogram of a cluster analyses of average taxonomic distance, using UPGMA, based on eight cranial measurements of eight different vespertilionid species (with additional type specimens of *Neoromicia africanus*). OTU and individual numbers and subspecies codes correspond to those in Tables 7.1 and 7.2. * = additional specimens. Cophenetic correlation coefficient = 0.750. Inset shows entire phenogram.

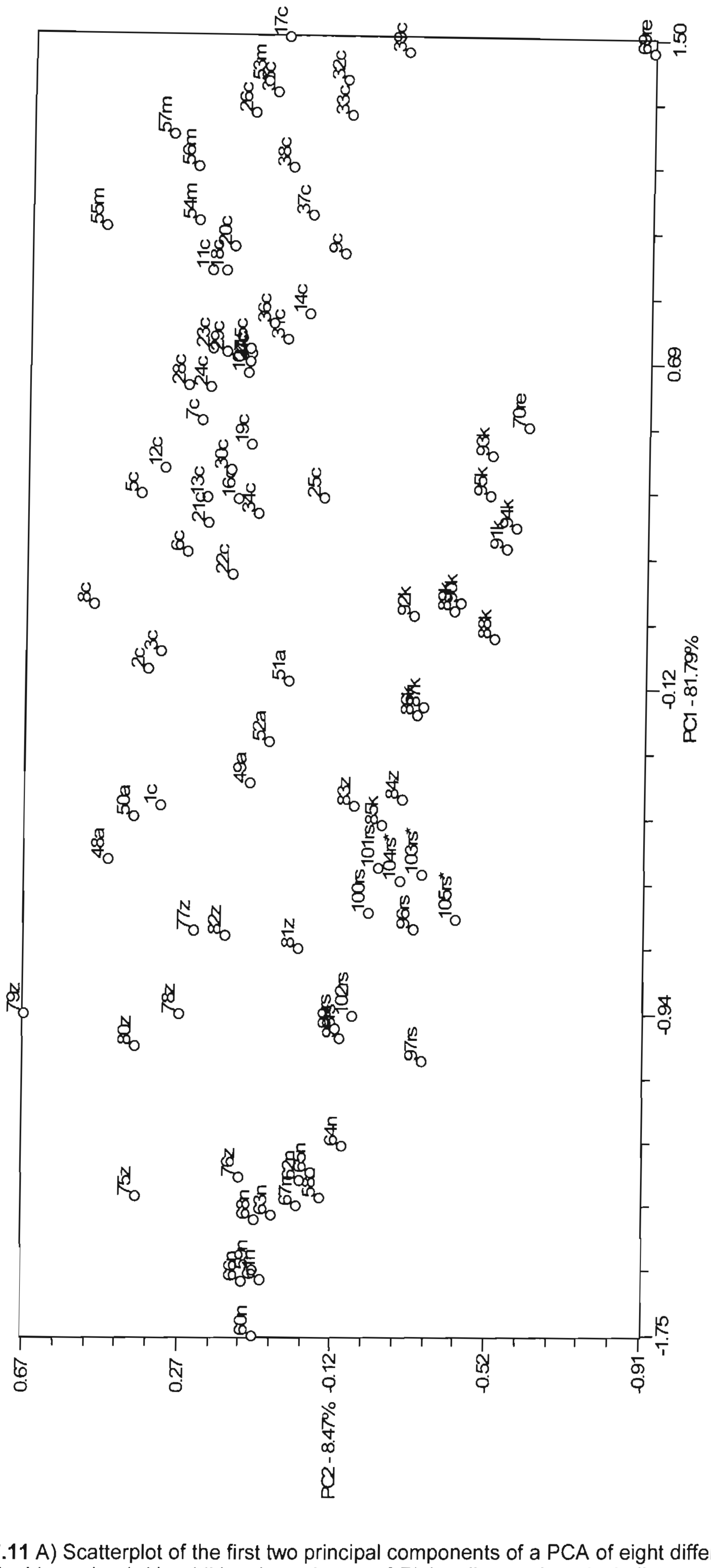


Figure 7.11 A) Scatterplot of the first two principal components of a PCA of eight different vespertilionid species (with additional specimens of *Pipistrellus rusticus,* including a type) based on eight cranial measurements. OTU and individual numbers and subspecies codes correspond to those in Tables 7.1 and 7.2. * = additional specimens.

Table 7.5 Variable loadings of various discriminant function analyses of vespertilionids. Numbers in bold type are the most important measurements on that axis.

		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
8 species	**DF1**	0.678	-0.619	**0.689**	0.474	-0.581	-0.274	0.202	0.377	**-0.684**	0.374	-0.091	0.336
OTUs	**DF2**	**-0.885**	-0.638	-0.080	0.564	-0.145	0.532	-0.447	0.955	**1.061**	0.420	-0.399	-0.360
10 species	**DF1**	**0.505**	-0.075	0.348	0.150	-0.120	-0.074	0.193	0.126	**-0.365**	0.229	0.136	0.210
Individuals	**DF2**	-0.566	0.750	0.050	0.001	0.296	-0.031	0.240	**-0.729**	**0.861**	-0.053	0.154	-0.159
8 species	**DF1**	**0.557**	-0.329	0.266	0.168	-0.113	-0.086	0.139	0.481	**-0.557**	0.316	0.022	0.265
Individuals	**DF2**	**-0.723**	-0.123	0.244	-0.157	0.392	0.342	-0.037	0.251	**0.760**	0.196	-0.064	-0.055

a UPGMA phenogram based on a distance matrix (Fig. 7.11 B) of eight measurements, placed the lectotype of *P. rusticus* (Tomes, 1861) from Olifants Vlei in Namibia, and the additional specimens from Kano Vlei in Namibia, together with other OTUs of *P. rusticus* from Namibia and Botswana (OTUs 96 and 97).

4) The reduction of the character suite to seven measurements, also obscured the distinction between *N. capensis* and *N.* cf. *melckorum* and between *P. hesperidus* and *N. zuluensis* (Fig. 7.12 A). Although not type specimens, three *H. anchietae* specimens from Zambia were added to provide further information for this relatively poorly represented species. In a scatterplot of the first two principal component axes (Fig. 7.12 A) a syntype of *H. anchietae* (BM6.1.3.1) (Seabra, 1900) from Cahata in Angola, plotted away from the other OTUs of *H. anchietae*. The angle of the distribution of some of the other species may suggest that the position of the additional specimens from Zambia in the PCA plot reflects the northerly extreme of a species characterised by latitudinal geographic variation. However, the UPGMA phenogram (Fig. 7.12 B) clustered the additional specimens of *H. anchietae* in a different cluster to the southern African OTUs of *H. anchietae*.

The important measurements on the first and second principal component axes in all these additional analyses were the same, other than the third analysis with the additional *P. rusticus* (Table 7.6). On the first principal component axes, all eigenvalues were positive and the measurements that loaded highest were, zygomatic breadth and braincase breadth. On the second principal component axis the eigenvalues were of mixed signs and the measurements that loaded highest were, length between the condylar and the coronoid processes of the mandible and post orbital width. In the third analysis, condylo-incisor skull length, rather than length between the condylar and the coronoid processes of the mandible, loaded highest. Most of these measurements were also important in the analyses of 10 and eight species with all 12 measurements, although width of the upper fourth premolar, important on the second principal component of the 12 measurements tests, was not included in this analysis.

7.3.4 Individual level analyses

The above analyses were based on OTU means with a few added individual specimens included to extend the geographic coverage of a species within southern Africa. The use of OTUs, however, masks the fact that within almost all the species the extremes of cranial variation presented by individuals were such that the species distinctions identified using OTUs fell away (Fig. 7.13 and Fig. 7.14). In analyses of 661 specimens of all 10 species, only individuals of *E. hottentotus* and *N. rueppellii* were sufficiently different for the species to be delineated in the PCA and DFA scatterplots, whereas individuals of the other eight species were sufficiently similar that PCA (Fig. 7.13) and DFA (Fig. 7.14) scatterplots did not delineate these species. Even when analysed without the distinct species of *E. hottentotus* and *N. rueppellii*, the 611 specimens of eight species showed no clear separations between the species in PCA (Fig. 7.13) and DFA (Fig. 7.14) scatterplots. The important measurements contributing to the first two axes of the PCA (Table 7.3) and DFA (Table 7.5) were the same or similar to those in the analyses with OTUs.

The *a posteriori* classification in the DFA of 10 species mis-classified 8.62% of the specimens, whereas in the DFA of eight species, 9.00% of the specimens were mis-classified. In the analyses of 10 species, four species showed 100% classification: *E. hottentotus*, *N.* cf. *melckorum*, *N. rendalli*, and *N. rueppellii*. Species having the greatest percentage of mis-classified specimens were *N. zuluensis* (18.60%), followed by *P. rusticus* (12.00%) and *N. capensis* (11.01%). *Neoromicia zuluensis* were most commonly mis-classified as *H. anchietae*, *P. rusticus* were mis-classified as either *N. zuluensis* or *N. africanus*, while *N. capensis* were most commonly mis-classified as *N.* cf. *melckorum*. In the analyses of eight species, none of the taxa were 100% classified. *Neoromicia rendalli*, by virtue of its small sample size, had the greatest percentage of mis-classified specimens (20.00%), whereas the order of the other most mis-classified species was the same as in the analysis of 10 species and the mis-classifications were similar, although the percentage of mis-classified specimens were slightly higher for *N. zuluensis* (16.28%) and *P. rusticus* (14.00%), but not for *N. capensis* (10.43%).

7.3.5 Pair-wise discrimination of species

Although half the taxa incorporated in this analysis could not be separated clearly in analyses with individual specimens, it was decided to make use of the separation provided by the analyses of OTUs. Thus, pair-wise discrimination function analyses were used to further maximize the separation between pairs of species that still showed some degree of overlap in

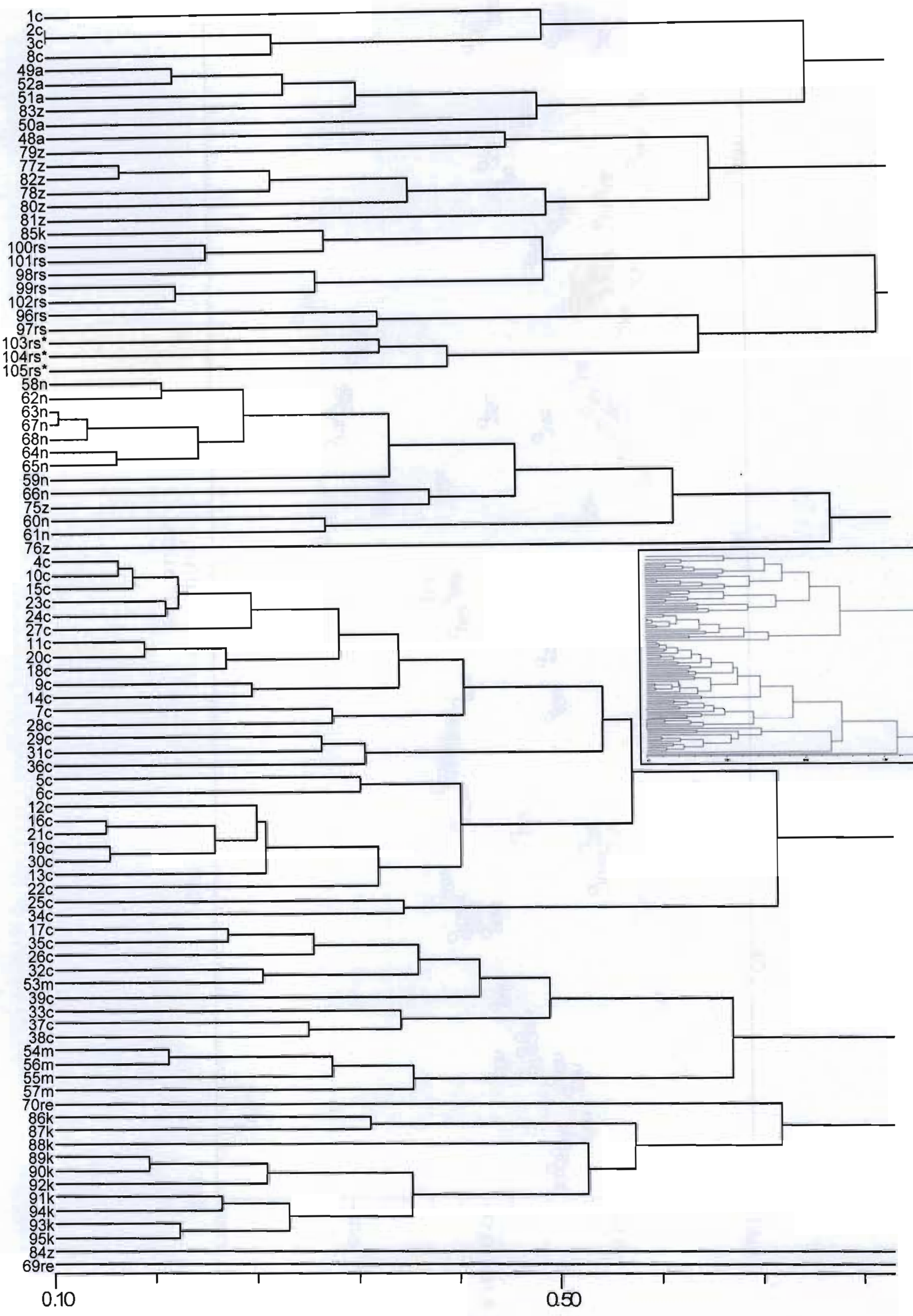


Figure 7.11 B) Distance phenogram of a cluster analyses of average taxonomic distance, using UPGMA, based on eight cranial measurements of eight different vespertilionid species (with additional specimens of *Pipistrellus rusticus*, including a type). OTU and individual numbers and subspecies codes correspond to those in Tables 7.1 and 7.2. * = additional specimens. Cophenetic correlation coefficient = 0.715. Inset shows entire phenogram.

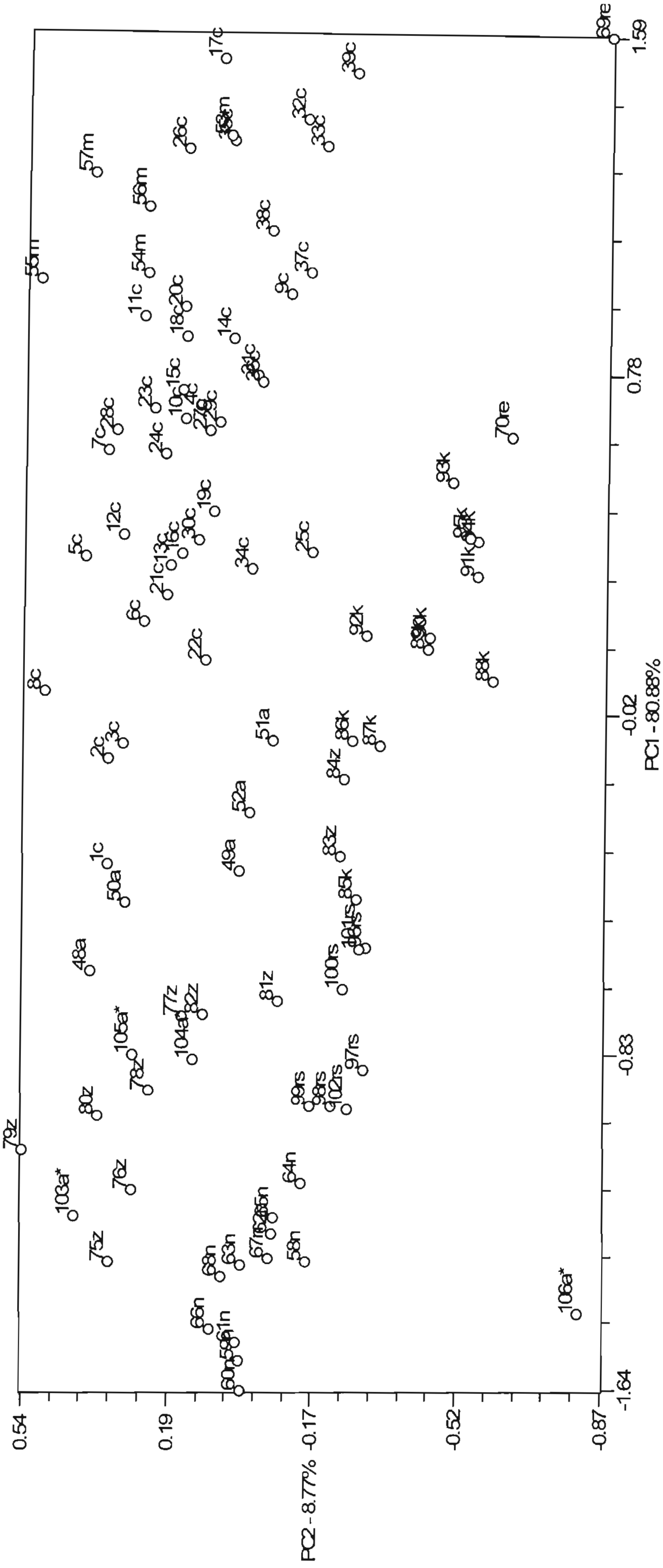


Figure 7.12 A) Scatterplot of the first two principal components of a PCA of eight different vespertilionid species (with additional specimens of *Hypsugo anchietae,* including a type) based on seven cranial measurements. OTU and individual numbers and subspecies codes correspond to those in Tables 7.1 and 7.2. * = additional specimens.

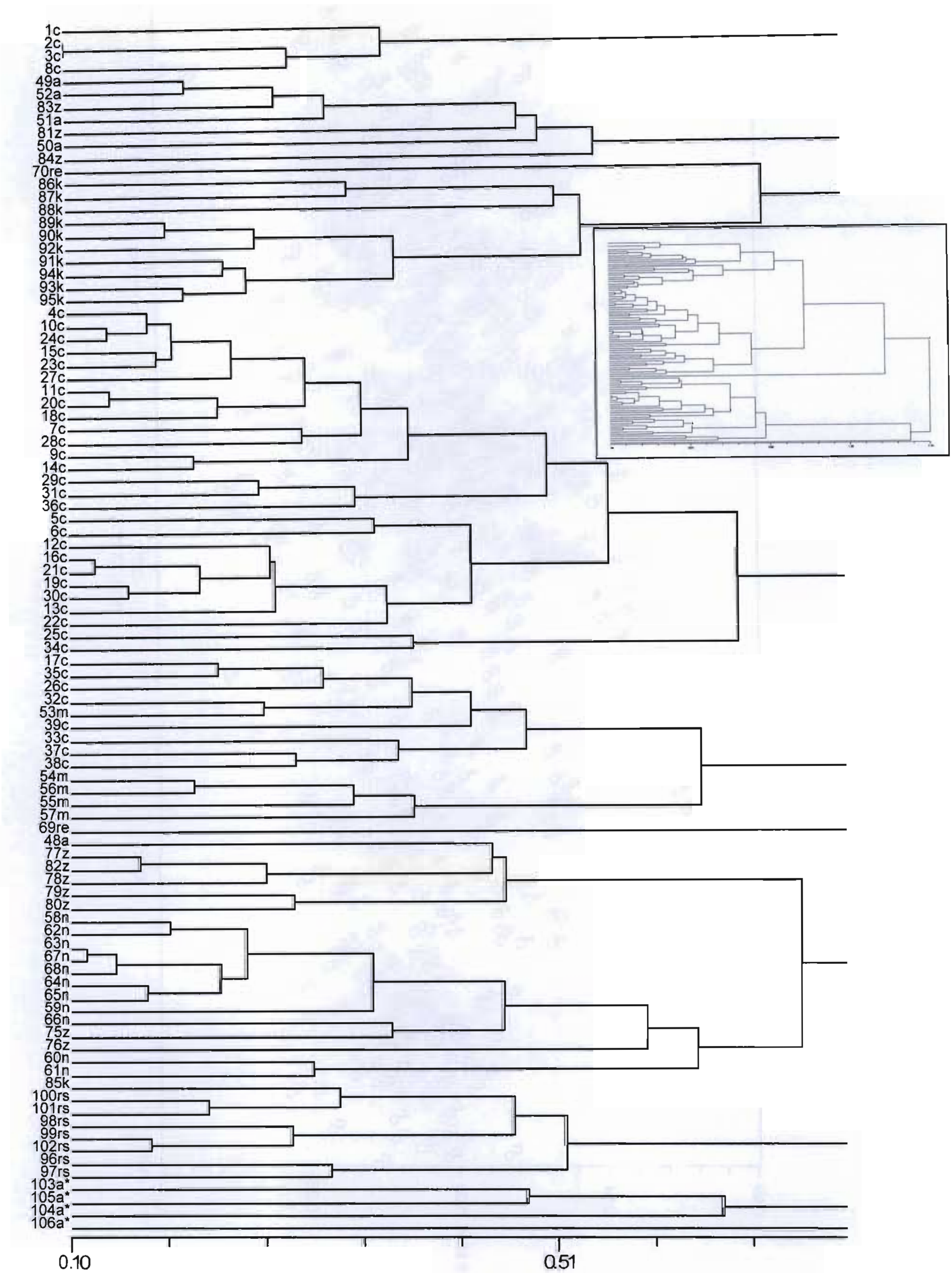


Figure 7.12 B) Distance phenogram of a cluster analyses of average taxonomic distance, using UPGMA, based on seven cranial measurements of eight different vespertilionid species (with additional specimens of *Hypsugo anchietae,* including a type). OTU and individual numbers and subspecies codes correspond to those in Tables 7.1 and 7.2. * = additional specimens. Cophenetic correlation coefficient = 0.742. Inset shows entire phenogram.

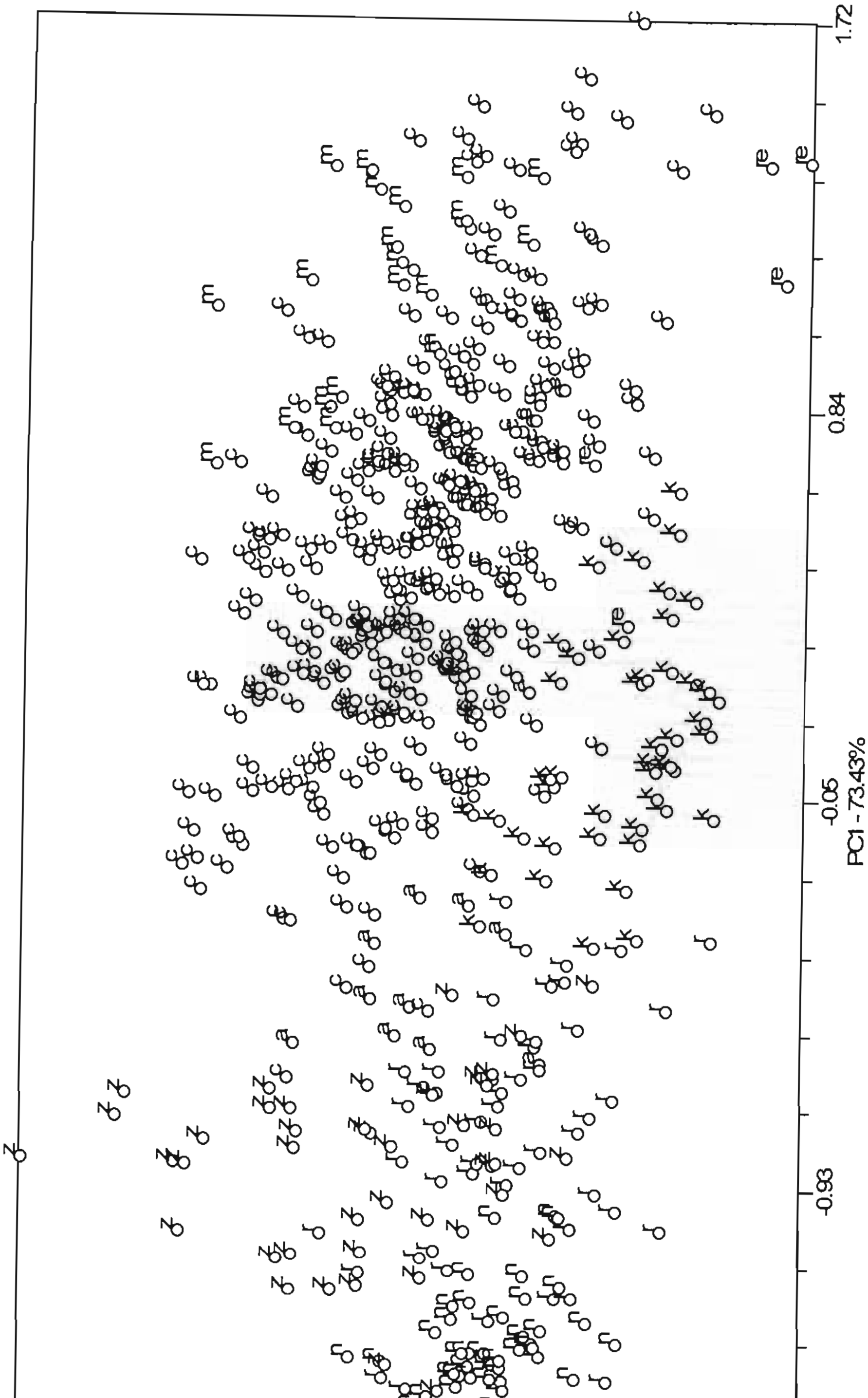


Figure 7.13 Scatterplot of the first two principal components of a PCA based on 12 cranial measurements of 611 specimens of eight vespertilionid species. Species codes: a = *Hypsugo anchietae*; c = *Neoromicia capensis*; m = *Neoromicia* cf. *melckorum*; n = *Neoromicia africanus*; re = *Neoromicia rendalli*; z = *Neoromicia zuluensis*; k = *Pipistrellus hesperidus*; r = *Pipistrellus rusticus*.

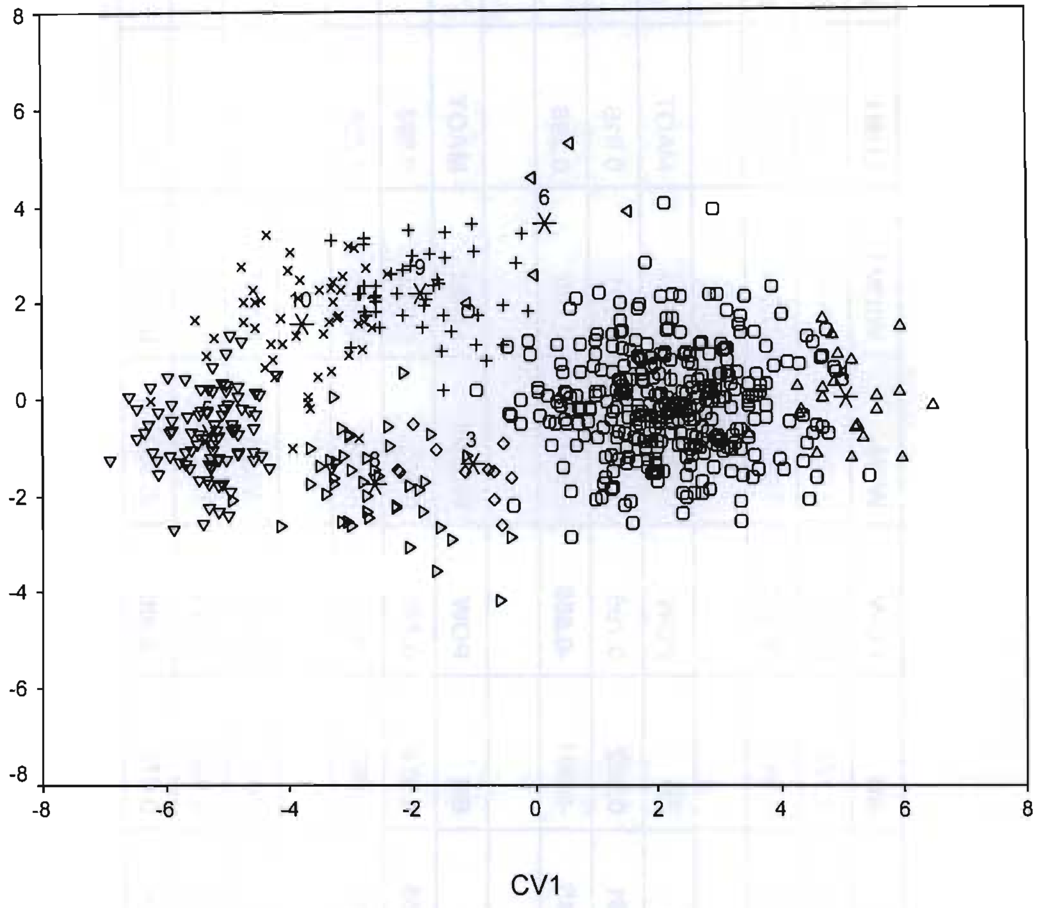


Figure 7.14 Plot of the first two discriminant function axes of discriminant function analysis based on 12 cranial measurements of 611 specimens of eight vespertilionid species. Centroid codes: 1 = *Neoromicia capensis*; 3 = *Hypsugo anchietae*; 4 = *Neoromicia* cf. *melckorum*; 5 = *Neoromicia africanus*; 6 = *Neoromicia rendalli*; 8 = *Neoromicia zuluensis*; 9 = *Pipistrellus hesperidus*; 10 = *Pipistrellus rusticus*. Species symbols: *Neoromicia capensis* = ○, *Hypsugo anchietae* = ◇, *Neoromicia* cf. *melckorum* =△, *Neoromicia africanus* = ▽, *Neoromicia rendalli* = ◁, *Neoromicia zuluensis* = ▷, *Pipistrellus hesperidus* = +, *Pipistrellus rusticus* = ×.

Table 7.6 Eigenvalues of principal component analyses with additional type specimens of vespertilionids. Numbers in bold type are the most important measurements on that axis.

Analysis		**CIL**	**BH**	**ZB**	**BB**	**POW**	**WFM**	**WIUM1**	**LUM1**	**MAOT**
1	**PC1**	0.956	0.896	**0.971**	**0.973**	0.784	0.926	0.830	0.917	0.901
	PC2	0.247	-0.155	0.090	0.041	**-0.553**	0.091	-0.359	0.178	**0.288**
		CIL	BH	ZB	BB	POW	WFM	LUM1	MAOT	
2	**PC1**	0.971	0.912	**0.981**	**0.982**	0.796	0.935	0.931	0.916	
	PC2	0.173	-0.193	0.045	-0.031	**-0.580**	0.050	0.146	**0.296**	
		CIL	**BH**	**ZB**	**BB**	**POW**	**WIUM1**	**LUM1**	**MAOT**	
3	**PC1**	0.954	0.910	**0.968**	**0.974**	0.798	0.803	0.912	0.898	
	PC2	**0.264**	-0.090	0.117	0.060	**-0.527**	-0.438	0.241	0.235	
		CIL	BH	ZB	BB	POW	WIUM1	MAOT		
4	**PC1**	0.942	0.923	**0.968**	**0.960**	0.818	0.831	0.840		
	PC2	0.255	-0.056	0.099	0.074	**-0.492**	-0.352	**0.405**		

PCA and cluster analyses and possibly provide a means of species identification for these taxa. The following outlier OTUs were removed prior to two-group discriminant function analyses given their uncertain identity: *N. capensis* - OTUs 1 and 9; *N. zuluensis* - OTUs 75-76 and 79; *P. rusticus* - OTU 97; and *P. hesperidus* - OTU 88.

The results of two-group discriminant function analyses of all 12 measurements, entered both simultaneously and stepwise, allowed positive identification of OTUs and specimens of the following pairs of species: *N. zuluensis* and *P. rusticus*; *H. anchietae* and *P. hesperidus*; *N. capensis* and *N.* cf. *melckorum*, *P. hesperidus* and *P. rusticus*, *H. anchietae* and *N. zuluensis*, *N. capensis* and *N. zuluensis*, *N. capensis* and *P. hesperidus*, *N. africanus* and *N. zuluensis*, and *N. africanus* and *P. rusticus*. The standardized canonical discriminant function coefficients for each measurement are given in Tables 7.7 to 7.15. In the stepwise analyses, the cranial measurements selected to maximize the separation between groups differed between the pair-wise comparisons. The discriminant scores plotted as frequency histograms are given in Figures 7.15 to 7.23. Separation between each species pair was marked, with no overlap in discriminant score ranges and with 100% *a posteriori* classification.

The discriminant score of an unidentified specimen can be calculated by taking the measurements in a Table (see Tables 7.7 to 7.15), for each measurement subtracting the overall mean from the measured value, multiplying the results with the standardized coefficient and then summing the values for each measurement. The resulting discriminant score compared with the plot of scores in the related figure identifies which species is associated with the discriminant score. It should be noted, however, that these classification tools were based largely on mean OTU measurements.

Neoromicia zuluensis and *P. rusticus* (Table 7.7; Fig. 7.15): For the analysis with all 12 measurements entered together, discriminant scores of *N. zuluensis* ranged from 8.577 to 11.243 (mean = 10.245); in *P. rusticus*, discriminant scores ranged from -13.647 to -10.642 (mean = -11.953). For the analysis of all 12 measurements entered in stepwise fashion, of which only four measurements were used, discriminant scores of *N. zuluensis* ranged from 4.980 to 8.293 (mean = 6.003), in *P. rusticus* discriminant scores ranged from -8.106 to -5.816 (mean = -7.003).

Hypsugo anchietae and *P. hesperidus* (Table 7.8; Fig. 7.16): For the analysis with all 12 measurements entered together, discriminant scores of *H. anchietae* ranged from -14.229 to -11.183 (mean = -12.358), in *P. hesperidus* discriminant scores ranged from 5.070 to 7.399 (mean = 6.179). For the analysis of all 12 measurements entered stepwise, of which only four measurements were used, discriminant scores of *H. anchietae* ranged from -10.398 to -7.263 (mean = -8.575), in *P. hesperidus* discriminant scores range from 2.786 to 5.885 (mean = 4.288).

Neoromicia capensis and *N.* cf. *melckorum* (Table 7.9; Fig. 7.17): For the analysis with all 12 measurements entered together, discriminant scores of *N. capensis* ranged from -3.094 to 1.280 (mean = -0.906), in *N.* cf. *melckorum* discriminant scores ranged from 5.324 to 7.760 (mean = 6.706). For the analysis of all 12 measurements entered stepwise, of which only five measurements were used, discriminant scores of *N. capensis* ranged from -3.569 to 1.155 (mean = -0.772), in *N.* cf. *melckorum* discriminant scores ranged from 4.716 to 6.916 (mean = 5.715).

Pipistrellus hesperidus and *P. rusticus* (Table 7.10; Fig. 7.18): For the analysis with all 12 measurements entered together, discriminant scores of *P. rusticus* ranged from -4.492 to -2.660 (mean = -3.582), in *P. hesperidus* discriminant scores ranged from -0.068 to 4.068 (mean = 2.149). For the analysis of all 12 measurements entered stepwise, of which only two measurements were used, discriminant scores of *P. rusticus* ranged from -3.862 to -2.294 (mean = -3.156), in *P. hesperidus* discriminant scores ranged from 0.188 to 3.552 (mean = 1.894).

Hypsugo anchietae and *N. zuluensis* (Table 7.11; Fig. 7.19): For the analysis with all 12 measurements entered together, discriminant scores of *N. zuluensis* ranged from -5.015 to -2.363 (mean = -3.512), in *H. anchietae* discriminant scores ranged from 3.858 to 6.420 (mean = 4.916). For the analysis of all 12 measurements entered stepwise, of which only four measurements were used, discriminant scores of *N. zuluensis* ranged from -11.042 to -7.679 (mean = -8.977), in *H. anchietae* discriminant scores ranged from 11.593 to 13.378 (mean = 12.568).

Neoromicia capensis and *N. zuluensis* (Table 7.12; Fig. 7.20): For the analysis with all 12 measurements entered together, discriminant scores of *N. zuluensis* ranged from -9.332 to -6.118 (mean = -7.941), in *N. capensis* discriminant scores ranged from -0.825 to 3.439 (mean = 1.588). For the analysis of all 12 measurements entered stepwise, of which only four measurements were used, discriminant scores of *N. zuluensis* ranged from -8.450 to -5.491 (mean = -7.627), in *N. capensis* discriminant scores ranged from -0.974 to 3.278 (mean = 1.525).

Neoromicia capensis and *P. hesperidus* (Table 7.13; Fig. 7.21): For the analysis with all 12

Table 7.7 Overall measurement means and standardized canonical discriminant function coefficients from A) a two-group DFA and B) a two-group stepwise DFA for *Neoromicia zuluensis* and *Pipistrellus rusticus* in southern Africa.

	Measurements	**Overall means**	**Standardised coefficient**
A)	**CIL**	11.766	-2.677
	BH	4.512	1.129
	ZB	7.002	4.292
	BB	6.301	-4.949
	POW	3.536	4.446
	WFM	3.196	-0.56
	WAS	1.378	0.677
	WOUC	3.851	6.951
	WIUM1	2.521	-10.803
	WUPM4	0.847	1.916
	LUM1	1.183	3.592
B)	**CIL**	11.766	1.112
	WIUM1	2.521	-2.065
	LUM1	1.183	0.940
	MAOT	2.698	1.116

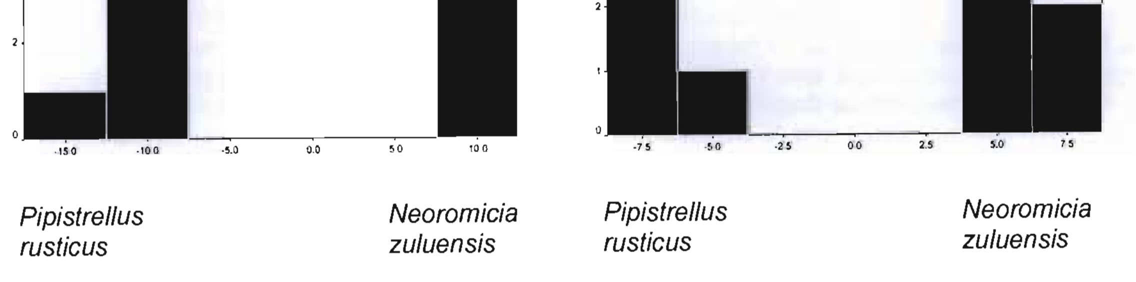


Figure 7.15 Histograms of discriminant scores from A) a two-group DFA, and B) a stepwise two-group DFA of *Pipistrellus rusticus* and *Neoromicia zuluensis* in southern Africa.

Table 7.8 Overall measurement means and standardized canonical discriminant function coefficients from A) a two-group DFA and B) a two-group stepwise DFA for *Hypsugo anchietae* and *Pipistrellus hesperidus* in southern Africa.

	Measurements	Overall means	Standardised coefficient
A)	CIL	12.412	-1.700
	BH	4.740	-0.914
	ZB	7.306	-1.193
	BB	6.613	0.520
	POW	3.675	1.049
	WFM	3.317	2.371
	WAS	1.485	-0.755
	WOUC	4.165	1.251
	WIUM1	2.667	0.656
	WUPM4	0.921	0.056
	LUM1	1.266	-1.286
	MAOT	2.888	0.648
B)	ZB	7.306	-0.761
	WFM	3.317	1.565
	WIUM1	2.667	1.109
	LUM1	1.266	-1.593

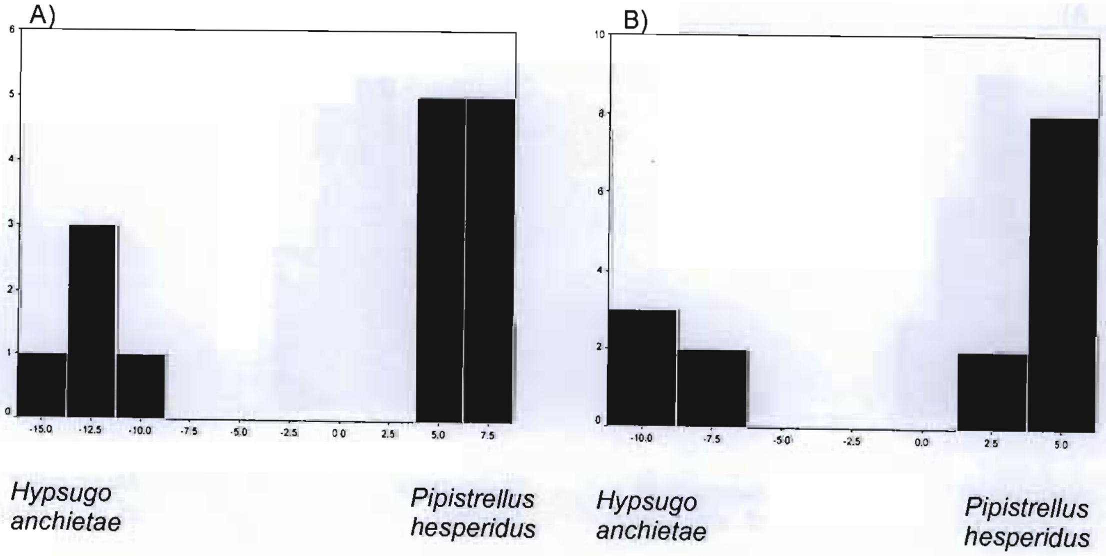


Figure 7.16 Histograms of discriminant scores from A) a two-group DFA, and B) a stepwise two-group DFA of *Hypsugo anchietae* (left) and *Pipistrellus hesperidus* (right) in southern Africa.

Table 7.9 Overall measurement means and standardized canonical discriminant function coefficients from A) a two-group DFA and B) a two-group stepwise DFA for *Neoromicia capensis* and *Neoromicia* cf. *melckorum* in southern Africa.

	Measurements	**Overall means**	**Standardised coefficient**
A)	**CIL**	13.930	1.365
	BH	4.869	-1.643
	ZB	8.009	0.718
	BB	7.047	-0.936
	POW	3.677	0.596
	WFM	3.576	0.900
	WAS	1.629	1.070
	WOUC	4.591	0.547
	WIUM1	2.709	-1.116
	WUPM4	1.015	0.792
	LUM1	1.397	-0.480
	MAOT	3.272	-0.364
B)	**BH**	4.869	-1.761
	ZB	8.009	0.938
	WFM	3.576	0.966
	WAS	1.629	0.520
	WUPM4	1.015	0.726

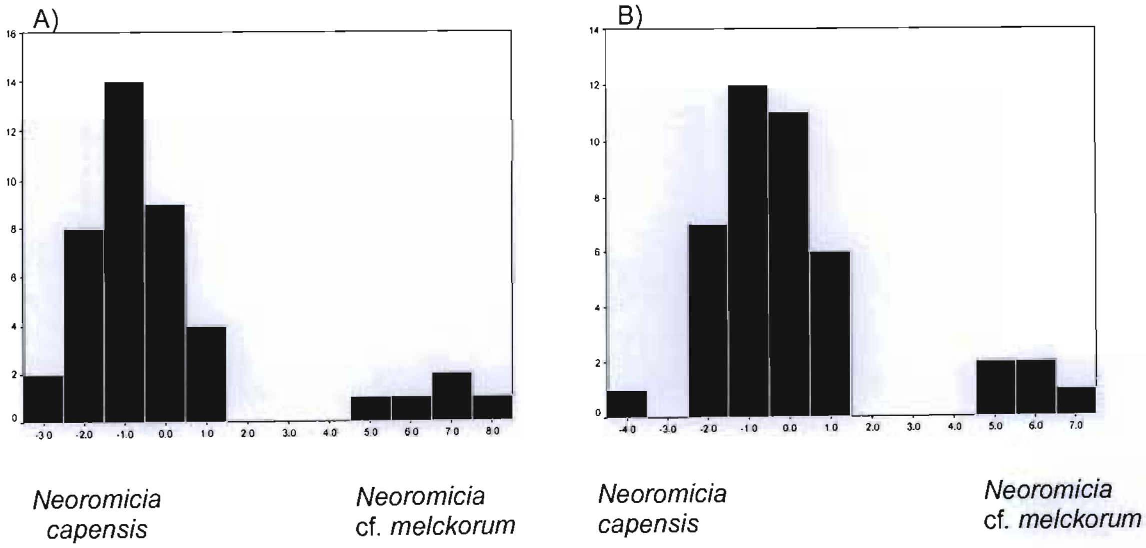


Figure 7.17 Histograms of discriminant scores from A) a two-group DFA, and B) a stepwise two-group DFA of *Neoromicia capensis* and *Neoromicia* cf. *melckorum* in southern Africa.

Table 7.10 Overall measurement means and standardized canonical discriminant function coefficients from A) a two-group DFA and B) a two-group stepwise DFA for *Pipistrellus hesperidus* and *Pipistrellus rusticus* in southern Africa.

	Measurements	Overall means	Standardised coefficient
A)	CIL	12.046	1.420
	BH	4.626	0.925
	ZB	7.207	-0.988
	BB	6.494	-1.129
	POW	3.656	0.220
	WFM	3.327	0.289
	WAS	1.412	0.552
	WOUC	4.139	0.309
	WIUM1	2.733	-0.344
	WUPM4	0.915	-0.500
	LUM1	1.230	-0.333
	MAOT	2.814	0.216
B)	CIL	12.046	0.921
	WAS	1.412	0.679

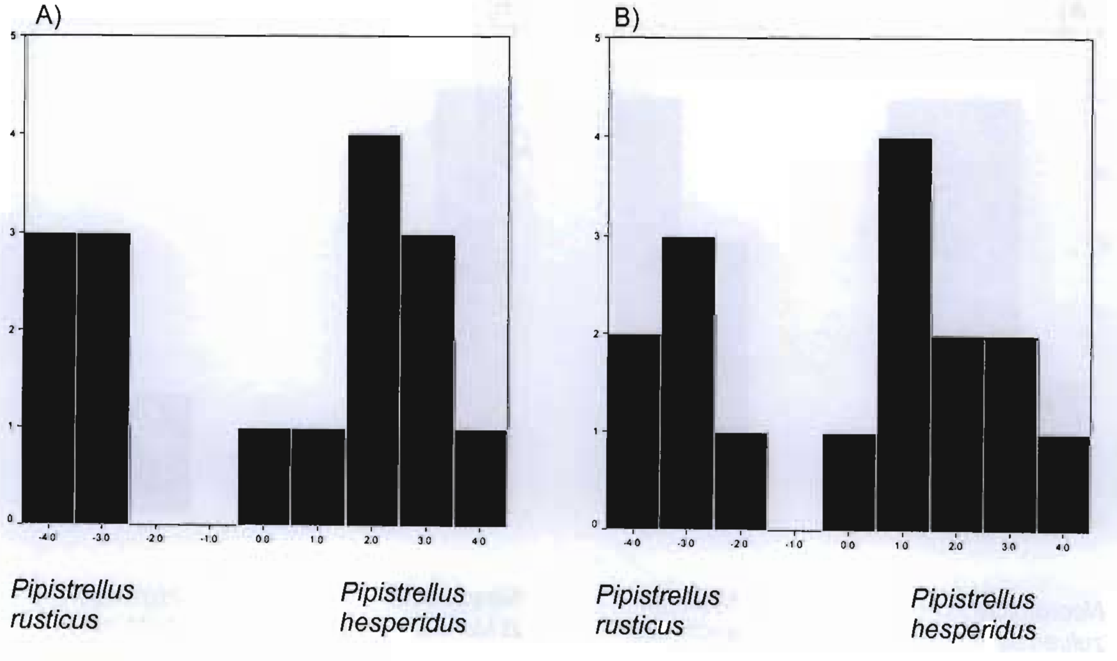


Figure 7.18 Histograms of discriminant scores from A) a two-group DFA, and B) a stepwise two-group DFA of *Pipistrellus rusticus* and *Pipistrellus hesperidus* in southern Africa.

Table 7.11 Overall measurement means and standardized canonical discriminant function coefficients from A) a two-group DFA and B) a two-group stepwise DFA for *Hypsugo anchietae* and *Neoromicia zuluensis* in southern Africa.

	Measurements	**Overall means**	**Standardised coefficient**
A)	**CIL**	12.200	1.106
	BH	4.645	3.470
	ZB	7.109	0.552
	BB	6.434	-0.532
	POW	3.550	-2.883
	WFM	3.172	1.632
	WAS	1.466	-2.925
	WOUC	3.860	4.104
	WIUM1	2.421	-0.281
	LUM1	1.225	-0.444
B)	**CIL**	12.200	2.708
	BH	4.645	1.106
	WAS	1.466	-3.872
	MAOT	2.781	2.813

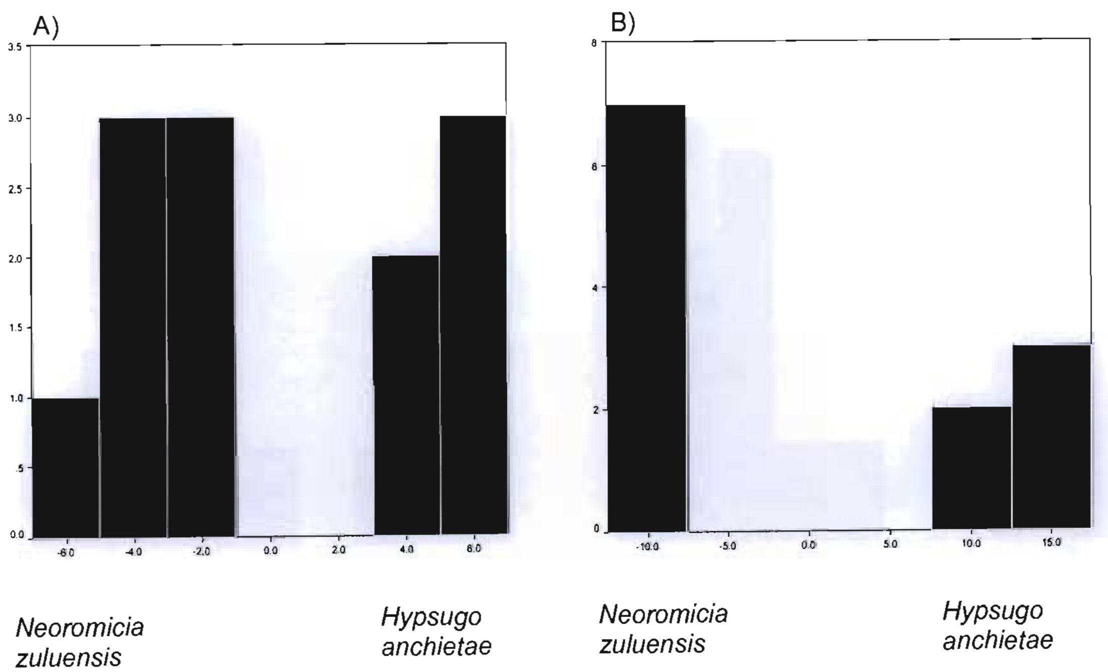


Figure 7.19 Histograms of discriminant scores from A) a two-group DFA, and B) a stepwise two-group DFA of *Neoromicia zuluensis* and *Hypsugo anchietae* in southern Africa.

Table 7.12 Overall measurement means and standardized canonical discriminant function coefficients from A) a two-group DFA and B) a two-group stepwise DFA for *Neoromicia capensis* and *Neoromicia zuluensis* in southern Africa.

	Measurements	**Overall means**	**Standardised coefficient**
A)	CIL	13.566	0.419
	BH	4.841	-1.142
	ZB	7.812	0.243
	BB	6.927	-0.103
	POW	3.658	-0.072
	WFM	3.494	0.403
	WAS	1.591	0.212
	WOUC	4.448	0.860
	WIUM1	2.661	-0.330
	WUPM4	0.968	0.797
	LUM1	1.357	0.061
	MAOT	3.159	0.124
B)	BH	4.841	-1.040
	WFM	3.494	0.562
	WOUC	4.448	1.071
	WUPM4	0.986	0.810

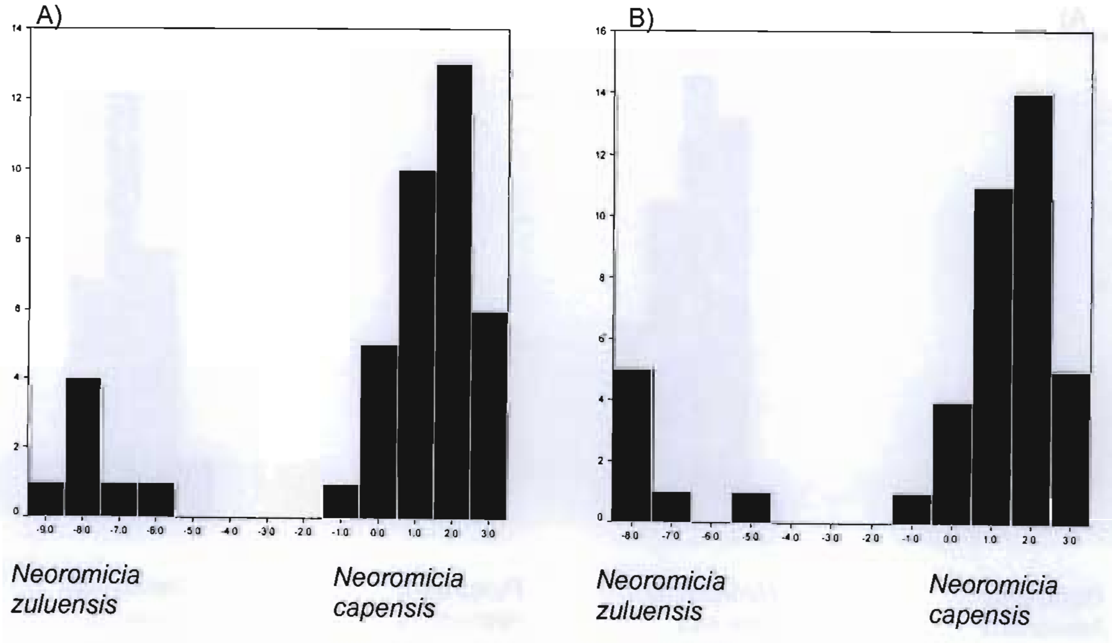


Figure 7.20 Histograms of discriminant scores from A) a two-group DFA, and B) a stepwise two-group DFA of *Neoromicia zuluensis* and *Neoromicia capensis* in southern Africa.

Table 7.13 Overall measurement means and standardized canonical discriminant function coefficients from A) a two-group DFA and B) a two-group stepwise DFA for *Neoromicia capensis* and *Pipistrellus hesperidus* in southern Africa.

	Measurements	Overall means	Standardised coefficient
A)	CIL	13.546	0.984
	BH	4.860	-0.679
	ZB	7.830	1.013
	BB	6.953	0.294
	POW	3.692	-0.663
	WFM	3.521	-0.486
	WAS	1.589	0.421
	WOUC	4.511	0.024
	WIUM1	2.727	-1.321
	WUPM4	0.984	0.142
	LUM1	1.362	0.588
	MAOT	3.170	0.292
B)	CIL	13.546	1.458
	BH	4.860	-0.879
	ZB	7.830	0.910
	WAS	1.589	0.717
	WIUM1	2.727	-1.568

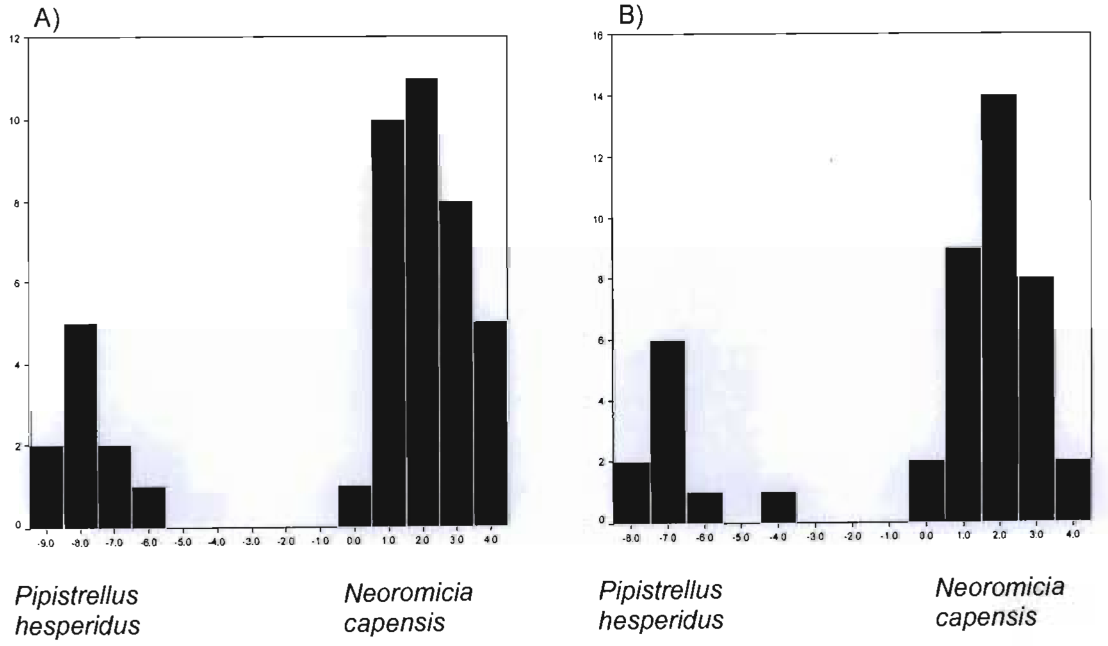


Figure 7.21 Histograms of discriminant scores from A) a two-group DFA, and B) a stepwise two-group DFA of *Pipistrellus hesperidus* and *Neoromicia capensis* in southern Africa.

Table 7.14 Overall measurement means and standardized canonical discriminant function coefficients from A) a two-group DFA and B) a two-group stepwise DFA for *Neoromicia africanus* and *Neoromicia zuluensis* in southern Africa.

	Measurements	**Overall means**	**Standardised coefficient**
A)	CIL	11.481	-0.306
	BH	4.483	2.049
	ZB	6.696	0.009
	BB	6.177	2.852
	POW	3.458	-1.032
	WFM	3.159	-1.437
	WAS	1.280	-0.687
	WOUC	3.661	0.198
	WIUM1	2.392	-3.260
	WUPM4	0.781	0.330
	LUM1	1.104	1.854
	MAOT	2.526	2.656
B)	BH	4.483	1.493
	BB	6.177	1.093
	WIUM1	2.392	-2.356
	LUM1	1.104	2.005
	MAOT	2.526	1.359

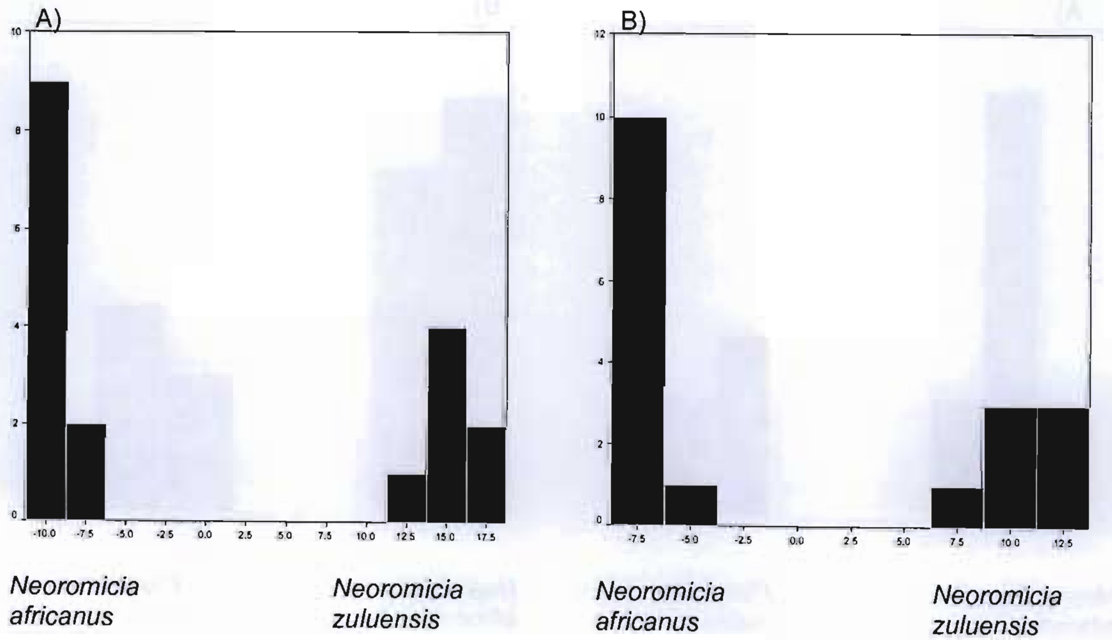
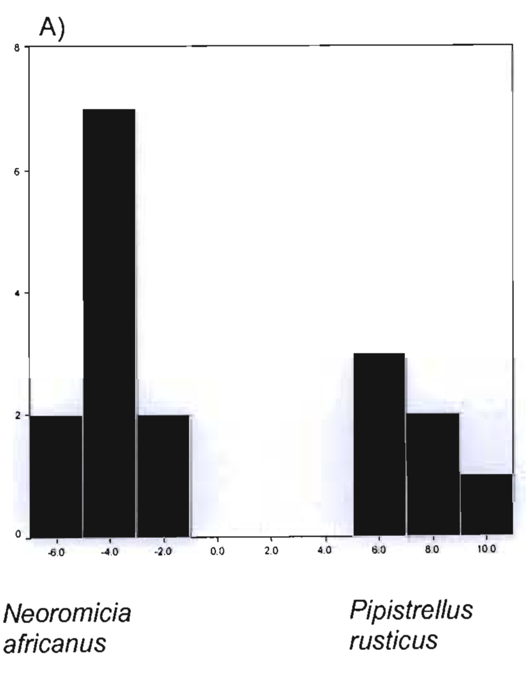


Figure 7.22 Histograms of discriminant scores from A) a two-group DFA, and B) a stepwise two-group DFA of *Neoromicia africanus* and *Neoromicia zuluensis* in southern Africa.

Table 7.15 Overall measurement means and standardized canonical discriminant function coefficients from A) a two-group DFA and B) a two-group stepwise DFA for *Neoromicia africanus* and *Pipistrellus rusticus* in southern Africa.

	Measurements	Overall means	Standardised coefficient
A)	CIL	11.274	-1.212
	BH	4.396	-0.026
	ZB	6.649	1.258
	BB	6.105	0.130
	POW	3.447	1.088
	WFM	3.166	-1.400
	WAS	1.214	0.424
	WOUC	3.694	1.225
	WIUM1	2.483	-1.797
	WUPM4	0.811	0.880
	LUM1	1.106	1.280
	MAOT	2.500	0.680
B)	ZB	6.649	1.661
	WOUC	3.694	-1.105
	LUM1	1.106	1.073



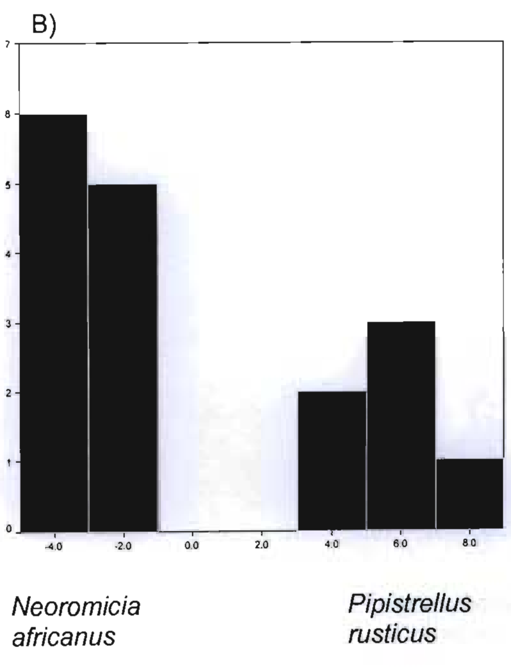


Figure 7.23 Histograms of discriminant scores from A) a two-group DFA, and B) a stepwise two-group DFA of *Neoromicia africanus* and *Pipistrellus rusticus* in southern Africa.

measurements entered together, discriminant scores of *P. hesperidus* ranged from -8.958 to -5.903 (mean = -7.640), in *N. capensis* discriminant scores ranged from 0.253 to 4.213 (mean = 2.183). For the analysis of all 12 measurements entered stepwise, of which only five measurements were used, discriminant scores of *P. hesperidus* ranged from -8.262 to -4.420 (mean = -6.844), in *N. capensis* discriminant scores ranged from 0.174 to 3.971 (mean = 1.955).

Neoromicia africanus and *N. zuluensis* (Table 7.14; Fig. 7.22): For the analysis with all 12 measurements entered together, discriminant scores of *N. africanus* ranged from -10.793 to -8.393 (mean = -9.632), in *N. zuluensis* discriminant scores ranged from 13.160 to 16.645 (mean = 15.136). For the analysis of all 12 measurements entered stepwise, of which only five measurements were used (but six were assessed), discriminant scores of *N. africanus* ranged from -8.285 to -6.214 (mean = -7.012), in *N. zuluensis* discriminant scores ranged from 8.088 to 12.884 (mean = 11.019).

Neoromicia africanus and *P. rusticus* (Table 7.15; Fig. 7.23): For the analysis with all 12 measurements entered together, discriminant scores of *N. africanus* ranged from -5.546 to -2.547 (mean = -3.942), in *P. rusticus* discriminant scores ranged from 6.120 to 9.065 (mean = 7.226). For the analysis of all 12 measurements entered stepwise, of which only three measurements were used, discriminant scores of *N. africanus* ranged from -4.490 to -1.725 (mean = -3.008), in *P. rusticus* discriminant scores ranged from 4.361 to 8.045 (mean = 5.515).

7.3.6 Univariate analysis

Basic statistics of 12 cranial measurements for the southern African distribution of 10 vespertilionid species are listed in Appendix 7.2. OTUs and individuals that plotted as outliers to the rest of the taxa in the PCA, cluster analyses and DFA were calculated separately (*N. capensis* - OTUs 1-3; *N. zuluensis* - OTUs 75-76; *P. rusticus* - OTU 97), or removed from the calculation of the basic statistics (*N. capensis* - OTU 9; *N. zuluensis* - OTU 79; *P. hesperidus* - OTU 88).

An ANOVA carried out on all OTUs and individuals of the 10 species, found significant difference ($P < 0.001$) between the species in all 12 cranial measurements (Appendix 7.2). The post-hoc Tukey tests identified similar significantly different subsets in most measurements (Appendix 7.3). *Eptesicus hottentotus* was always the largest, and *N. africanus* was usually the smallest, the exceptions were two measurements (width between the inner surfaces of the upper first molars and greatest width of the foramen magnum) where it was second smallest to *N. zuluensis*. Most measurements showed a gradual increase in size across the different species. However, two exceptions to this were, post-orbital width, which was wider in *N. rendalli*, *N. rueppellii* and *E. hottentotus* than in the other species, and width between the inner surfaces of the upper first molars which was smaller in *N. zuluensis, N. africanus* and *H. anchietae* than all the other species. Post-orbital width was also an important measurement on the first two discriminant function axes, and width between the inner surfaces of the upper first molars was an important measurement on the second principal component axes of the PCAs.

7.4 DISCUSSION

Using PCA and CA, traditional morphometric methods using 12 cranial measurements were able to distinguish between half of the vespertilionid species tested using OTUs (*E. hottentotus, N. capensis, N.* cf. *melckorum, N. rueppellii*, and *N. africanus*), whereas the distinctions of the remaining five species tested (*H. anchietae*, *N. rendalli*, *N. zuluensis*, *P. hesperidus* and *P. rusticus*) were not always resolved. Using DFA in OTUs, all species could be distinguished with 100% accuracy. In analyses of individuals, however, only *E. hottentotus* and *N. rueppellii* were sufficiently different in the 12 cranial measurements to allow clear distinction of the individuals tested, whereas individuals of the other eight vespertilionid species did not allow delineation of the different species.

The broad intra-specific scatter shown in the PCA plots is consistent with the intra-specific variation reported in chapter 6, where significant latitudinal variation was demonstrated within *H. anchietae*, *N. capensis*, *N. zuluensis*, *P. hesperidus* and *P. rusticus.* Furthermore, chapter 5 documented intra-specific OTU arrangements according to latitude, as well as significant longitudinal variation within *N. capensis* and *N. zuluensis*. In all the analyses, most of the cranial variation was in relation to size and hence, most of the differences among species did not reflect the phylogenetic relationships suggested by chromosome banding and DNA analyses (Hoofer and Van Den Bussche, 2003; Volleth *et al.* 2001; Kearney *et al.*, 2002). Instead, as in the shape analysis (Chapter 3), there was a high degree of homoplasy in the skull morphology of eight of the taxa in question that constrained species separation. This homoplasy, as in the shape analysis (see discussion in Chapter 3), presumably resulted from the observed allometric scaling between the species and possible ecological constraints (Jacobs, 1996; Freeman 1998; Pedersen 1998; Sanchez-Villagra and Williams, 1998; Stadelmann *et al.* 2004).

Huxley (1932) initially devised allometry as a tool to study relative growth of parts of various organisms, allometry being considered as bivariate change in shape correlated with change in size (Pimental, 1979; Klingenberg, 1996). It was subsequently realised that growth is not the only origin of variation in overall size and associated variation in shape, since evolutionary changes and individual variation can also generate allometric relationships, and hence three types of allometry have since been described: static, ontogenetic and evolutionary (Klingenberg, 1996). The model of allometry may be applied, as in this study, to show if evolutionary variation is constrained in its dimensionality (Klingenberg, 1996). The allometric scaling between the crania of the different species is probably the result of a correlated response by shape to selection on size (Cheverud, 1982), and as in the shape analysis (Chapter 3) the different species appeared to have slightly different scaling patterns. In addition, the patterns of allometry were different for the different measurements with 41.6% and 50% of the measurements in the analyses with 10 and eight species, respectively showing significant negative allometry, where rates of shape and size change were not simultaneous. The other measurements, although not significant, all showed positive allometry (where rates of change in shape and size occur simultaneously) since the coefficient values were above one. The allometric constraints were confined to the first principal components of the PCAs which showed considerable influence of size rather than shape, since regression analyses and bivariate plots of the second and third principal component scores with the chosen measure reflecting overall size, condylo-incisor length, did not show significant allometry.

The use of log-transformed size measures in assessments of allometry relates to Huxley's (1932) formula for allometry being log-transformed on both axes to allow the curved line resulting from the scatterplot of two trait measurements in growing organisms to become linear. Whether a correction which takes into account progressive decrease of rate of shape change during growth is necessary in an assessment between species has probably led to the variation noted in the literature, since the measure of size is log-transformed in some analyses comparing species (Singleton, 2002) but not in others (Milne and O'Higgens, 2002; Viguier, 2002). Log-transformed data was used in this study across species because the multiplicative nature of growth processes may also be important for these levels because all variation in morphological structures is due to variation in the developmental processes that generate them (Klingenberg, 1996).

Unlike the results of the shape analysis which did not find any separation between the 10 vespertilionid species in question, the traditional morphometric methods based on 12 cranial measurements identified a significant difference in size between *E. hottentotus* and the other species. This method also distinguished *P. rueppellii*, and to some extent *N. rendalli*, from the other species largely on the basis of a broader post-orbital region than other species of a similar overall skull length. The distinction of *N. rueppellii* is valuable because this species was recognised in a subgenus, *Vansonia*, distinct from *Pipistrellus* (Meester *et al.*, 1986) as a result of Roberts (1946) having transferred *N. rueppellii vernayi* to the genus *Vansonia*. However, in the description of the genus *Vansonia* Roberts (1946) makes no mention of the post-orbital region of the skull. Instead, height of the cranium relative to the muzzle, and various dental characters were used for the distinction of *Vansonia*. Albeit small and subtle, the only observed cranial variation in shape that possibly reflected a phylogenetic relationship, was the distinction of both *Pipistrellus* species from the other genera on the third principal component of a scatterplot of the first three principal component axes.

The addition of type specimens to some of the species sampled was useful to confirm the identifications given to specimens made on morphological characters following the published identification keys (Meester *et al.*, 1986) and/or additional characters of more recently described bacular morphology and diploid chromosome number, which are usually not known for the type specimen. While some of the types confirmed the species association given to the southern African OTUs, there were also a few unanswered questions raised by the addition of the type material. The holotype specimen of the subspecies *P. h. fuscatus* plotted together with southern African *P. hesperidus* confirming Kock's (2001a) findings that the characters of *P. hesperidus* agreed with specimens previously identified as *P. kuhlii fuscatus* and *P. k . broomi*. This brings into question the validity of the *fuscatus* subspecies. However, further analyses with additional specimens of *P. h. fuscatus* are required to resolve this question.

The position of the holotype of *N. somalicus* from Somalia relative to the OTUs of southern

African *N. zuluensis*, was suggestive of the geographic variation noted within many of the species, except that *N. zuluensis* and *N. somalicus* are known to have different diploid chromosome numbers, which is why *N. zuluensis* was recognised as a distinct species (Rautenbach *et al.*, 1993). Although there is considerable geographic distance between the type locality of *N. rendalli* in Bathurst, Gambia and the southern African localities, the holotype of *N. rendalli* showed a close similarity to the larger specimen of *N. rendalli* from KwaZulu-Natal, while the paratype showed a closer similarity to the smaller Zimbabwe specimen of *N. rendalli*. The holotype of the subspecies of *N. c. gracilior* from Eshowe does not relate to OTUs of *N. capensis* from close to Eshowe, instead it appears more similar to *H. anchietae*. However, further work on this specimen and others from localities close to Eshowe will be required to clarify this distinction. The holotype of *N. a. fouriei* from north-western Ovamboland in Namibia was very distinct from the other southern African OTUs of *N. africanus*, whereas the syntype of *N. a. nanus* from Inhambane in Mozambique was similar to the closest OTUs of *N. africanus* in KwaZulu-Natal. The lectotype of *P. rusticus* from Olifants Vlei in Namibia was also similar to OTUs of *P. rusticus* from the same area. The syntype of *H. anchietae* from Cahata in Angola, on the other hand, was considerably different to other southern African OTUs of *H. anchietae* and the distribution of additional specimens of *H. anchietae* from Zambia on the PCA might be explained as a northward geographical extension of the species. Both the syntype and the additional specimens plotted separately from the southern African OTUs of *H. anchietae* drawing into question the distinction of this species. However, while this study was able to draw attention to such discrepancies, it did not have sufficient information to provide answers to the problem which will have to be addressed in further studies.

Pair-wise DFA of OTUs, which by virtue of using mean values excluded the extreme ranges of measurements of individuals within each species, allowed the formulation of classification calculations based on 12 cranial measurements to distinguish between eight pairs of similar species.

Several other studies of cranial morphometric variation in species of *Eptesicus*, *Pipistrellus* and *Hypsugo* from other parts of the world show similarities to the results of this study regarding southern African representatives of these genera. Various analyses have been made on Australian *Eptesicus* and *Pipistrellus* species. Three species of Australian forest dwelling *Eptesicus* were distinguished using DFA on a suite of skull and body features (Tidemann *et al.*, 1981). Among the important measurements contributing most to the variation, those that were similar to this analysis were: inter-orbital breadth of the skull and greatest length of the skull. Although Tidemann *et al.* (1981) also found forearm length, width of the foramen magnum, length of the maxillary tooth row and height of the skull to be important, it was only after the introduction of ratios of measurements into the DFA that all specimens were accurately grouped. Kitchener *et al.* (1986) used Canonical Variate Analysis (CVA) on skull, dentary and external body measurements to separate five species of Australian *Pipistrellus*. As in this study, one of the important measurements on the first canonical variate related to greatest skull length. On the second canonical variate, greatest skull length and braincase width were important in both analyses. The third canonical variate also provided some separation of the species. Additional important measurements that were found in the study by Kitchener *et al.* (1986), but not in this analysis, on the first canonical variate related to post palatal width and tooth row lengths, and on the third canonical variate, palatal length, and third digit and first phalanx lengths. Kitchener *et al.* (1987) also used a CVA on skull, dentary and external body measurements to separate nine Australian *Eptesicus* species, the measurements that were important in the separation of the species on the first and second canonical variates in both analysis were: greatest skull length, least orbital width, and mastoid width (similar to brain case width).

In North Africa, a multivariate analysis of Ethiopian *P. rusticus* and *P. hesperidus* using cranial measurements, also separated these taxa along the first principal component axis with overall cranial length being the most important factor in their separation (Lavrenchenko *et al.*, 2004). In a study of various mainland African and Madagascan species of *Eptesicus* and *Pipistrellus* by Petersen *et al.* (1995) using cranial measurements, the *Eptesicus* species showed separation along the first principal component with size being the overall component of variation, as well as the separation on the second principal component of *N. rendalli* (Petersen *et al.*, 1995). However, in the present analysis, the distribution of *N. zuluensis* was separated more from *N. rendalli* on the second principal component axis than the single OTU of *N. zuluensis* in the study by Petersen *et al.* (1995). The analysis of Petersen *et al.* (1995) also showed a fairly close relationship between *N. africanus* from Kenya, Uganda, Zambia, Zimbabwe, and South Africa.

Traditional morphometric methods on 12 cranial measurements were more efficient, in allowing some distinction between the 10 vespertilionid species, than the chosen landmarks in the shape analysis (Chapter 3). Nevertheless, craniometric variation was dominated by allometrically constrained size variation, which held little phylogenetic information. Hence, as is the case in bacular morphology, some of these cranial variations may be useful for species identification of certain taxa, but they provide little information about the phylogeny of the genera (Chapter 2), which GTG-banded chromosomes were able to provide (Chapter 2).

APPENDIX 7.1

Type and additional vespertilionid specimens used in this analysis.

Acronyms: BM - The Natural History Museum, London, United Kingdom; PM - Paris Museum, Paris, France.

* denotes type specimen.

Hypsugo anchietae: **ANGOLA:** Cahata (12°22'S, 14°52'E): BM6.1.3.1*. **ZAMBIA:** Barotseland (Chavuma area), Balovale (13°01'S, 22°44'E): PM70.2632, PM70.2633. Ngoma (15°54'S, 25°51'E): PM69.1248.

Neoromicia africanus: **MOZAMBIQUE:** Inhambane (23°45'S, 35°28'E): BM7.1.1.422*. **NAMIBIA:** 32 km NW Rehoboth, Rehoboth Mission (23°05'S, 17°16'E): BM25.12.4.20*.

Neoromicia capensis: **SOUTH AFRICA:** KWAZULU-NATAL PROVINCE: Eshowe (28°53'S, 31°28'E): BM4.8.31.3*.

Neoromicia rendalli: **GAMBIA:** Bathurst (13°27'11"N, 16°34'39"W): BM89.12.12.1*; PM89.3.2.3*.

Neoromicia somalicus: **SOMALIA:** Hargeisa (10°00'N, 44°00'E): BM98.6.9.1*.

Pipistrellus hesperidus: **KENYA:** Naivasha (00°43'S, 36°26'E): BM1.8.9.96*.

Pipistrellus rusticus: **NAMIBIA:** Ovamboland, Olifant's Vlei (17°30'S, 18°00'E): BM7.1.1.419*. Otjozondjupa, Tsumkwe (syn. Grootfontein) District, Kano Vlei (19°22'S, 19°07'E): PM35.9.1.101, PM35.9.1.102.

APPENDIX 7.2

Basic statistics

Basic statistics of 12 cranial measurements for the southern African distribution of 10 vespertilionid species. SD = standard deviation; CV = coefficient of variation; Min = minimum value; Max = maximum value; *n* = number of specimens. See the material and methods section of Chapter 5 for an explanation of the measurement codes.

Species		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Eptesicus hottentotus	**Mean**	19.05	6.54	11.16	9.05	4.35	4.36	2.62	6.20	3.54	1.45	1.97	4.58
(*n* = 42)	**SD**	0.787	0.28	0.50	0.33	0.22	0.19	0.19	0.36	0.19	0.15	0.12	0.297
	CV	4.11	4.37	4.47	3.71	5.15	4.48	7.42	5.83	5.39	10.45	6.32	6.30
	Min	16.99	5.94	10.09	8.42	3.94	3.89	2.24	5.40	3.05	1.197	1.73	4.02
	Max	20.07	7.17	12.36	9.82	4.91	4.84	3.00	6.92	3.97	1.976	2.27	5.19
Hypsugo anchietae	**Mean**	12.52	4.69	7.23	6.53	3.60	3.14	1.52	3.99	2.46	0.90	1.29	2.87
(*n* = 12)	**SD**	0.29	0.13	0.31	0.10	0.11	0.11	0.16	0.17	0.08	0.10	0.04	0.12
	CV	2.32	2.88	4.31	1.56	3.17	3.54	10.91	4.37	3.26	11.73	3.48	4.11
	Min	12.12	4.46	6.92	6.38	3.34	2.97	1.32	3.69	2.29	0.78	1.22	2.70
	Max	13.01	4.90	7.98	6.75	3.77	3.32	1.83	4.33	2.60	1.09	1.36	3.05
Neoromicia capensis	**Mean**	13.83	4.87	7.95	7.02	3.66	3.55	1.62	4.57	2.70	1.00	1.39	3.25
(*n* = 312)	**SD**	0.53	0.20	0.33	0.25	0.16	0.17	0.13	0.21	0.15	0.09	0.09	0.22
	CV	3.85	4.03	4.13	3.53	4.33	4.80	7.97	4.49	5.56	8.94	6.09	6.63
	Min	12.19	4.07	6.79	6.38	3.15	3.02	1.19	3.92	2.29	0.81	1.12	2.29
	Max	15.25	5.46	8.93	7.74	4.14	4.09	1.93	5.19	3.21	1.35	1.70	3.82
Neoromicia capensis	**Mean**	12.92	4.55	7.53	6.58	3.47	3.37	1.52	4.28	2.57	1.02	1.30	3.09
(OTUs 1-3)	**SD**	0.26	0.11	0.18	0.15	0.13	0.15	0.08	0.17	0.12	0.112	0.09	0.17
(*n* = 30)	**CV**	2.04	2.44	2.46	2.36	3.75	4.60	5.04	3.94	4.70	11.38	7.16	5.39
	Min	12.45	4.32	6.99	6.28	3.25	2.97	1.37	4.02	2.34	0.81	1.15	2.55
	Max	13.49	4.75	7.82	6.87	3.65	3.71	1.68	4.68	2.84	1.25	1.49	3.41
Neoromicia* cf. *melckorum	**Mean**	14.64	4.87	8.49	7.31	3.73	3.80	1.75	4.78	2.72	1.09	1.44	3.48
(*n* = 22)	**SD**	0.28	0.18	0.27	0.21	0.16	0.15	0.09	0.14	0.11	0.06	0.06	0.16
	CV	1.94	3.76	3.23	2.86	4.33	3.98	5.10	2.97	4.20	5.60	4.33	4.55
	Min	14.23	4.43	7.98	6.90	3.46	3.48	1.63	4.48	2.49	0.95	1.32	3.21
	Max	15.09	5.20	8.84	7.68	4.04	4.06	1.88	5.09	2.95	1.19	1.59	3.87

Species		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Neoromicia africanus	**Mean**	11.12	4.33	6.46	6.09	3.41	3.15	1.18	3.53	2.37	0.76	1.06	2.41
(*n* = 89)	**SD**	0.26	0.19	0.20	0.15	0.09	0.11	0.09	0.19	0.11	0.10	0.05	0.11
	CV	2.33	4.39	3.10	2.48	2.69	3.59	7.93	5.38	4.54	12.60	4.61	4.51
	Min	10.46	3.82	5.85	5.74	3.18	2.90	0.97	2.90	2.09	0.54	0.92	2.09
	Max	11.93	4.74	6.87	6.44	3.68	3.40	1.43	3.97	2.66	0.97	1.15	2.65
Neoromicia rendalli	**Mean**	13.47	5.14	8.32	7.11	4.06	3.69	1.77	4.56	3.01	1.02	1.36	3.11
(*n* = 5)	**SD**	0.50	0.08	0.38	0.27	0.19	0.15	0.19	0.17	0.17	0.06	0.04	0.20
	CV	3.87	1.60	4.77	3.93	4.94	4.32	11.17	3.94	6.07	6.55	3.22	6.89
	Min	12.75	5.04	7.77	6.74	3.80	3.47	1.58	4.28	2.75	0.95	1.29	2.80
	Max	13.95	5.25	8.71	7.37	4.24	3.82	2.04	4.68	3.21	1.12	1.39	3.31
Neoromicia rueppellii	**Mean**	13.37	5.31	7.80	7.52	4.34	3.59	1.51	4.20	3.04	0.94	1.26	2.96
(*n* = 8)	**SD**	0.41	0.22	0.28	0.21	0.25	0.16	0.08	0.30	0.19	0.13	0.07	0.18
	CV	3.17	4.17	3.70	2.92	5.85	4.51	5.52	7.23	6.40	14.27	5.45	6.40
	Min	12.62	4.81	7.31	7.14	3.94	3.36	1.37	3.67	2.75	0.71	1.18	2.70
	Max	13.81	5.47	8.11	7.75	4.70	3.83	1.63	4.58	3.36	1.12	1.39	3.16
Neoromicia zuluensis	**Mean**	11.94	4.56	6.99	6.29	3.46	3.15	1.40	3.79	2.40	0.81	1.19	2.72
(*n* = 30)	**SD**	0.21	0.10	0.18	0.18	0.14	0.15	0.12	0.14	0.09	0.07	0.08	0.09
	CV	1.75	2.16	2.63	2.89	4.02	4.86	8.47	3.75	3.69	8.58	6.77	3.28
	Min	11.41	4.37	6.66	5.91	3.22	2.77	1.22	3.51	2.24	0.68	1.02	2.60
	Max	12.37	4.76	7.37	6.67	3.79	3.42	1.66	4.17	2.60	0.95	1.36	2.952
Neoromicia zuluensis	**Mean**	11.53	4.53	6.56	6.14	3.29	2.97	1.34	3.49	2.37	0.74	1.02	2.61
(OTUs 75-76)	**SD**	0.09	0.06	0.21	0.13	0.04	0.17	0.03	0.04	0.18	0.01	0.10	0.20
(*n* = 2)	**CV**	0.83	1.58	3.64	2.33	1.21	6.43	2.38	1.24	8.53	1.05	10.84	8.69
	Min	11.47	4.48	6.41	6.05	3.26	2.85	1.32	3.46	2.24	0.74	0.95	2.46
	Max	11.59	4.57	6.71	6.23	3.31	3.09	1.36	3.51	2.49	0.75	1.09	2.75

Species		CIL	BH	ZB	BB	LIW	WFM	WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
Pipistrellus hesperidus	**Mean**	12.51	4.82	7.50	6.71	3.78	3.44	1.49	4.32	2.82	0.90	1.28	2.92
(*n* = 45)	**SD**	0.34	0.13	0.23	0.17	0.12	0.13	0.14	0.15	0.11	0.08	0.06	0.12
	CV	2.69	2.66	3.12	2.55	3.30	3.84	9.52	3.43	3.76	8.60	4.65	4.08
	Min	11.81	4.57	6.90	6.28	3.54	3.15	1.17	4.02	2.55	0.78	1.15	2.70
	Max	13.24	5.08	8.05	7.08	4.00	3.87	1.83	4.63	3.00	1.07	1.39	3.16
Pipistrellus rusticus	**Mean**	11.49	4.39	6.97	6.23	3.53	3.21	1.33	3.94	2.66	0.88	1.18	2.70
(*n* = 48)	**SD**	0.31	0.17	0.26	0.17	0.13	0.14	0.15	0.18	0.13	0.09	0.07	0.16
	CV	2.75	3.95	3.80	2.75	3.70	4.44	11.12	4.53	4.88	9.76	5.53	5.81
	Min	10.75	4.07	6.40	5.85	3.23	2.90	1.17	3.56	2.39	0.71	1.05	2.29
	Max	12.23	4.89	7.49	6.56	3.80	3.58	1.94	4.33	2.95	1.02	1.32	2.95
Pipistrellus rusticus	**Mean**	11.13	4.57	6.71	6.28	3.53	3.06	1.22	3.74	2.57	0.66	1.02	2.55
(OTU 97)	**SD**	0.16	0.03	0.11	0.19	0.13	0.08	0.07	0.11	0.04	0.07	-	-
(*n* = 2)	**CV**	1.57	0.70	1.78	3.42	4.29	2.86	6.63	3.25	1.58	12.24	-	-
	Min	11.02	4.55	6.63	6.14	3.43	3.00	1.17	3.67	2.55	0.61	1.02	2.55
	Max	11.24	4.59	6.78	6.41	3.62	3.11	1.27	3.82	2.60	0.71	1.02	2.55

APPENDIX 7.3

One-way ANOVA results

One-way ANOVA results of 12 cranial measurements to test for variation between 10 vespertilionid species (across their southern African distribution). df = degrees of freedom; P = significance; *** denotes significance at $P < 0.001$. SS = sum of squares. See the material and methods section of Chapter 5 for an explanation of the measurement codes.

Species		CIL	BH	ZB	BB	LIW	WFM
ANOVA	SS	389.036	27.857	127.240	54.658	6.501	10.574
	df	9	9	9	9	9	9
	F	224.995	133.637	240.758	159.728	46.973	94.816
	P	0.00E-16***	0.00E-16***	0.00E-16***	0.00E-16***	0.00E-16***	0.00E-16***

Species		WAS	WOUC	WIUM1	WUPM4	LUM1	MAOT
ANOVA	SS	11.656	43.328	8.564	2.705	4.922	28.156
	df	9	9	9	9	9	9
	F	148.085	156.900	94.305	57.673	137.696	168.910
	P	0.00E-16***	0.00E-16***	0.00E-16***	0.00E-16***	0.00E-16***	0.00E-16***

APPENDIX 7.4

Post-hoc Tukey test results

Post-hoc Tukey non-significant subsets between different vespertilionid species (with the mean for each species) for 12 cranial measurements. Species codes: 1 = *Neoromicia capensis*; 2 = *E. hottentotus*; 3 = *Hypsugo anchietae*; 4 = *Neoromicia* cf. *melckorum*; 5 = *Neoromicia africanus*; 6 = *Neoromicia rendalli*; 7 = *Neoromicia rueppellii*; 8 = *Neoromicia zuluensis*; 9 = *Pipistrellus hesperidus*; 10 = *Pipistrellus rusticus*. *n* = number of OTUs and individuals per species.

CIL								
Species	***n***	**1**	**2**	**3**	**4**	**5**	**6**	**7**
5	11	11.15						
10	7	11.44						
8	10	11.91	11.91					
9	11		12.37	12.37				
3	5		12.49	12.49	12.49			
6	2			13.20	13.20	13.20		
7	4				13.27	13.27		
1	39					13.80		
4	5						14.66	
2	8							19.04
Significance		0.112	0.435	0.051	0.085	0.370	1.000	1.000

ZB								
Species	***n***	**1**	**2**	**3**	**4**	**5**	**6**	**7**
5	11	6.48						
8	10	6.91	6.91					
10	7	6.93	6.93					
3	5		7.21	7.21				
9	11			7.39	7.39			
7	4				7.70	7.70		
1	39					7.94		
6	2					8.11	8.11	
4	5						8.48	
2	8							11.12
Significance		0.067	0.539	0.964	0.468	0.120	0.230	1.000

BB								
Species	***n***	**1**	**2**	**3**	**4**	**5**	**6**	**7**
5	11	6.05						
10	7	6.22	6.22					
8	10	6.31	6.31	6.31				
3	5		6.51	6.51				
9	11			6.66	6.66			
1	39				7.01	7.01		
6	2					7.04		
4	5					7.29	7.29	
7	4						7.45	
2	8							9.03
Significance		0.401	0.260	0.093	0.084	0.286	0.932	1.000

APPENDIX 7.4 continued

POW						
Species	***n***	**1**	**2**	**3**	**4**	**5**
5	11	3.40				
8	10	3.46	3.46			
10	7	3.53	3.53	3.53		
3	5	3.56	3.56	3.56		
1	39		3.67	3.67		
4	5			3.73		
9	11			3.74		
6	2				4.00	
7	4					4.28
2	8					4.32
Significance		0.521	0.158	0.129	1.000	1.000

WFM						
Species	***n***	**1**	**2**	**3**	**4**	**5**
8	10	3.13				
5	11	3.14				
3	5	3.16				
10	7	3.19	3.196			
9	11		3.406	3.40		
1	39			3.55		
7	4			3.59		
6	2			3.61	3.61	
4	5				3.80	
2	8					4.35
Significance		0.995	0.055	0.054	0.098	1.000

WAS							
Species	***n***	**1**	**2**	**3**	**4**	**5**	**6**
5	11	1.17					
10	7	1.28	1.28				
8	10		1.43	1.43			
9	11			1.46	1.46		
3	5			1.49	1.49		
7	4			1.50	1.50		
1	39				1.61	1.61	
6	2					1.72	
4	5					1.75	
2	8						2.61
Significance		0.572	0.239	0.929	0.184	0.330	1.000

APPENDIX 7.4 continued

WOUC								
Species	*n*	**1**	**2**	**3**	**4**	**5**	**6**	**7**
5	11	3.57						
8	10	3.72	3.72					
10	7	3.89	3.89	3.89				
3	5		3.95	3.95	3.95			
7	4			4.07	4.07			
9	11				4.25	4.25		
6	2					4.45		
1	39					4.55	4.55	
4	5						4.80	
2	8							6.20
Significance		0.080	0.464	0.770	0.113	0.112	0.314	1.000

WIUM1						
Species	*n*	**1**	**2**	**3**	**4**	**5**
8	10	2.39				
5	11	2.39				
3	5	2.45				
10	7		2.65			
1	39		2.71			
4	5		2.73	2.73		
9	11		2.78	2.78		
6	2			2.91	2.91	
7	4				3.01	
2	8					3.54
Significance		0.986	0.429	0.071	0.816	1.000

WUPM4						
Species	*n*	**1**	**2**	**3**	**4**	**5**
5	11	0.77				
8	10	0.81	0.81			
10	7	0.86	0.86			
7	4	0.89	0.89	0.89		
3	5		0.91	0.91		
9	11		0.92	0.92		
1	39			1.01	1.01	
6	2			1.02	1.02	
4	5				1.09	
2	8					1.43
Significance		0.093	0.278	0.113	0.634	1.000

APPENDIX 7.4 continued

LUM1							
Species	*n*	1	2	3	4	5	6
5	11	1.06					
8	10	1.16	1.16				
10	7	1.17	1.17				
7	4		1.25	1.25			
9	11		1.26	1.26			
3	5			1.29	1.29		
6	2			1.33	1.33	1.33	
1	39				1.39	1.39	
4	5					1.44	
2	8						1.98
Significance		0.119	0.229	0.452	0.279	0.085	1.000

MAOT							
Species	*n*	1	2	3	4	5	6
5	11	2.40					
10	7	2.66	2.66				
8	10		2.70				
3	5		2.87	2.87			
9	11		2.87	2.87			
7	4		2.90	2.90			
6	2			2.99	2.99		
1	39				3.24	3.24	
4	5					3.49	
2	8						4.57
Sig.		0.062	0.081	0.886	0.075	0.065	1.000

BH						
Species	*n*	1	2	3	4	5
5	11	4.40				
10	7	4.42				
8	10	4.60	4.60			
3	5	4.69	4.69			
9	11		4.76			
1	39		4.86	4.86		
4	5		4.88	4.88		
6	2			5.10	5.10	
7	4				5.24	
2	8					6.54
Sig.		0.056	0.069	0.178	0.903	1.000

CHAPTER 8

SYNTHESIS

8.1 OVERVIEW OF THE STUDY

Chromosomal GTG-band characters (Chapter 2) were used to support the proposed elevation to generic rank of *Neoromicia*. The presence of the same three Robertsonian fusion chromosomes (7/11, 8/9, 10/12) in *Hypsugo nanus sensu lato* indicated the move to the genus *Neoromicia*. Gross bacular morphology (small triangular or medium to large elongated) also supported the separation of *N. rendalli, N. capensis, N. zuluensis* and *N.* cf. *melckorum* from *Eptesicus*, leaving *E. hottentotus* as the only true *Eptesicus* occurring in southern Africa (Chapter 2). Bacular morphology, however, was not suitable for phylogeny estimates above the species level for taxa with medium to large elongated bacular, although it still allowed species identification (albeit a character available only for male specimens).

Although it was considered that the assessments of cranial morphology with shape (Chapter 3) and traditional morphometrics (Chapters 4-7) would provide additional characters to support the genera *Neoromicia* and *Hypsugo*, none were found in these analyses. Morphometric analyses found little support for the phylogeny suggested by the GTG-chromosome banding characters due to considerable homoplasy in morphology, which appears to result from allometric and ecological constraints. Hence, the relationships suggested by cranial morphology separate the species in relation to their size.

However, the analyses of cranial morphology using shape and traditional morphometric techniques were able to document, for the first time, differences within and between species in cranial variation due to age or sex, and differences between and within a species in cranial variation across their southern African distributions. Many of the species showed considerable variation in cranial morphology across their distribution in relation to latitude and longitude. The value of an understanding of variation that exists in the morphology of a species is nowhere better demonstrated than in the mis-classification of *N. capensis* as *N. melckorum* at that point in the distribution of *N. capensis* where they are largest due to a longitudinal clinal variation in size and shape.

It is recognised that while this study has made some contribution to the resolution of differences at both generic and specific levels, and provided an insight into the extent of cranial variation within and between the taxa studied, additional taxonomic tools, such as molecular sequencing, are necessary to further resolve the taxonomy of these genera and species given that morphological differences between species are sometimes minor. This study has also identified numerous additional problems that can only be resolved through further analyses. For example, does a difference in roost type and numbers of individuals in a roost influence sexual dimorphism within *N. capensis*?; what causes geographic variation within species such as *E. hottentotus* and *N. africanus* where the variation is not related to latitude and/or longitude?; how much has the historical distribution of the species affected patterns of geographic variation?; which ecological constraints influence inter-specific cranial homoplasy?; and why are the type specimens of *H. anchietae* and *N. africanus fouriei* so distinct from other specimens identified as *H. anchietae* and *N. africanus*?

8.2 REVISED IDENTIFICATION KEY TO SOUTHERN AFRICAN GENERA AND SPECIES

Includes elements of the identification keys in Meester *et al.* (1986) that are still valid. $2n$ = diploid number; FN = fundamental number.

Generic identification key

1. Larger external and cranial size (see Tables 8.1 and 8.2), for example larger forearm length (> 48.0 mm) and condylo-incisor length (> 16.0 mm); small triangular bacular; 2n = 50, FN = 48 .... ***Eptesicus***

\- Smaller external and cranial size (see Tables 8.1 and 8.2); elongated, 'stick-like' bacular; variable diploid number (2n = 26 - 42) .... **2.**

2. Presence of Robertsonian fusion chromosomes 7/11, 8/9, 10/12. .... ***Neoromicia***

\- Absence of Robertsonian fusion chromosomes 7/11, 8/9, 10/12. .... **3.**

3. Robertsonian fusion of chromosomes 11 and 12............. ***Pipistrellus***

\- Absence of Robertsonian fusion of chromosomes 11 and 12. Distinct morphological (Horacek and Hanak, 1986), and allozyme characteristics (Ruedi and Arletaz, 1991). .... ***Hypsugo***

Species identification key

Genus *Eptesicus*

1. Larger external and cranial size (see Tables 8.1 and 8.2), for example larger forearm length (> 48.0 mm) and condylo-incisor length (> 16.0 mm); small triangular bacular; 2n = 50, FN = 48 .... ***Eptesicus hottentotus***

Genus *Neoromicia*

1. Wing membranes white or translucent............................. ***Neoromicia rendalli***

\- Wing membranes dark .... **2.**

2. First upper incisor markedly bifid; greyish brown above and white below. Broad inter-orbital width (3.94-4.70 mm), and width between the inner surfaces of the upper first molar teeth (2.75-3.36 mm), extremes of ranges overlap with *N. capensis* and *N.* cf. *melckorum*, but larger than *N. africanus* and *N. zuluensis* (see Tables 8.1 and 8.2). .... ***Neoromicia rueppellii***

\- First incisor not, or scarcely bifid, dorsal and ventral colour not distinctly separated into greyish brown and white, usually some shade of brown.... **3.**

3. Outer upper incisor more than half the length of the inner upper incisor, forehead strongly concave, tragus hatchet-shaped. May be separated from *N. zuluensis* using discriminant function score calculation (see Table 7.14 and Figure 7.22). Smaller condylo-incisor length (< 12.00 mm) than *N. capensis* and *N.* cf. *melckorum*....... ***Neoromicia africanus***

\- Outer upper incisor not more than half the length of the inner upper incisor, forehead not strongly concave. .... **4.**

4. Chromosome FN = 48. May be separated from *N. capensis* using discriminant function score calculation (see Table 7.12 and Figure 7.20). Smaller overall size than *N.* cf. *melckorum* (see Tables 8.1 and 8.2); for example, smaller forearm length (< 31.5 mm) and condylo-incisor length (< 12.5 mm)................................. ***Neoromicia zuluensis***

\- Chromosome FN = 50... **5.**

5. Chromosome $2n$ = 32. May be separated from *N.* cf. *melckorum* using discriminant function score calculation (see Table 7.9 and Fig. 7.17). .... ***Neoromicia capensis***

\- Chromosome $2n$ = 40... ***Neoromicia* cf. *melckorum***

Genus *Pipistrellus*

1. Usually darker, dorsal hair tip colour blackish-brown; dorsal pelage length slightly longer (ca. 5 mm). Associated with forest habitats. Overall larger cranial and external size (see Tables 8.1 and 8.2), measurements that overlap the least are length of the third metacarpal (28.86-33.20 mm), braincase breadth (6.28-7.08 mm), and length between the condylar and coronoid processes of the mandible (2.70-3.16 mm). Discriminant score using pair-wise DFA with *P. rusticus* of 12 cranial measurements -0.068 to 4.068 (mean = 2.149) (Table 7.10; Fig. 7.18) .... ***Pipistrellus hesperidus***

\- Usually paler, dorsal hair tip colour reddish-brown; dorsal pelage length slightly shorter (ca. 4 mm). Associated with savanna habitats. Overall smaller cranial and external size (see Tables 8.1 and 8.2) measurements that overlap the least are length of the third metacarpal (23.17-28.91 mm), braincase breadth (5.85-6.56 mm), and length between the condylar and coronoid processes of the mandible (2.29-2.95 mm). Discriminant score using pair-wise DFA with *P. hesperidus* of 12 cranial measurements 4.492 to -2.660 (mean = -3.582) (Table 7.10; Fig. 7.18) .... ***Pipistrellus rusticus***

Genus *Hypsugo*

1. Absence of Robertsonian fusion of chromosomes 11 and 12. Distinct morphological (Horacek and Hanak, 1986), and allozyme characteristics (Ruedi and Arletaz, 1991). .... ***Hypsugo anchietae***

8.2.1 General note about identification of species

All four genera have dorsal and ventral pelage that shows two colours along the hair shaft. See Kearney and Seamark (2004 - Appendix I) for use of this character to indicate a misidentified specimen in a collection. Bacular morphology can be used to identify males to any of the southern African species within these three genera (see Figure 2.1). However, the bacular morphology of *P. hesperidus* and *P. rusticus* are very similar, as are those of *N. capensis* and *N.* cf. *melckorum*.

8.3 ACCOUNTS OF SPECIES EXAMINED

8.3.1 *Eptesicus*

Genus ***EPTESICUS*** **Rafinesque, 1820**

1820. *Eptesicus* Rafinesque, Annals of Nature: 2. *Eptesicus melanops* Rafinesque = *Vespertilio fuscus* Beauvois, from North America.
1829. *Cnephaeus* Kaup, Skizzirte Entwicklungs-Geschichte...der Europäischen Thierwelt 1: 103. *Vespertilio serotinus* Schreber, from France.
1837. *Noctula* Bonaparte, Iconografia della fauna italica 1: fasc. 21. Noctula serotina Bonaparte = *Vespertilio serotinus* Schreber, from France.
1856. *Cateorus* Kolenati, Allgemeine Deutsche naturhistorische Zeitung (2) 2: 131. *Vespertilio serotinus* Schreber, from France.
1858. *Amblyotus* Kolenati, Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien 29: 252. *Amblyotus atratus* Kolenati = *Vespertilio nilssonii* Keyserling & Blasius, from Sweden.
1866. *Pachyomus* Gray, Annals and Magazine of Natural History (3) 17: 90. *Scotophilus pachyomus* Tomes, from India = *Vespertilio serotinus* Schreber.
1870. *Nyctiptenus* Fitzinger, Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien 62 (1): 424. *Vespertilio smithii* Wagner = *Vespertilio hottentota* A. Smith.
1892. *Adelonycteris* H. Allen, Proceedings of the Academy of Natural Sciences of Philadelphia (1891): 466 (part). Substitute for *Vesperus* Keyserling & Blasius, 1839, which is preoccupied by *Vesperus* Latreille, 1829, and which contained species of both *Eptesicus* and *Vespertilio*.
1917. *Pareptesicus* Bianchi, Annuaire du Musée zoologique de l'Académie impériale des sciences de St. Pétersbourg 21: lxxvi. *Vesperugo pachyotis* Dobson, from Assam.
1917. *Rhyneptesicus* Bianchi, Annuaire du Musée zoologique de l'Académie impériale des sciences de St. Pétersbourg 21: lxxvi. *Vesperugo nasutus* Dobson, from west India.
1931. *Tuitatus* Kishida & Mori, Zoological Magazine, Tokyo 43: 372-391. *Nomen nudum*.
1943. *Vespadelus* Troughton, Furred Animals of Australia 2nd edn: 348. *Eptesicus pumilus* Gray, from Australia. Based on *Vespadelus* Iredale & Troughton, Australian Museum Memoirs 6: 95, 1934. a *nomen nudum*. See Hill (Mammalia 30: 306, 1966) on the status of this name.
1943. *Registrellus* Troughton, Furred Animals of Australia 2nd edn: 349. *Pipistrellus regulus* Thomas, from Australia. See Hill (Mammalia 30: 306, 1966) on the status of the status of this name.

Eptesicus hottentotus **(A. Smith, 1833)**

1833. *Vespertilio hottentota* A. Smith, South African Quarterly Journal 2: 59. Uitenhage and Albany, eastern Cape Province; restricted to Uitenhage by Ellerman *et al.* (1953).
1840. *Vespertilio megalurus* Temminck, Monographies de mammalogie 2: 206. Interior of South Africa.
1849. *Vespertilio minutus* A. Smith, Illustrations of the Zoology of South Africa, Mammals: pl. 51 and text. Not Vespertilio minutus Montagu, 1808; not Vespertilio minuta Temminck, 1840.
1855. *Vespertilio smithii* Wagner, in Schreber's Säugthiere, Supplementband 5: 747, footnote. South Africa. For status see Roberts (1951).
1938. *Scotophilus angusticeps* Shortridge & Carter, Annals of the South African Museum 32: 282. Hex River Estate, 16 km north of Citrusdal, Western Cape Province.
1942. *Eptesicus megalurus pallidior* Shortridge, Annals of the South African Museum 36: 37. Goodhouse, Orange River, Little Namaqualand, Northern Cape Province. Valid as a subspecies (Meester *et al.*, 1986)
1946. *Eptesicus hottentotus bensoni* Roberts, Annals of the Transvaal Museum 20: 305. Ntcheu, Malawi. Valid as a subspecies (Meester *et al.*, 1986).
1986. *Eptesicus hottentotus portavernus* Schlitter & Aggundey, 1986. Kenya, Rift Valley Province, Naivasha.

Type material examined. None examined in this study.

Distribution. Patchy distribution in western Namibia, Zimbabwe, Mozambique, Lesotho, and in the following Provinces in South Africa, in the west of the Northern Cape and Western Cape, Eastern Cape, Free State, KwaZulu-Natal, Mpumalanga, Limpopo and North-West.

Geographic variation (subspecies). These analyses confirmed the lack of geographic variation and hence the lack of subspecies distinction between *E. h. pallidior* and *E. h. hottentotus* as indicated by Schlitter and Aggundey (1986). These analyses also found overlap between the Lesotho and KwaZulu-Natal populations of *E. h. bensoni* and *E. h. hottentotus*, suggesting the subspecies of *E. h. bensoni* needs reconsideration. The shape analysis identified a stepped cline in the variation of centroid size with specimens from Zimbabwe and Limpopo Province in South Africa being smaller than the other specimens from South Africa, Lesotho and Namibia, which was significantly correlated with latitude and longitude with size increasing in localities to the south and west. The traditional morphometric analysis identified a size change across the distribution that was not significantly correlated with latitude or longitude, where the largest specimens were from Algeria in the Western Cape, the Namibian, Lesotho and KwaZulu-Natal specimens were generally intermediate in size, and the specimens from the Limpopo Province in South Africa and Zimbabwe were smallest.

Diagnosis (Table 8.1). Small triangular bacula, as in Fig 2.1; $2n = 50$, FN = 48; largest species of all three genera in southern Africa, in all 12 cranial measurements, and most external measurements, other than hind foot length and tragus breadth.

Specimens examined (Fig. 8.1). See Appendices 2.1; 2.2; 3.1; 5.1; 6.1.

8.3.2 *Hypsugo*

Genus ***HYPSUGO* Kolenati, 1856**

1856. *Hypsugo* Kolenati, Allgemeine Deutsche naturhistorische Zeitung (2)2: 131. *Vespertilio maurus* Blasius, from the central Alps = *Vespertilio savii* Bonapart, from Pisa, Italy; and *Vesperugo krascheninikowii* Eversmann, from Russia.

***Hypsugo anchietae* (Seabra, 1900)**

1900. *Vesperugo anchieta* Seabra, Journal de Sciencias mathematicas, physicas e naturaes, Lisboa (2) 6: 26, 120. Cahata, 12°20'S, 14°50'E, Angola.

Type material examined. Syntype BM6.1.3.1 skull measured. Syntype BMGC1900-538 skull measured but not included in this analysis due to missing measurements.

Distribution. Scattered, sparse distribution in Zimbabwe, and in South Africa in Mpumalanga and KwaZulu-Natal Provinces. Known from as far south in the KwaZulu-Natal Province as Umkomaas. Two specimens from Limpopo Province previously identified as *H. anchietae* were re-identified as *P. rusticus* (TM40287 and TM40291).

Geographic variation (subspecies). There was a significant negative correlation with latitude indicating an overall north to south clinal pattern of variation of increasing size in the 12 cranial measurements of *H. anchietae* in southern Africa.

Diagnosis (Table 8.2). Bacular shape as in Fig 2.1; $2n = 26$, FN = 32.

Comparison with difficult to distinguish related species. Forearm length smaller (< 32.5 mm) than *N. rendalli*, *N. rueppellii*, *N.* cf. *melckorum*, *E. hottentotus*. Condylo-incisor length (< 13.5 mm) smaller than *N.* cf. *melckorum*, *E. hottentotus*. Condylo-incisor length (> 12.0 mm) larger than *N. africanus*. Post-orbital width smaller (< 3.8 mm) than *N. rendalli*, *N. rueppellii*, *E. hottentotus*. Otherwise, ranges of all 12 cranial and nine external measurements overlap with *N. capensis*, *N. zuluensis*, *P. hesperidus*, and *P. rusticus*.

May be separated from the following similar species using discriminant function score calculations: *P. hesperidus* (Table 7.8; Fig. 7.16); *N. zuluensis* (Table 7.11; Fig. 7.19).

Specimens examined (Fig. 8.2). See Appendices 2.1; 2.2; 3.1; 5.1; 6.1; 7.1.

8.3.3 *Neoromicia*

Genus ***NEOROMICIA* Roberts, 1926**

1867. *Alobus* Peters, Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin: 707. *Vespertilio temminckii* Cretzschmar, from Dongola, Sudan = *Vespertilio rueppellii* Fischer. Not of Leconte, 1856.
1906. *Rhinopterus* Miller, Proceedings of the Biological Society of Washington 19: 85. *Glauconycteris floweri* De Winton, from the Sudan. Valid as a subgenus.
1907. *Scabrifer* G.M. Allen, Bulletin of the Museum of Comparative Zoology at Harvard College 52: 46. Substitute for *Rhinopterus* Miller; not *Rhinoptera* Kuhl.
1925. *Neoromica* Roberts, Annals of the Transvaal Museum 11: 245. *Eptesicus zuluensis* Roberts.
1946. *Vansonia* Roberts, Annals of the Transvaal Museum 20: 304. *Pipistrellus venayi* Roberts,

Table 8.1 External and cranial measurements (Meas) for *Eptesicus hottentotus* examined. SD = standard deviation; *n* = sample size. See the material and methods section of Chapter 5 for an explanation of the measurement codes.

Meas	*n*	Mean	SD	Range
External				
TOT	5	129.6	7.3	120.0-136.0
T	10	54.0	5.4	46.0-65.0
TL	12	48.22	4.46	38.27-53.67
HFL	10	10.8	1.4	9.0-13.0
HF	15	9.59	0.73	8.60-10.77
FAL	5	51.6	1.8	49.0-54.0
FA	15	49.55	1.96	46.63-52.63
E	10	18.3	1.2	17.0-20.0
TIB	15	19.19	1.38	17.31-21.32
TMETA	15	48.70	2.71	43.59-53.05
TRL	15	8.71	0.64	7.66-9.97
TRB	15	2.07	0.27	1.45-2.47
Cranial				
CIL	42	19.05	0.78	16.99-20.07
BH	42	6.54	0.28	5.94-7.17
ZB	42	11.16	0.50	10.09-12.36
BB	42	9.05	0.33	8.42-9.82
POW	42	4.35	0.22	3.94-4.91
WFM	42	4.36	0.19	3.89-4.84
WAS	42	2.62	0.19	2.24-3.00
WOUC	42	6.20	0.36	5.40-6.92
WIUM1	42	3.54	0.19	3.05-3.97
WUPM4	42	1.45	0.15	1.19-1.97
LUM1	42	1.97	0.12	1.73-2.27
MAOT	42	4.58	0.29	4.02-5.19

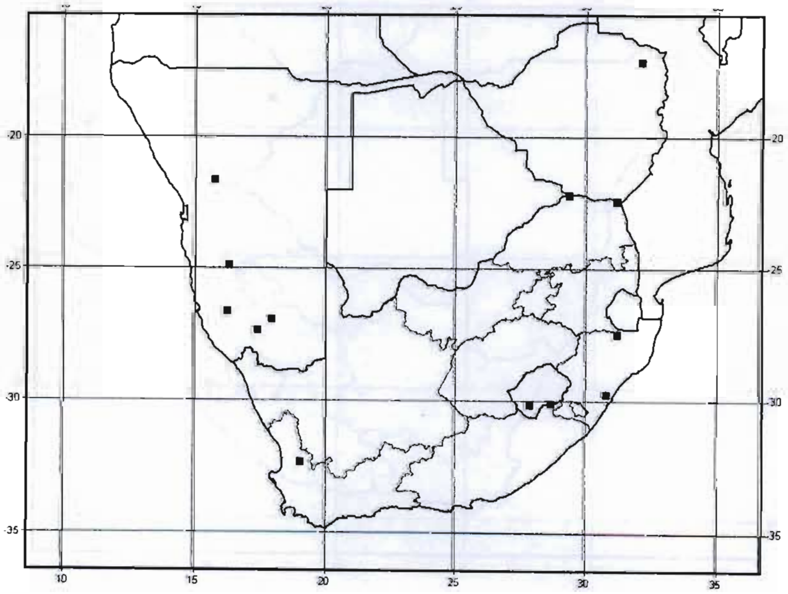


Figure 8.1 Distribution in southern Africa of *Eptesicus hottentotus* specimens included in this study.

Table 8.2 External and cranial measurements (Meas) for *Hypsugo anchietae* examined. SD = standard deviation; *n* = sample size. See the material and methods section of Chapter 5 for an explanation of the measurement codes.

Meas	*n*	Mean	SD	Range
External				
TOT	6	81.8	3.4	78.0-87.0
T	6	35.3	2.7	32.0-39.0
TL	6	35.41	2.02	33.72-38.77
HFL	6	6.3	0.4	6.0-7.0
HF	8	6.09	0.41	5.56-6.80
FAL	6	30.9	1.2	29.0-32.0
FA	7	30.06	1.52	28.42-31.56
E	6	11.2	1.0	10.0-13.0
TIB	6	11.13	0.69	10.60-12.29
TMETA	8	30.40	1.43	27.34-31.80
TRL	8	5.26	0.37	4.79-5.77
TRB	8	1.69	0.48	1.24-2.63
Cranial				
CIL	12	12.52	0.29	12.12-13.01
BH	12	4.69	0.13	4.46-4.90
ZB	12	7.23	0.31	6.92-7.98
BB	12	6.53	0.10	6.38-6.75
POW	12	3.60	0.11	3.34-3.77
WFM	12	3.14	0.11	2.97-3.32
WAS	12	1.52	0.16	1.32-1.83
WOUC	12	3.99	0.17	3.69-4.33
WIUM1	12	2.46	0.08	2.29-2.60
WUPM4	12	0.90	0.10	0.78-1.09
LUM1	12	1.29	0.04	1.22-1.36
MAOT	12	2.87	0.12	2.70-3.05

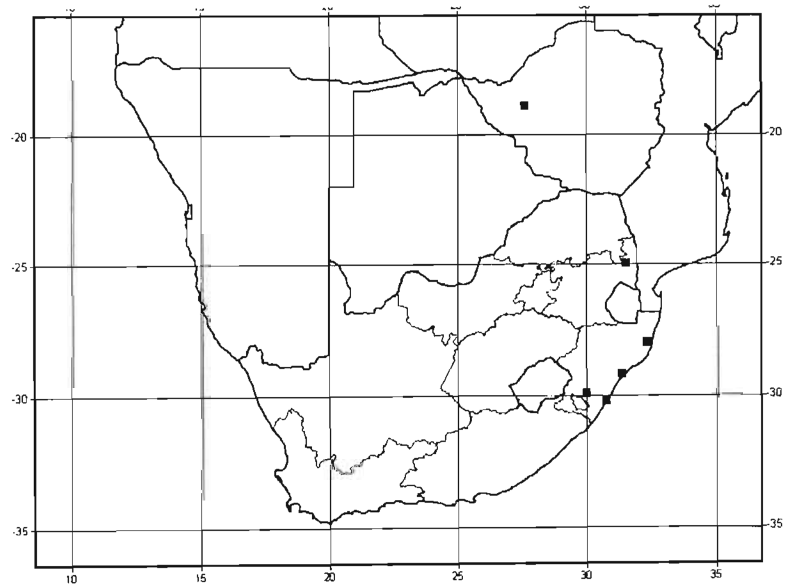


Figure 8.2 Distribution in southern Africa of *Hypsugo anchietae* specimens included in this study.

a subspecies of *Vespertilio rueppellii* Fischer. Valid as a subgenus.

***Neoromicia capensis* (A. Smith, 1829)**
1829. *Vespertilio capensis* A. Smith, Zoological Journal 4: 435. Cape Province. Restricted to Grahamstown, Eastern Cape, by Roberts (1951).
1840. *Vespertilio minuta* Temminck, Monographies de mammalogie 2: 209. Cape of Good Hope. Not *Vespertilio minutus* Montagu, 1808.
1889. *Vesperus damarensis* Noack, Zoologische Jahrbücher, systematik 4: 213. Omburu and Golabie, Damaraland, Namibia.
1905. *Vespertilio capensis gracilior* Thomas & Schwann, Proceedings of the Zoological Society, London 1: 257. Eshowe, Zululand, Natal.
1908. *Scabrifer notius* G.M. Allen, Bulletin of the Museum of Comparative Zoology, Harvard 52: 46. Cape Town, Western Cape Province.
1919. *Eptesicus melckorum* Roberts, Annals of the Transvaal Museum 6: 113. Kersefontein, Berg River, Western Cape Province.
1932. *Eptesicus capensis nkatiensis* Roberts, Annals of the Transvaal Museum 15: 16. Nkate, northern Botswana.

Type material examined. Lectotype *Vespertilio capensis* BM48.6.12.1.81 skull measured. Holotype *Vespertilio capensis gracilior* BM4.8.31.3 skull measured. Holotype *Eptesicus melckorum* TM2283 skull measured; all four adult paratypes (taken from the roost at the same time were measured but only three had all measurements and were included in the analysis – TM2280, TM2281, TM2284. Holotype *Eptesicus capensis nkatiensis* TM6549 skull measured.

Distribution. Widespread distribution in Zimbabwe, Botswana, Namibia, South Africa, and Lesotho.

Geographic variation (subspecies). Of the southern African taxa analysed, this species showed the greatest degree of variation in cranial morphology across their distribution. Cranial morphology was negatively correlated with latitude and longitude, such that size and shape increase from localities in the north-east to the localities in the south-west. This variation in cranial morphology does not support the subspecies identified by Thorn (1988) or Koopman (1994).

Diagnosis (Table 8.3). Medium-size elongated, 'stick-like' bacular, as in Fig 2.1; $2n = 32$, FN = 50.

Comparison with difficult to distinguish related species. Largest range of all 12 cranial and nine external measurements due to geographic variation in size, overlaps most species (other than *E. hottentotus*). Larger condylo-incisor length (> 12.0 mm) than *N. africanus*. Otherwise, ranges of all 12 cranial and nine external measurements overlap with the other species.

May be separated from the following similar species using discriminant function score calculations: *N.* cf. *melckorum* (Table 7.9; Fig. 7.17); *N. zuluensis* (Table 7.12; Fig. 7.20); *P. hesperidus* (Table 7.13; Fig. 7.21).

Specimens examined (Fig. 8.3). See Appendices 2.1; 2.2; 3.1; 4.1; 5.1; 6.1; 7.1.

Neoromicia.* cf. *melckorum *sensu* Rautenbach *et al.* (1993)
Still being formally described by Dr Duane Schlitter (pers. comm.)

Distribution. Limited records from Zimbabwe and north-eastern part of Limpopo Province in South Africa.

Geographic variation (subspecies). None identified between the two areas analysed.

Diagnosis (Table 8.4). Medium-size elongated, 'stick-like' bacular, of shape as in Fig 2.1; $2n = 40$, FN = 50 (Rautenbach *et al.*, 1993).

Comparison with difficult to distinguish related species. Smaller forearm length (< 40.0 mm), and condylo-incisor length (< 16.0 mm) than *E. hottentotus*. Larger forearm length (> 36.0 mm) than *H. anchietae*, *N. rueppellii*, *N. africanus*, *N. zuluensis*, *P. hesperidus* and *P. rusticus*. Larger condylo-incisor length (> 14.1 mm) than *H. anchietae*, *N. africanus*, *N. rendalli*, *N. rueppellii*, *N. zuluensis*, *P. hesperidus* and *P. rusticus*. Ranges of all 12 cranial and nine external measurements overlap with *N. capensis*.

May be separated from *N. capensis* using discriminant function score calculations (Table 7.9; Fig. 7.17).

Specimens examined (Fig. 8.4). See Appendices 2.2; 3.1; 5.1; 6.1.

Table 8.3 External and cranial measurements (Meas) for *Neoromicia capensis* examined. SD = standard deviation; *n* = sample size. See the material and methods section of Chapter 5 for an explanation of the measurement codes.

	n	Mean	SD	Range
External				
TOT	189	87.5	6.1	70.0-112.0
T	232	34.2	3.4	23.0-45.0
TL	157	30.95	2.92	23.23-37.95
HFL	232	7.9	1.1	5.0-10.0
HF	224	6.79	0.69	4.80-8.78
FAL	179	34.5	2.0	29.0-39.0
FA	228	33.93	1.96	28.66-38.24
E	232	12.0	1.6	8.0-15.0
TIB	191	11.41	0.82	8.85-14.24
TMETA	223	31.44	1.89	26.68-37.27
TRL	223	5.85	0.71	3.72-7.37
TRB	226	1.56	0.23	1.09-2.38
Cranial				
CIL	342	13.75	0.57	12.19-15.25
BH	342	4.84	0.21	4.07-5.46
ZB	342	7.91	0.34	6.79-8.93
BB	342	6.98	0.27	6.28-7.74
POW	342	3.65	0.17	3.15-4.14
WFM	342	3.54	0.18	2.97-4.09
WAS	342	1.61	0.13	1.19-1.93
WOUC	342	4.55	0.22	3.92-5.19
WIUM1	342	2.69	0.15	2.29-3.21
WUPM4	342	1.0	0.1	0.8-1.4
LUM1	342	1.38	0.09	1.12-1.70
MAOT	342	3.23	0.22	2.29-3.82

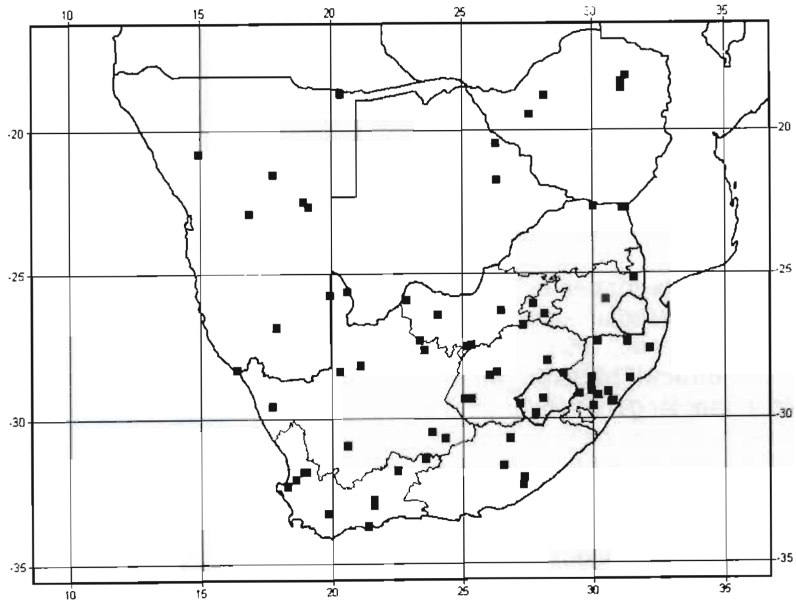


Figure 8.3 Distribution in southern Africa of *Neoromicia capensis* specimens included in this study.

Table 8.4 External and cranial measurements (Meas) for *Neoromicia* cf. *melckorum* examined. SD = standard deviation; *n* = sample size. See the material and methods section of Chapter 5 for an explanation of the measurement codes.

Meas	*n*	Mean	SD	Range
External				
TOT	3	99.0	2.7	96.0-101.0
T	3	40.3	3.2	38.0-44.0
TL	13	34.93	2.59	29.65-37.53
HFL	3	7.3	0.6	7.0-8.0
HF	15	6.46	0.48	5.74-7.51
FAL	3	37.3	1.2	36.0-38.0
FA	17	36.08	1.33	33.68-38.70
E	3	11.0	1.0	10.0-12.0
TIB	15	12.77	0.54	12.07-14.14
TMETA	15	35.11	1.01	33.24-37.24
TRL	15	6.59	0.27	6.23-7.17
TRB	15	1.85	0.13	1.68-2.06
Cranial				
CIL	22	14.64	0.28	14.23-15.09
BH	22	4.87	0.18	4.43-5.20
ZB	22	8.49	0.27	7.98-8.84
BB	22	7.31	0.21	6.90-7.68
POW	22	3.73	0.16	3.46-4.04
WFM	22	3.80	0.15	3.48-4.06
WAS	22	1.75	0.09	1.63-1.88
WOUC	22	4.78	0.14	4.48-5.09
WIUM1	22	2.72	0.11	2.49-2.95
WUPM4	22	1.09	0.060	0.95-1.19
LUM1	22	1.44	0.06	1.32-1.59
MAOT	22	3.48	0.16	3.21-3.87

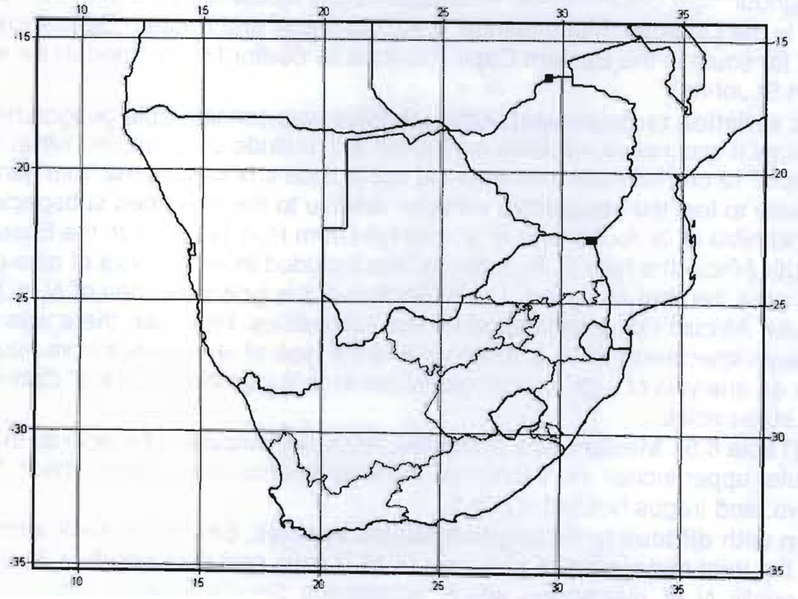


Figure 8.4 Distribution in southern Africa of *Neoromicia* cf. *melckorum* specimens included in this study.

Neoromicia africanus (Rüppell, 1842)

1842. *Vespertilio pipistrellus* var. *africanus* Rüppell, Museum Senckenbergianum 3: 156. Shoa Province, Ethiopia (Koopman 1975: 399-400); if correct, *africaus* would have priority; see also Swanepoel *et al.* (1980: 158). Kock (*in litt.*) regards africanus as a composite species, with lectotype representing *nanus*, paralectotype representing *kuhlii*, and possibly antedated by *Vespertilio hesperida* Temminck, 1840.

1852. *Vespertilio nanus* Peters, Reise nach Mossambique, Säugethiere: 63, pl. 16, fig. 2. Inhambane, Mozambique.

1870. *Vesperugo pusillulus* Peters, Jornal de sciencias mathematicas, physicas e naturaes, Lisboa (1)3: 124. Loanga, Angola.

1888. *Vesperugo stampflii* Jentink, Notes from the Leyden Museum 10: 54. Farmington River, Liberia.

c. 1889. *Vesperus pusillus* Noack, Zoologische Jahrbücher, Systematik 4: 216. Boma, Zaire River mouth, Zaire.

c. 1889. *Vesperugo pagenstecheri* Noack, Zoologische Jahrbücher, Systematik 4: 220. Neotonna, Zaire River Mouth, Zaire.

1900. *Pipistrellus minusculus* Miller, Proceedings of the Washington Academy of Science 2: 647, fig. 43. Mount Coffee, Liberia.

1911. *Pipistrellus culex* Thomas, Annals and Magazine of Natural History (8)7: 458. Kabwir, northern Nigeria.

1912. *Pipistrellus helios* Heller, Smithsonian Miscellaneous Collections 60(12): 3. Merelle Water, 48 km south of Mount Marsabit, Kenya. Possibly a valid subspecies (Koopman 1975).

1913. *Pipistrellus nanus australis* Roberts, Annals of the Transvaal Museum 4: 67. Port St Johns, Transkei. Not *Pipistrellus hesperus australis* Miller, 1897.

1917. *Pipistrellus abaensis* J.A. Allen, Bulletin of the American Museum of Natural History 37: 442. Aba, north-eastern Zaire.

1926. *Pipistrellus fouriei* Thomas, Proceedings of the Zoological Society, London: 288. Ukualukasi, north-western Ovamboland, Namibia.

2001. *Pipistrellus africanus meesteri* Kock, Acta Chiropterologica 3(2): 245-248. Port St Johns, Transkei.

Type material examined. Syntypes *Vespertilio nanus* BM7.1.1.421 and BM7.1.1.422 skulls measured, only the latter included in the analysis due to missing measurements on the former. Holotype *Pipistrellus nanus australis* nom nov. *Pipistrellus africanus meesteri* TM1076 skull measured. Holotype *Pipistrellus fouriei* BM25.12.4.20 skull measured.

Distribution. Broad distribution across the most northern parts of Namibia and Botswana, scattered throughout most of Zimbabwe, in Swaziland and Mozambique and in the eastern parts of South Africa in the Limpopo, Mpumalanga, KwaZulu-Natal, and Eastern Cape Provinces. Known from as far south in the Eastern Cape Province as Bedford (confirmed as far south in this analysis as Port St Johns).

Geographic variation (subspecies). Although there was considerable geographic variation in cranial morphology it was not significantly correlated with latitude or longitude. While the intra-specific analysis of 12 cranial measurements did not include any specimens from north-western Namibia to be able to test the geographic variation relative to the described subspecies from north-western Namibia *N. a. fouriei* and *N. a. meesteri* from Port St Johns in the Eastern Cape Province of South Africa, the type of *N. a. fouriei* was included in an analysis of nine cranial measurements of all the taxa analysed. The distinction of the type specimen of *N. a. fouriei* from the other southern African indicates support for this subspecies. However, there was little distinction between specimens of *N. a. meesteri* and the type of *N. a. nanus* from Inhambane in Mozambique in an analysis of eight cranial measurements suggesting a lack of distinction between these subspecies.

Diagnosis (Table 8.5). Medium-size elongated, 'stick-like' bacular, of shape as in Fig 2.1; $2n$ = 36, FN = 50; outer upper incisor more than half the length of the inner upper incisor; forehead strongly concave; and tragus hatchet shaped.

Comparison with difficult to distinguish related species. Smaller forearm length (< 31.5 mm), length of the third metacarpal of phalange (< 31.0 mm), and tibia length (< 31.0 mm) than *N. rendalli*, *N. rueppellii*, *N.* cf. *melckorum*, and *E. hottentotus*. Smaller condylo-incisor skull length (<

Table 8.5 External and cranial measurements (Meas) for *Neoromicia africanus* examined. SD = standard deviation; n = sample size. See the material and methods section of Chapter 5 for an explanation of the measurement codes.

Meas	*n*	Mean	SD	Range
External				
TOT	19	75.84	4.43	68.0-83.0
T	22	34.5	3.1	29.0-39.0
TL	25	29.76	2.27	24.04-34.34
HFL	22	6.1	0.8	4.0-7.0
HF	31	5.27	0.64	4.25-6.57
FAL	20	30.3	1.9	27.0-31.5
FA	31	29.59	1.12	27.34-31.18
E	22	10.2	1.1	8.0-12.0
TIB	30	11.06	0.68	9.66-12.28
TMETA	30	28.26	1.22	24.68-30.66
TRL	31	4.35	0.56	3.47-6.10
TRB	31	1.30	0.34	0.73-2.22
Cranial				
CIL	89	11.12	0.26	10.46-11.93
BH	89	4.33	0.19	3.82-4.74
ZB	89	6.46	0.20	5.85-6.87
BB	89	6.09	0.15	5.74-6.44
POW	89	3.41	0.09	3.18-3.68
WFM	89	3.15	0.11	2.90-3.40
WAS	89	1.18	0.09	0.97-1.43
WOUC	89	3.53	0.19	2.90-3.97
WIUM1	89	2.37	0.11	2.09-2.66
WUPM4	89	0.76	0.10	0.54-0.97
LUM1	89	1.06	0.05	0.92-1.15
MAOT	89	2.41	0.11	2.09-2.65

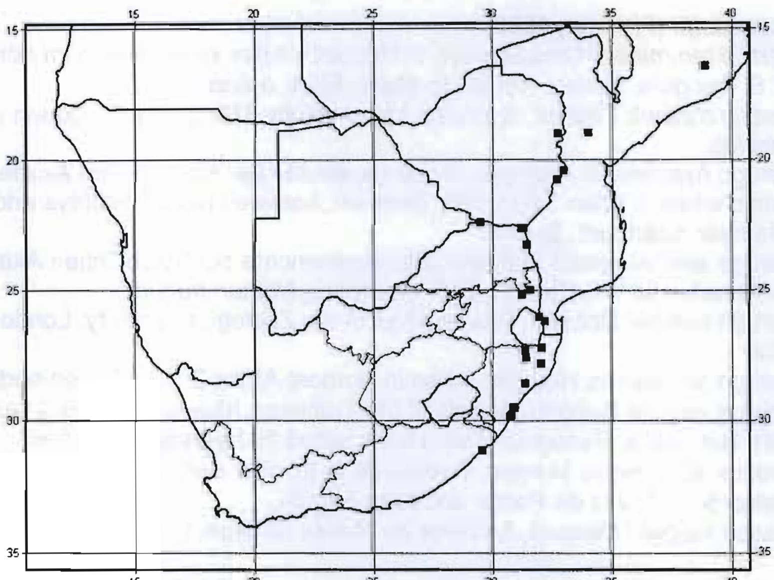


Figure 8.5 Distribution in southern Africa of *Neoromicia africanus* specimens included in this study.

12.0 mm) than *H. anchietae*, *N. capensis*, *N. rendalli*, *N. rueppellii*, *N.* cf. *melckorum*, and *E. hottentotus*. Smaller zygomatic breath (< 6.9 mm) than *P. hesperidus*, *H. anchietae*, *N. capensis*, *N. rendalli*, *N. rueppellii*, *N.* cf. *melckorum*, and *E. hottentotus*. Ranges of all 12 cranial and nine external measurements overlap with *N. zuluensis* and *P. rusticus*.

May be separated from the following similar, small species using discriminant function score calculations: *N. zuluensis* (Table 7.14; Fig. 7.22); *P. rusticus* (Table 7.15; Fig. 7.23).

Specimens examined (Fig. 8.5). See Appendices 2.1; 2.2; 3.1; 4.1; 5.1; 6.1; 7.1.

***Neoromicia rendalli* (Thomas, 1889)**

1889. *Vesperugo* (*Vesperus*) *rendalli* Thomas, Annals and Magazine of Natural History (6)3: 362. Bathurst, Gambia.
1911. *Eptesicus phasma* G.M. Allen, Bulletin of the Museum of Comparative Zoology, Harvard 54: 327. Meru River, northern Guaso Nyiro, Kenya. May be valid as a subspecies (Koopman 1975).
1917. *Eptesicus faradjius* J.A. Allen, Bulletin of the American Museum of Natural History 37: 444. Faradje, north-eastern Zaire. Synonym of *phasma* (Koopman 1975).

Type material examined. Holotype BM89.3.2.3 and paratype PM89.12.12.1 skulls measured.

Distribution. Known from few well-watered localities, in the northern parts of the Okavango Delta in Bostwana, Mana Pools on the Zambezi in Zimbabwe, south of the Zambezi in Mozambique, with a southerly locality in South Africa on the northern KwaZulu-Natal Province coast.

Geographic variation (subspecies). All but one of the 12 cranial measurements of the Zimbabwe specimen were smaller relative to the mean for the South African specimens. However, only further analyses with more specimens from additional localities will clarify whether this is a reflection of clinal longitudinal variation in size between the localities, possibly associated with change in altitude, in which specimens from south-easterly localities are larger than specimens from north-westerly localities.

Diagnosis (Table 8.6). Large size elongated, 'stick-like' bacular, as in Fig 2.1 ; 2n = 38, FN = 50; wing membranes white or translucent.

Comparison with difficult to distinguish related species. Larger third metacarpal of phalange (> 34.0 mm) than *H. anchietae*, *N. africanus*, *N. zuluensis*, *P. hesperidus* and *P. rusticus*. Larger forearm length (> 33.0 mm) than *H. anchietae*, *N. africanus*, *N. zuluensis* and *P. rusticus*. Larger condylo-incisor length (> 12.6 mm) than *N. africanus*, *N. zuluensis* and *P. rusticus*. Smaller condylo-incisor length (> 14.0 mm) than *N.* cf. *melckorum* and *E. hottentotus*.

Ranges of all 12 cranial and nine external measurements overlap with *N. rueppellii* and *N. capensis*.

Specimens examined (Fig. 8.6). See Appendices 2.1; 2.2; 3.1; 6.1; 7.1.

***Neoromicia rueppellii* (Fischer, 1829)**

1827. *Vespertilio temminckii* Cretzschmar, in Rüppell's Atlas zu der Reise im nördlichen Afrika: 17, pl. 6. Dongola, Sudan. Not of Horsfield, 1824, a *Scotophilus*.
1829. *Vespertilio rüppellii* Fischer, Synopsis Mammalium: 109. Dongola, Sudan (renaming of *temminckii*).
1866. *Vesperugo hypoleucus* Fitzinger, Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien 54(1): 546. Sennaar, between Kéréri, Halfäye and Surerát, on the Nile near Khartoum, Sudan.
1866. *Vesperugo sennaariensis* Fitzinger, Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien 54 (1): 546. Khartoum. *Nomen nudum*.
1875. *Vesperugo pulcher* Dobson, Proceedings of the Zoological Society, London: 471. Zanzibar.
1877. *Vesperugo senarensis* Heuglin, Reise in Nordost-Afrika 2: 32. *Nomen nudum*.
1932. *Pipistrellus vernayi* Roberts, Annals of the Transvaal Museum 15: 16. Maun, Ngamiland, northern Botswana. Recognized as a subspecies by Meester *et. al.*,1986.
1933. *Pipistrellus leucomelas* Monard, Bulletin de la Société des sciences naturelles de Neuchâtel 57: 47. Vila da Ponte, southern Angola.
1935. *Scotozous rüppellii* Monard, Archivos do Museu Bocage, Lisboa 6: 31.

Type material examined. Holotype *Pipistrellus vernayi* TM6546 skull measured.

Table 8.6 External and cranial measurements (Meas) for *Neoromicia rendalli* examined. SD = standard deviation; *n* = sample size. See the material and methods section of Chapter 5 for an explanation of the measurement codes.

Meas	*n*	Mean	SD	Range
External				
TOT	5	95.2	4.1	91.0-100.0
T	5	39.2	2.2	37.0-42.0
TL	1	28.3	-	-
HFL	4	7.5	1.3	6.0-9.0
HF	5	7.19	0.54	6.51-7.91
FAL	5	35.6	2.0	33.0-37.9
FA	5	34.89	1.78	32.93-37.59
E	4	11.5	0.6	11.0-12.0
TIB	5	11.10	0.84	10.03-11.99
TMETA	5	35.35	0.87	34.06-36.28
TRL	3	4.05	1.27	2.66-5.16
TRB	5	1.52	0.20	1.29-1.75
Cranial				
CIL	5	13.47	0.50	12.75-13.95
BH	5	5.14	0.08	5.04-5.25
ZB	5	8.32	0.38	7.77-8.71
BB	5	7.11	0.27	6.74-7.37
POW	5	4.06	0.19	3.80-4.24
WFM	5	3.69	0.15	3.47-3.82
WAS	5	1.77	0.19	1.58-2.04
WOUC	5	4.56	0.17	4.28-4.68
WIUM1	5	3.01	0.17	2.75-3.21
WUPM4	5	1.02	0.06	0.95-1.12
LUM1	5	1.36	0.04	1.29-1.39
MAOT	5	3.11	0.20	2.80-3.31

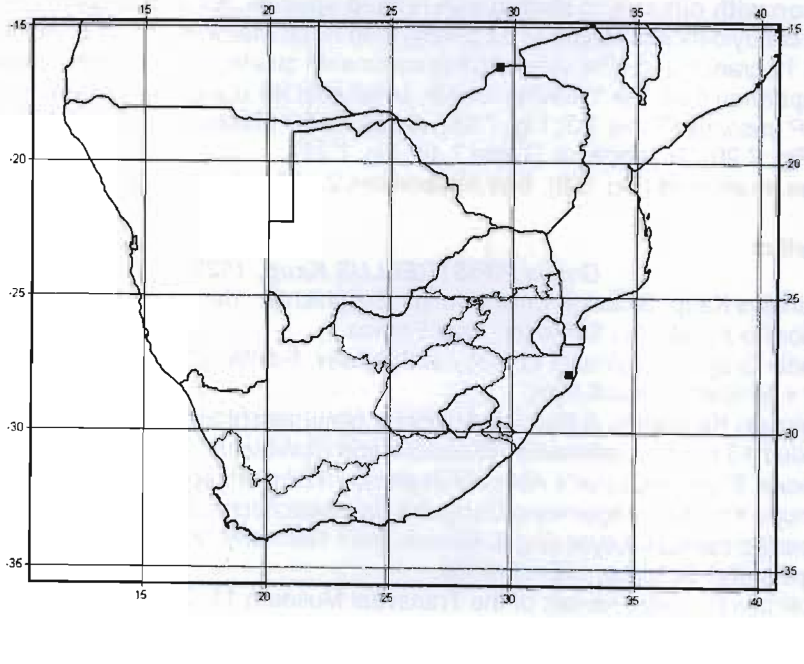


Figure 8.6 Distribution in southern Africa of *Neoromicia rendalli* specimens included in this study.

Distribution. Known from a few localities in Botswana, Zimbabwe, and north-eastern Limpopo Province and Northern Cape Provinces in South Africa.

Geographic variation (subspecies). No geographic variation was recorded in the 12 cranial measurements of *N. rueppellii* across the four localities analysed.

Diagnosis (Table 8.7). Large-size elongated, 'stick-like' bacular, as in Fig 2.1; 2*n* = 36, FN = 54 (Rautenbach *et al.*, 1993); first upper incisor markedly bifid; and distinct colour difference between dorsal (greyish brown) and ventral (white) pelage.

Comparison with difficult to distinguish related species. Larger forearm length (> 34.0 mm), and broader least inter-orbital width (> 3.94 mm) than *H. anchietae*, *N. africanus*, *N. zuluensis*, and *P. rusticus*. Larger third metacarpal of phalange (> 31.0 mm), and condylo-incisor length (> 12.5 mm) than *N. africanus*, *N. zuluensis*, and *P. rusticus*. Smaller forearm length (< 35.0 mm), and condylo-incisor length (> 14.0 mm) than *N.* cf. *melckorum* and *E. hottentotus*.

Ranges of all 12 cranial and nine external measurements overlap with *N. capensis*, *N. rendalli* and *P. hesperidus*.

Specimens examined (Fig. 8.7). See Appendices 2.2; 3.1; 5.1; 6.1.

***Neoromicia zuluensis* (Roberts, 1924)**

1924. *Eptesicus zuluensis* Roberts, Annals of the Transvaal Museum 10: 60, text-fig. I. White Umfolosi Game Reserve, Zululand, KwaZulu-Natal.

1932. *Neoromicia vansoni* Roberts, Annals of the Transvaal Museum 15: 15. Zweizwe waterhole, north of Tsotsoroga Pan, Ngamiland, northern Botswana.

Type material examined. Holotype *Eptesicus zuluensis* TM3024 skull measured. Holotype *Neoromicia vansoni* TM6553 skull measured.

Distribution. Sparsely scattered in Namibia, northern Botswana and Zimbabwe, and in South Africa in Limpopo, the eastern parts of Mpumalanga and the north-eastern parts of KwaZulu-Natal Provinces. The record from the North-West Province indicated in Friedmann and Daly (2004) could not be identified for verification of the species occurring that far west in South Africa.

Geographic variation (subspecies). Both analyses with or without additional localities showed clinal longitudinal variation in the overall size of the 12 cranial measurements of *N. zuluensis* with OTUs in the east being larger than OTUs in the west. Clinal latitudinal variation, with increasing size in more southerly OTUs, was only observed when the additional specimens from more northerly and southerly localities were added. Given that single individuals were representative of the more northerly and southerly localities, the observed pattern of latitudinal clinal change in overall size of the 12 skull measurements of *N. zuluensis* will need to be tested with additional specimens to confirm that this is not just due to outlier individuals.

Diagnosis (Table 8.8). Medium size elongated, 'stick-like' bacular as in Fig 2.1; 2*n* = 28, FN = 48.

Comparison with difficult to distinguish related species. Smaller forearm length (< 31.5 mm), smaller condylo-incisor length (< 12.5 mm) than *N.* cf. *melckorum* and *E. hottentotus*. Ranges of all 12 cranial and nine external measurements overlap with the other species.

May be separated from the following similar, small species using discriminant function score calculations: *P. rusticus* (Table 7.7; Fig. 7.15); *H. anchietae* (Table 7.11; Fig. 7.19); *N. capensis* (Table 7.12; Fig. 7.20); *N. africanus* (Table 7.14; Fig. 7.22).

Specimens examined (Fig. 8.8). See Appendices 2.1; 2.2; 3.1; 4.1; 5.1; 6.1.

8.3.4 *Pipistrellus*

Genus ***PIPISTRELLUS Kaup, 1829***

1829. *Pipistrellus* Kaup, Skizzirte Entwicklungs-Geschichte...der Europäischen Thierwelt 1: 98. *Vespertilio pipistrellus* Schreber, from France.

1838. *Romicia* Gray, Magazine of Zoology and Botany, Edinburgh 2: 495. *Romicia calcarata* Gray = *Vespertilio kuhlii* Kuhl.

1839. *Vesperugo* Keyserling & Blasius, Archiv für Naturgeschichte, Berlin 5(1): 312 (in part). Included 13 species referred to *Eptesicus* and *Pipistrellus*.

1840. *Romicius* Blyth, in Cuvier's Animal Kingdom: 75. Variant spelling of *Romicia* Gray.

1856. *Nannugo* Kolenati, Allgemeine Deutsche naturhistorische Zeitung (2)2: 131. Including *Vespertilio nathusii* Keyserling & Blasius, from Germany; *V. kuhlii* Kuhl, from Trieste, and *V. pipistrellus* Schreber, from France.

1926. *Eptesicops* Roberts, Annals of the Transvaal Museum 11: 245. *Scotohilus rusticus*

Table 8.7 External and cranial measurements (Meas) for *Neoromicia rueppellii* examined. SD = standard deviation; *n* = sample size. See the material and methods section of Chapter 5 for an explanation of the measurement codes.

Meas	*n*	Mean	SD	Range
External				
TOT	2	93.5	5.0	90.0-97.0
T	2	41.5	0.7	41.0-42.0
TL	4	32.67	3.60	28.58-37.23
HFL	2	8.5	0.7	8.0-9.0
HF	5	7.16	0.70	6.17-8.02
FAL	1	34.0	-	-
FA	5	34.79	1.57	33.00-37.02
E	2	13.0	1.4	12.0-14.0
TIB	5	13.56	1.19	11.52-14.65
TMETA	4	33.38	1.13	31.97-34.73
TRL	4	5.61	0.15	5.42-5.77
TRB	4	1.48	0.14	1.28-1.58
Cranial				
CIL	8	13.37	0.41	12.62-13.81
BH	8	5.31	0.22	4.81-5.47
ZB	8	7.80	0.28	7.31-8.11
BB	8	7.52	0.21	7.14-7.75
POW	8	4.34	0.25	3.94-4.70
WFM	8	3.59	0.16	3.36-3.83
WAS	8	1.51	0.08	1.37-1.63
WOUC	8	4.20	0.30	3.67-4.58
WIUM1	8	3.04	0.19	2.75-3.36
WUPM4	8	0.94	0.13	0.71-1.12
LUM1	8	1.26	0.07	1.18-1.39
MAOT	8	2.96	0.18	2.70-3.16

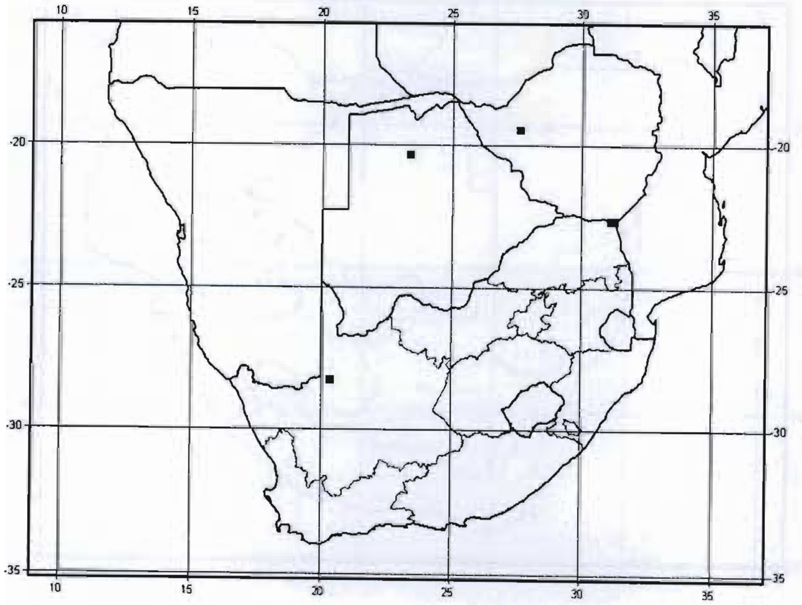


Figure 8.7 Distribution in southern Africa of *Neoromicia rueppellii* specimens included in this study.

Table 8.8 External and cranial measurements (Meas) for *Neoromicia zuluensis* examined. SD = standard deviation; *n* = sample size. See the material and methods section of Chapter 5 for an explanation of the measurement codes.

Meas	*n*	Mean	SD	Range
External				
TOT	6	79.7	3.2	74.0-82.0
T	6	35.8	2.9	31.0-40.0
TL	6	30.84	2.87	27.41-35.23
HFL	6	6.9	0.2	6.5-7.0
HF	12	5.54	0.39	5.02-6.06
FAL	3	30.2	0.8	29.5-31.0
FA	12	29.89	1.09	27.45-31.26
E	6	10.8	0.4	10.0-11.0
TIB	11	11.52	0.60	10.28-12.22
TMETA	10	29.55	0.92	27.96-30.89
TRL	12	4.96	0.52	4.29-5.91
TRB	12	1.24	0.11	1.11-1.49
Cranial				
CIL	30	11.94	0.21	11.41-12.37
BH	30	4.56	0.10	4.37-4.76
ZB	30	6.99	0.18	6.66-7.37
BB	30	6.29	0.18	5.91-6.67
POW	30	3.46	0.14	3.22-3.79
WFM	30	3.15	0.15	2.77-3.42
WAS	30	1.40	0.12	1.22-1.66
WOUC	30	3.79	0.14	3.51-4.17
WIUM1	30	2.40	0.09	2.24-2.60
WUPM4	30	0.81	0.07	0.68-0.95
LUM1	30	1.19	0.08	1.02-1.36
MAOT	30	2.72	0.09	2.60-2.95

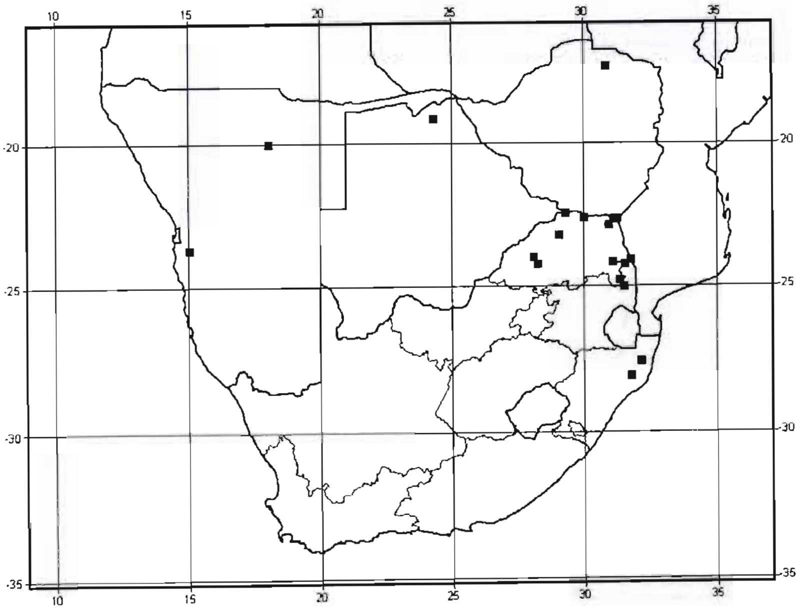


Figure 8.8 Distribution in southern Africa of *Neoromicia zuluensis* specimens included in this study.

Tomes.
1943. *Falsistrellus* Toughton, Furred Animals of Australia 2nd edn: 349. *Vespertilio tasmaniensis* Gould, from Tasmania.

***Pipistrellus hesperidus* (Temminck, 1840)**
1840. *Vespertilio hesperida* Temminck, Monographies de mammalogie 2: 392. Shewa Province, Ethiopia.
?1832. *Vespertilio platycephalus* Temminck, in Smuts's Dissertatio zoologica, enumerationem Mammalium Capensium continens: 107. Cape Town, South Africa. (Roberts 1951; however, both Allen 1939 and Ellerman *et al.* 1953 regard this taxon as unidentifiable, besides which it appears to fall outside the known distribution of the species).
1846. *Vesperugo subtilis* Sundevall, Öfversigt af Kungliga Svenska Vetenskapsakademiens Förhandlingar, Stockholm 3(4): 119. Interior of Caffraria.
1901. *Pipistrellus kuhlii fuscatus* Thomas, Annals and Magazine of Natural History 7(8): 34. Naivasha, Kenya.
1948. *Pipistrellus* (*Romicia*) *kuhlii broomi* Roberts, Special Publications of the Royal Society of South Africa, Robert Broom Commemorative Volume: 9. Malvern, Durban, Natal, according to Roberts (1948, 1951), locality confirmed by Smithers *et al.*, 1987.

Type material examined. Holotype *Pipistrellus kuhlii fuscatus* BM1.8.9.96 skull measured. Holotype *Pipistrellus* (*Romicia*) *kuhlii broomi* TM1085 skull measured.

Distribution. Easterly distribution in Zimbabwe, from the Maputo District in Mozambique, and in South Africa from Limpopo, Mpumalanga, Free State, KwaZulu-Natal and Eastern Cape Provinces. Although recorded from as far south in South Africa as King Williams Town in the Eastern Cape, this analysis only included specimens from as far south as Ngqeleni in the Eastern Cape, and even this specimen was left out of the final analysis of *P. hesperidus* because it was an outlier. The distribution in the Limpopo Province is not as widespread westerly as previously reported given the re-identification by K. Koopman (Transvaal Museum specimen records) of specimens recorded from these areas as *P. rusticus* (see Introduction for more details).

Geographic variation (subspecies). The shape morphometric analysis identified significant correlation between centroid size and latitude and longitude with size increasing in localities to the south and west. Traditional morphometric analyses identified significant clinal latitudinal variation in the overall size of the 12 cranial measurements with increasing size in more southerly localities, but no significant correlation with longitude. Although this variation in size has some resemblance to a subspecies distinction between east coast *P. h. broomi* and *P. h. subtilis* from the "Interior of Caffraria", however, the clinal variation in cranial size with latitude precludes the subspecies distinction.

Diagnosis (Table 8.9). Elongated, 'stick-like' bacular morphology as in Fig. 2.1; $2n = 42$, FN = 50.

Comparison with difficult to distinguish related species. Ranges of all 12 cranial and external measurements overlap with similar *P. rusticus*, they also share the same chromosome diploid and FN, and both have similar bacular morphologies. *Pipistrellus hesperidus* may be separated from *P. rusticus* using discriminant function score calculations (Table 7.10; Fig. 7.18) and geographic distribution, given *P. hesperidus* appears to have a more forest restricted distribution, whereas *P. rusticus* appears to be more woodland savanna specific in its distribution.

Smaller forearm length (< 35.5 mm), smaller condylo-incisor length (< 13.5 mm) than *N.* cf. *melckorum* and *E. hottentotus*. Larger zygomatic breadth (> 6.90 mm) and length between the condylar and the coronoid processes of the mandible (> 2.67 mm) than *N. africanus*. Ranges of all 12 cranial and nine external measurements overlap with the other species.

May be separated from the following similar, small species using discriminant function score calculations: *H. anchietae* (Table 7.8; Fig. 7.16); *N. capensis* (Table 7.13; Fig. 7.21).

Specimens examined (Fig. 8.9). See Appendices. 2.1; 2.2; 3.1; 4.1; 5.1; 6.1; 7.1.

***Pipistrellus rusticus* (Tomes, 1861)**
1861. *Scotophilus rusticus* Tomes, Proceedings of the Zoological Society, London: 31, 35. Damaraland; Allen (1939) records a lectotype from Olifants Vlei.

Type material examined. Lectotype *Scotophilus rusticus* BM7.1.1.419 skull measured. Paralectotype *Scotophilus rusticus* BM7.1.1.420 skull measured, but not included in this analysis

Table 8.9 External and cranial measurements (Meas) for *Pipistrellus hesperidus* examined. SD = standard deviation; *n* = sample size. See the material and methods section of Chapter 5 for an explanation of the measurement codes.

Meas	*n*	Mean	SD	Range
External				
TOT	26	82.9	4.2	70.0-91.0
T	28	33.3	2.7	25.0-38.0
TL	21	30.66	3.65	23.25-40.56
HFL	26	7.5	1.0	6.0-11.0
HF	29	6.42	0.57	5.22-7.43
FAL	28	32.7	1.0	30.6-35.0
FA	30	31.15	1.13	29.07-32.87
E	26	11.29	0.67	10.0-12.0
TIB	28	10.54	0.69	8.55-11.67
TMETA	26	31.11	1.14	28.86-33.20
TRL	28	4.97	0.44	3.87-5.57
TRB	28	1.59	0.35	1.14-2.84
Cranial				
CIL	45	12.51	0.34	11.81-13.24
BH	45	4.82	0.13	4.57-5.08
ZB	45	7.50	0.23	6.90-8.05
BB	45	6.71	0.17	6.28-7.08
POW	45	3.78	0.12	3.54-4.00
WFM	45	3.44	0.13	3.15-3.87
WAS	45	1.49	0.14	1.17-1.83
WOUC	45	4.32	0.15	4.02-4.63
WIUM1	45	2.82	0.11	2.55-3.00
WUPM4	45	0.90	0.08	0.78-1.07
LUM1	45	1.28	0.06	1.15-1.39
MAOT	45	2.92	0.12	2.70-3.16

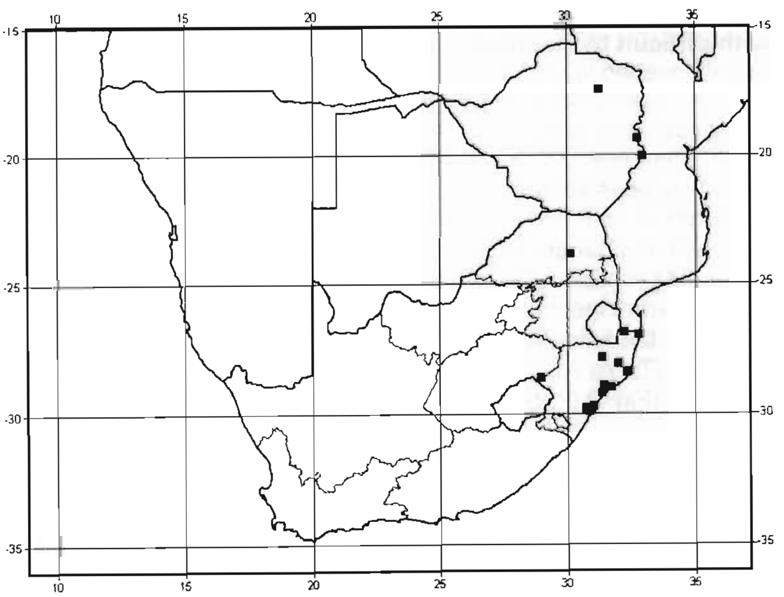


Figure 8.9 Distribution in southern Africa of *Pipistrellus hesperidus* specimens included in this study.

due to missing measurements.

Distribution. Northern parts of Namibia and Botswana, throughout most of Zimbabwe, and in the northern part of South Africa in Limpopo, Gauteng, Mpumalanga, and North-West Provinces.

Geographic variation (subspecies). Traditional morphometric analyses identified clinal latitudinal variation in the overall size of the 12 cranial measurements with increasing size in southerly localities.

Diagnosis (Table 8.10). Elongated, 'stick-like' bacular morphology as in Fig. 2.1; $2n$ = 42, FN = 50.

Comparison with difficult to distinguish related species. Ranges of all 12 cranial and nine external measurements overlap with *P. hesperidus*, they also share the same chromosome diploid and FN, and both have similar bacular morphologies. *Pipistrellus rusticus* may be separated from *P. hesperidus* using discriminant function score calculations (Table 7.10; Fig. 7.18) and geographic distribution, given *P. rusticus* appears to have a more savanna woodland restricted distribution, whereas *P. hesperidus* appears to be more forest specific in its distribution.

Smaller forearm length (< 31.5 mm) and condylo-incisor length (< 12.4 mm) than *N. rendalli*, *N. rueppellii*, *N.* cf. *melckorum*, and *E. hottentotus*. Ranges of all 12 cranial and nine external measurements overlap with the other species.

May be separated from the following similar, small species using discriminant function score calculations: *N. zuluensis* (Table 7.7; Fig. 7.15); *N. africanus* (Table 7.15; Fig. 7.23).

Specimens examined (Fig. 8.10). See Appendices 2.1; 2.2; 3.1; 5.1; 6.1; 7.1.

Table 8.10 External and cranial measurements (Meas) for *Pipistrellus rusticus* examined. SD = standard deviation; *n* = sample size. See the material and methods section of Chapter 5 for an explanation of the measurement codes.

Meas	*n*	Mean	SD	Range
External				
TOT	14	74.3	4.8	65.0-85.0
T	16	29.8	2.0	25.0-33.0
TL	20	25.19	2.68	18.93-30.54
HFL	16	6.6	0.8	5.0-8.0
HF	22	5.35	0.53	4.33-6.19
FAL	14	28.7	0.9	27.5-31.0
FA	22	27.87	1.59	25.60-31.02
E	16	10.3	0.6	10.0-12.0
TIB	22	9.11	0.90	7.29-10.81
TMETA	22	26.87	1.29	23.17-28.91
TRL	22	4.27	0.47	3.26-5.01
TRB	22	1.50	0.43	0.66-2.34
Cranial				
CIL	48	11.49	0.31	10.75-12.23
BH	48	4.39	0.17	4.07-4.89
ZB	48	6.97	0.26	6.40-7.49
BB	48	6.23	0.17	5.85-6.56
POW	48	3.53	0.13	3.23-3.80
WFM	48	3.21	0.14	2.90-3.58
WAS	48	1.33	0.15	1.17-1.94
WOUC	48	3.94	0.18	3.56-4.33
WIUM1	48	2.66	0.13	2.39-2.95
WUPM4	48	0.88	0.09	0.71-1.02
LUM1	48	1.18	0.07	1.05-1.32
MAOT	48	2.70	0.16	2.29-2.95

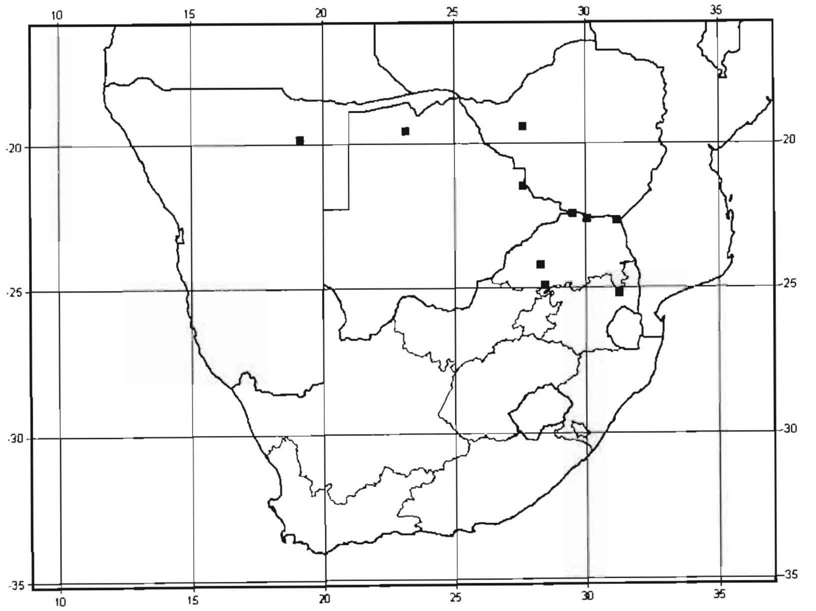


Figure 8.10 Distribution in southern Africa of *Pipistrellus rusticus* specimens included in this study.

CHAPTER 9

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APPENDIX I

PUBLICATIONS EMANATING FROM THIS STUDY

Acta Chiropterologica, 4(1): 55–76, 2002
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Systematic implications of chromosome GTG-band and bacula morphology for Southern African *Eptesicus* and *Pipistrellus* and several other species of Vespertilioninae (Chiroptera: Vespertilionidae)

Teresa C. Kearney[1, 2], Marianne Volleth[3], Giancarlo Contrafatto[4], and Peter J. Taylor[5]

[1]*Biology Department, University of Natal, Private Bag X10, Dalbridge, Durban, 4014, Republic of South Africa*
[2]*Present address: Vertebrate Department, Transvaal Museum, P.O. Box 413, Pretoria, 0001, Republic of South Africa; E-mail: kearney@nfi.co.za*
[3]*Dept. of Human Genetics, Otto-von-Guericke-University, D-39120 Magdeburg, Germany*
[4]*Biology Department, University of Natal, Private Bag X10, Dalbridge, Durban, 4014, Republic of South Africa*
[5]*Durban Natural Science Museum, P.O. Box 4085, Durban 4000, Republic of South Africa*

Phylogenetic analyses of bacular and chromosomal GTG-band characters verify the suggestion that *Eptesicus hottentotus* (A. Smith, 1833) is the only true *Eptesicus* Rafinesque, 1820 of the six southern African species (*capensis*, cf. *melckorum*, *rendalli*, *somalicus* and *zuluensis*) formerly classified as *Eptesicus*. GTG-banded chromosomes studied in *rendalli*, *zuluensis* and *capensis* confirm the affiliation of all of them to the genus *Neoromicia*; these species were previously placed in the *Pipistrellus* Kaup, 1829, subgenus *Neoromicia* based on bacular morphology. For karyological reasons, the elevation of the subgenus *Neoromicia* to generic rank is established by the presence of three Robertsonian fusion chromosomes (7/11, 8/9, 10/12) as distinguishing characters. The move of *Hypsugo nanus* and cf. *melckorum* to the genus *Neoromicia* is indicated by chromosomal analysis and bacular morphology, respectively. The close phylogenetic relationship between *Pipistrellus* cf. *kuhlii* and *P. rusticus* is shown by a shared Robertsonian fusion element (11/12).

Key words: bacula, GTG-banded chromosomes, *Eptesicus*, *Pipistrellus*, *Neoromicia*

Introduction

Differences between *Eptesicus* Rafinesque, 1820 and *Pipistrellus* Kaup, 1829, two genera of insectivorous bats of the family Vespertilionidae have long been problematic (Koopman, 1975; Horáček and Hanák, 1986). Heller and Volleth (1984) proposed that *Eptesicus* is chromosomally conservative, all species having a diploid number of 50, while *Pipistrellus* is chromosomally variable, having diploid numbers of 44 or less. At the time of Heller's and Volleth's (1984) work the only species occurring in southern Africa that had been karyotyped were *E. hottentotus* (A. Smith, 1833) and *E. capensis* (A. Smith, 1829) (Peterson and Nagorsen, 1975). *Eptesicus capensis* with a diploid number of 32 was placed in the genus *Pipistrellus*.

On the basis of bacular morphology Heller and Volleth (1984) and Hill and

Harrison (1987) suggested the *Eptesicus* and *Pipistrellus* could be distinguished from each other by *Eptesicus* having a small, triangular baculum, and *Pipistrellus* having a medium to large, 'stick-like', elongated baculum. Applying these characters, Hill and Harrison (1987) transferred all, but one southern African species of *Eptesicus* [*capensis, melckorum* Roberts, 1919, *somalicus* (Thomas, 1901), *zuluensis* Roberts, 1924 and *rendalli* (Thomas, 1889)], with an exception of *E. hottentotus*, to a new subgenus, *Neoromicia*, in the genus *Pipistrellus*. A subsequent allozyme analysis by Morales *et al.* (1991), which included several southern African species of *Eptesicus* (*hottentotus*, *capensis*, *zuluensis*, cf. *melckorum*) and *Pipistrellus* (*nanus*), showed biochemical relationships between the taxa to be consistent with the suggestions of Heller and Volleth (1984) and Hill and Harrison (1987).

Several authors (Ansell and Dowsett, 1988; Cotterill, 1996; Fenton and Rautenbach, 1998; Taylor, 2000) and at least one museum (Natural History Museum of Zimbabwe, Bulawayo) have followed the suggestions of Heller and Volleth (1984) and Hill and Harrison (1987). But for the most part the caution by Meester *et al.* (1986: 56) appears to have been followed, that until all southern African species of *Eptesicus* and *Pipistrellus* have been tested against the bacula and chromosome criteria "it would be premature to depart from established generic synonymy".

Various studies have subsequently confirmed on the basis of diploid number (from non-differential staining) that *E. rendalli*, *E. somalicus* (McBee *et al.*, 1987; Rautenbach and Fenton, 1992), *E.* cf. *melckorum* (sensu Rautenbach *et al.*, 1993), and *E. zuluensis* (Rautenbach *et al.*, 1993) all have diploid numbers less than 50.

Chromosome banding has also proved a useful source of characters, enabling Volleth and Heller (1994) to infer a phylogenetic relationship for Vespertilionidae. Two chromosomal characters, i.e., the banding pattern of chromosomes 11 and 23, were found to separate the tribes Vespertilionini and Pipistrellini. According to those characters, *Pipistrellus* (*Neoromicia*) *capensis* is a member of the tribe Vespertilionini, and not Pipistrellini. In order to prevent a polyphyletic classification for the genus *Pipistrellus*, Volleth *et al.* (2001) suggested the subgenus *Neoromicia* be elevated to generic rank, as had been done before for all other *Pipistrellus* subgenera sensu Hill and Harrison (1987) (*Hypsugo* — Horáček and Hanák, 1986; *Perimyoti* — Menu, 1984; *Vespadelus* — Volleth and Tidemann, 1991; *Falsistrellus* — Kitchener, 1986; *Arielulus* — Csorba and Lee, 1999). We follow the above-mentioned authors and treat all subgenera of *Pipistrellus* (sensu Hill and Harrison, 1987) as separate genera.

In this study, we present the first GTG-banded karyotypes of five southern African *Pipistrellus*-like species, and the outgroup *Myotis tricolor* (Temminck, 1832). We revisited bacular morphology to confirm the usefulness of this structure for identifying relationships. GTG-banded chromosomes and bacular morphology provided characters for cladistic analyses to assess inter- and intrageneric relationships among southern African *Pipistrellus*-like species.

Materials and Methods

Taxonomic Designations

We followed Volleth *et al.* (2001) in calling *Pipistrellus kuhlii*-like specimens with a diploid number of 42, *P.* cf. *kuhlii*. Both Meester *et al.* (1986) and Koopman (1993) recognised that *N. melckorum* had not been clearly distinguished from *N. capensis*. Rautenbach *et al.* (1993) in questioning the taxonomic validity of *N. melckorum* suggested it as a synonym of *N. capensis*. This suggestion was made on the basis of unpublished morphometric data, which showed a clinal variation within these species. We followed Rautenbach *et al.* (1993), in considering specimens (DM5630, DM5636) from Kersefontein (the type locality for *N. melckorum*) as *N. capensis*. Kersefontein specimens had the same chromosome number, GTG-banding pattern, and bacula size and shape as other *N. capensis* specimens.

Rautenbach *et al.* (1993) found specimens of *Pipistrellus* from the 'interior of South Africa' being intermediate in size between *N. capensis* and *E. hottentotus*, which matched the description of *N. melckorum*. These specimens have a different chromosome number (i.e., $2n = 40$) to *N. capensis* (Rautenbach and Schlitter, 1985), and allozyme results (Morales *et al.*, 1991) have shown them to be biochemically well differentiated, although closely allied to *N. capensis*. We accepted the suggestion by Rautenbach *et al.* (1993) that specimens found in northern South Africa and Zimbabwe be called *P.* cf. *melckorum*. Kearney and Taylor (1997) described a specimen of *Laephotis* Thomas, 1901 as *Laephotis* cf. *wintoni* since the validity of *L. wintoni* Thomas, 1901 in South Africa remains ambiguous.

Chromosomes

GTG-banded (Seabright, 1971) karyotypes were constructed from bone-marrow metaphase spreads (for method see Green *et al.*, 1980) of *E. hottentotus, N. capensis, N. rendalli, N. zuluensis, N. nanus, P.* cf. *kuhlii, P. rusticus* (Tomes, 1861), and *M. tricolor*, from specimens captured at various localities in South Africa (Appendix I). Chromosomes were arranged following a standardised numbering system introduced by Bickham (1979*a*) for *Myotis*, where chromosome arms instead of chromosomes are numbered. This numbering system has been used subsequently in analyses of European and Asian Vespertilionidae, including *Eptesicus* and *Pipistrellus* species, by Zima (1982), Volleth (1987), Volleth and Heller (1994), and Volleth *et al.* (2001). Since complete chromosomal arms are conserved extensively in the family, it should be possible to trace the changes that have given rise to different diploid numbers, and thus infer phylogenetic relationships. Most often the chromosome changes are due to Robertsonian rearrangements, but occasionally due to inversions and tandem fusions (Baker *et al.*, 1982; Zima, 1982; Volleth and Heller, 1994).

Seven chromosome rearrangements (see Appendix II), i.e., the presence or absence of five synapomorphic Robertsonian fusion products, the state of chromosome 11 due to a small paracentric inversion (Volleth and Tidemann, 1989; Volleth and Heller, 1994; Volleth *et al.*, 2001), and the state of the X chromosome, were used to construct a data matrix (Appendix III). Following Ando *et al.* (1977), Bickham (1979*b*), Zima (1982), Baker *et al.* (1985), and Volleth and Heller (1994) who all considered the *Myotis* karyotype, $2n = 44$, FN = 52, as closest to the hypothetical ancestral karyotype of Vespertilionidae, we used *M. tricolor* ($2n = 44$, FN = 52) as the outgroup.

Robertsonian fusion chromosomes are denoted as the fusion chromosome numbers linked by a forward slash. Tandem fusions are denoted as the fusion chromosome numbers linked by a hyphen.

Bacula

Bacula were dissected, stained (Hill and Harrison 1987), cleared in glycerin (Lidicker, 1968), and drawn (Fig. 1) for *E. hottentotus, N. capensis, N. rendalli, N. zuluensis, N.* cf. *melckorum, N. nanus, P. rusticus, P.* cf. *kuhlii, P. rueppellii*, and *Hypsugo anchietae* (Seabra, 1900). Bacula from *M. tricolor*, *Laephotis* cf. *wintoni* (sensu Kearney and Taylor, 1997), *L. namibensis* Setzer, 1971, *L. botswanae* Setzer, 1971, *Nycticeinops schlieffenii* (Peters, 1859) and *Scotophilus dinganii* (A. Smith, 1833) were also included — these are all genera within the same subfamily Vespertilioninae, as *Pipistrellus* and *Eptesicus*. Specimen details are given in Appendix I. Since bacula of different *Laephotis* species are almost identical, their results were combined as *Laephotis* spp.

For each baculum seven qualitative characters were scored, two of which were multistate (see Appendix II), and a matrix of bacula characters was created (Appendix IV). As described for the chromosome analysis above, *Myotis tricolor* was used as the outgroup.

Analyses

Data matrices of phylogenetically informative bacula and chromosome characters, and a matrix combining bacula and chromosome characters were analysed with Hennig86 (version 1.5; Farris, 1988). Character polarity was determined by the outgroup. Multistate characters were run as nonadditive. Characters were not weighted. The shortest possible trees were found using implicit enumeration (the 'ie*' command in Hennig86).

In order to assess whether there was a lack of congruence between the bacula and chromosome data sets, two measures of incongruence were used, the Mickevich-Farris incongruence metric (i_{MF}) (Kluge, 1989), and the incongruence length difference

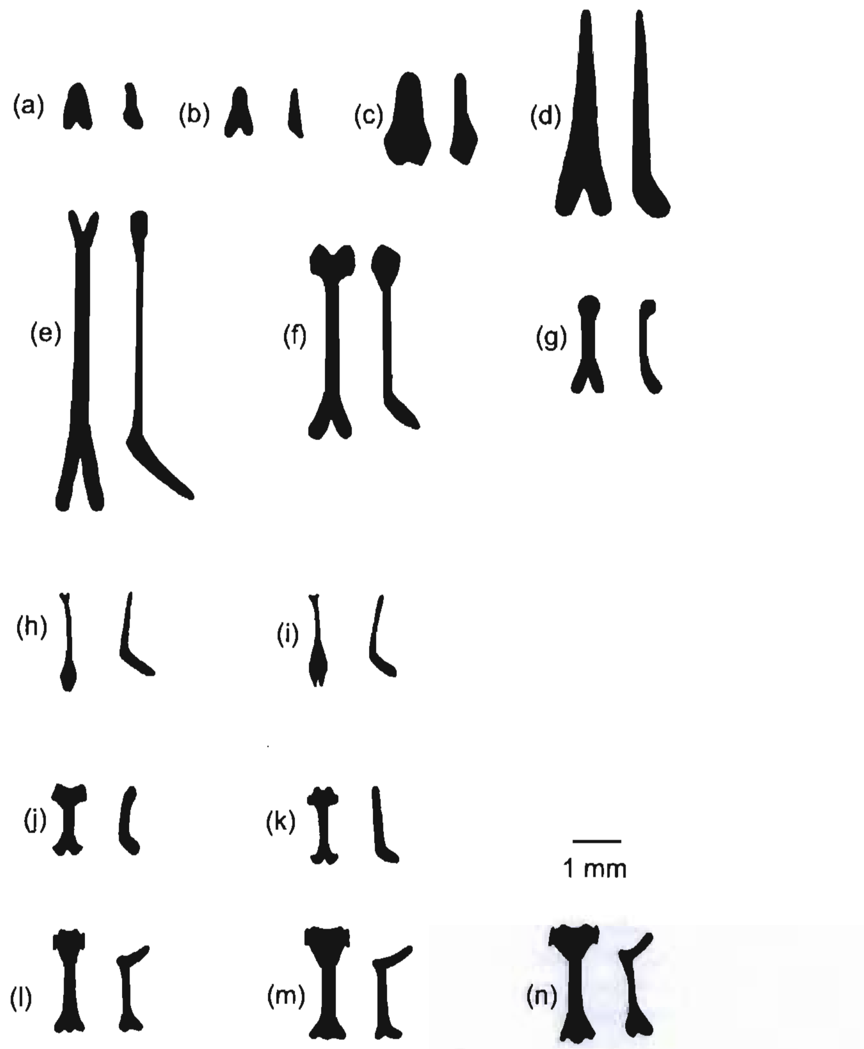

FIG. 1. Dorsal (left) and lateral (right) views of bacula from: (a) *Myotis tricolor*, (b) *Eptesicus hottentotus*, (c) *Scotophilus dinganii*, (d) *Nycticeinops schlieffenii*, (e) *Pipistrellus rueppellii*, (f) *Neoromicia rendalli*, (g) *Neoromicia nanus*, (h) *Pipistrellus rusticus*, (i) *Pipistrellus* cf. *kuhlii*, (j) *Hypsugo anchietae*, (k) *Neoromicia zuluensis*, (l) *Neoromicia capensis*, (m) *Neoromicia* cf. *melckorum*, (n) *Laephotis* cf. *wintoni*

(D_{xy}; Mickevich and Farris, 1981). The robustness of the resulting trees was assessed using the '\\x;' command in Dos-equis mode of Hennig86. This identifies the additional length gained when branches are lost, by successively collapsing nodes leading to at least two taxa in the tree. This is analogous to Bremer's branch support (Bremer, 1994), which although not useful for comparison between analyses, because it is positively correlated with the number of characters in a particular analysis, it is informative within an analysis (Bremer, 1996). As a further measure of topology support, the number of unique and unreversed synapomophies supporting each node were counted.

RESULTS

Chromosome morphology

Unfortunately bone marrow does not provide the same high GTG-band resolution that cell cultured spreads do. Thus, not all the GTG-bands obtained were of a resolution to allow detection and confirmation of possible inversions and intraspecific variations, other than a possible polymorphism in *N. rendalli*. The banding patterns of the smallest chromosomes (including the Y chromosome) were also often difficult to detect.

Myotis tricolor ($2n = 44$, FN = 52)

The GTG-banded karyotype (Fig. 2) shows three large metacentric, one small submetacentric, and 17 acrocentric autosomal pairs. GTG-banding shows the four biarmed chromosomes are composed of chromosome arms: 1/2, 3/4, 5/6 and 16/17. The X chromosome is a medium sized submetacentric.

Eptesicus hottentotus ($2n = 50$, FN = 48)

The GTG-banded karyotype of *E. hottentotus* (Fig. 3) shows all 24 pairs of autosomes are acrocentric. Chromosome arms 16 and 17 form a single acrocentric chromosome. The X chromosome is a medium sized submetacentric.

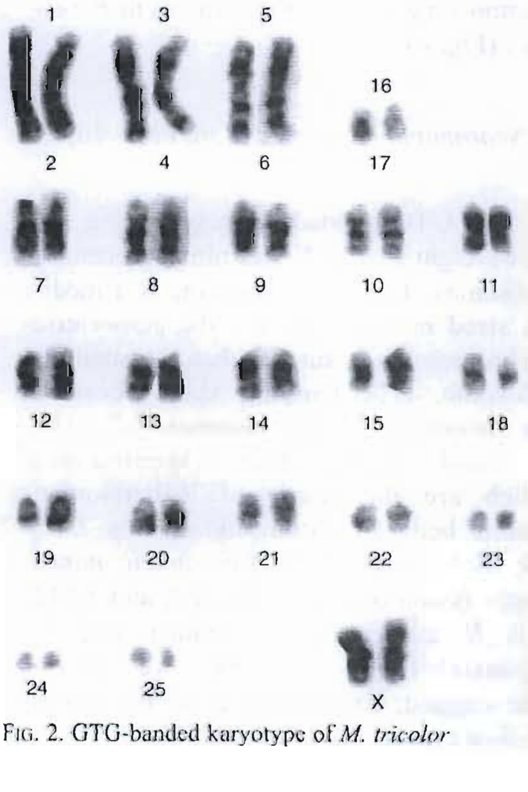

FIG. 2. GTG-banded karyotype of *M. tricolor*

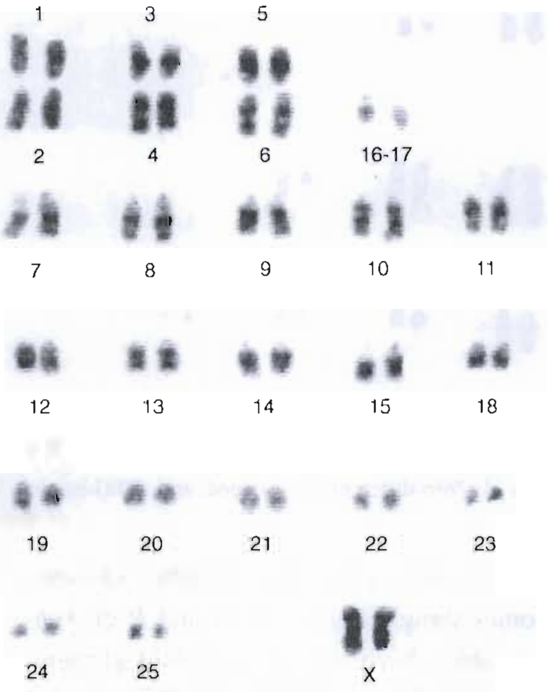

FIG. 3. GTG-banded karyotype of *E. hottentotus*

Hypsugo anchietae ($2n = 26$, FN = 32)

The non-differentially stained karyogram of a male and GTG-banded karyogram of a female *H. anchietae* (Fig. 4) show one medium sized submetacentric, one small metacentric, two large and one medium sized subtelocentric, and seven acrocentric autosomes. The X chromosome is a small metacentric, and the Y a tiny acrocentric.

Pipistrellus rusticus ($2n = 42$, FN = 50)

The GTG-banded karyotype (Fig. 5) shows five biarmed, and 15 acrocentric autosomes. The X chromosome is a medium sized metacentric, and the acrocentric Y is the same size as the smallest autosome. The five metacentric chromosomes are composed of chromosome arms: 1/2, 3/4, 5/6,

FIG. 4. Non-differentially stained and GTG-banded karyotypes of a male (left) and a female (right) of *H. anchietae*

16/17, and 11/12. GTG-banded chromosomes show that *P. rusticus* and *P.* cf. *kuhlii*, which have the same diploid chromosome number, share the same fusion pairs, including 11/12, which is not present in the basic karyotype (Fig. 6).

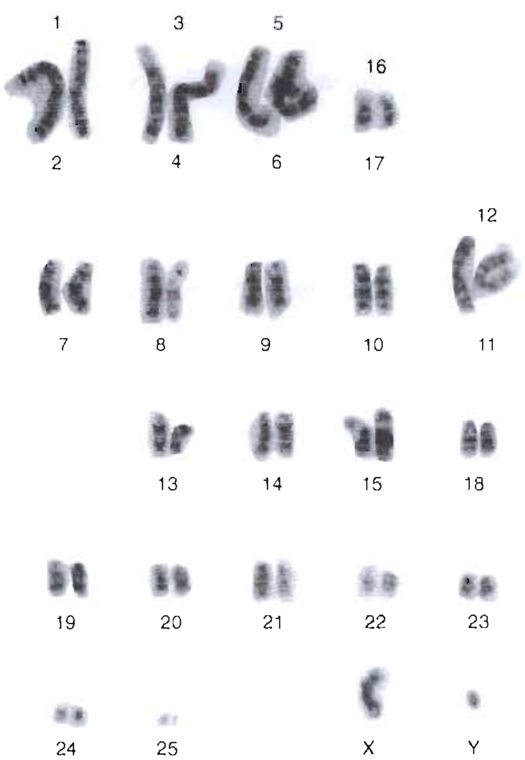

FIG. 5. GTG-banded karyotype of *P. rusticus*

Pipistrellus cf. *kuhlii* ($2n = 42$, FN = 50)

The GTG-banded karyotype (Fig. 7) shows five biarmed, and 15 acrocentric autosomes. The X chromosome is a medium sized metacentric. The biarmed chromosomes are composed of arms 1/2, 3/4, 5/6, 16/17, and 11/12. The Robertsonian fusion chromosome 11/12 is the same as in *P. rusticus* (Fig. 6).

Neoromicia nanus ($2n = 36$, FN = 50)

The GTG-banded karyotype (Fig. 8) shows eight biarmed, and nine acrocentric autosomes. The X chromosome is a medium sized metacentric, and the acrocentric Y chromosome is smaller than the smallest autosome. GTG-banding shows besides the metacentric chromosomes 1/2, 3/4, 5/6 and 16/17, four chromosomes which are the result of Robertsonian fusions between chromosome arms 7/11, 8/9, 10/12, and 13/14. *Neoromicia nanus* shares fusion of pairs 7/11, 8/9, and 10/12 with *N. zuluensis*, *N. rendalli*, and *N. capensis* (Fig. 6), and we therefore suggest transferring it to the genus *Neoromicia*.

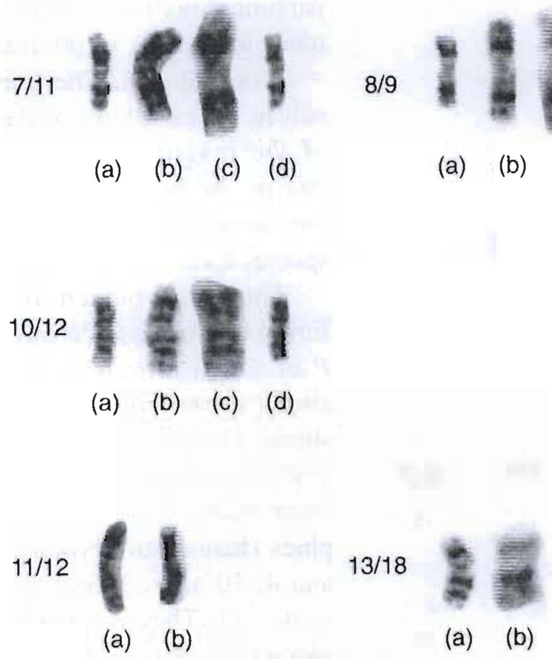

FIG. 6. Comparison of GTG-banded chromosome pairs between species: 7/11, 8/9, 10/12: (a) *Neoromicia nanus*, (b) *N. zuluensis*, (c) *N. capensis*, (d) *N. rendalli*; 11/12: (a) *Pipistrellus rusticus*, (b) *P.* cf. *kuhlii*; 13/18: (a) *N. zuluensis*, (b) *N. capensis*

Neoromicia zuluensis ($2n = 28$, FN = 48)

This GTG-banded karyotype (Fig. 9) shows 12 biarmed, and one acrocentric autosomes. The X chromosome is a medium sized subtelocentric. GTG-bands show the reduced chromosome number in *N. zuluensis* is due to Robertsonian fusion pairs between chromosome arms 7/11, 8/9, 10/12, 13/18, 14/21, 15/19, 20/22, and 23/24. *Neoromicia zuluensis* shares pairs 7/11, 8/9, 10/12 with *N. nanus*, *N. rendalli*, and *N. capensis*, and pair 13/18 with *N. capensis* (Fig. 6).

Neoromicia capensis ($2n = 32$, FN = 50)

The GTG-banded karyotype (Fig. 10) shows 10 biarmed and 5 acrocentric autosomes. The X chromosome is a medium sized metacentric. Robertsonian fusion pairs are between chromosome arms: 1/2, 3/4, 5/6, 16/17, 7/11, 8/9, 10/12, and 13/18.

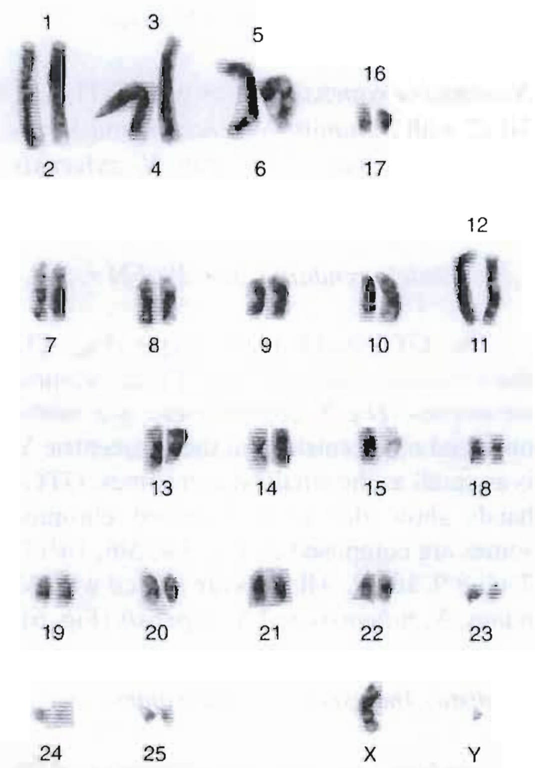

FIG. 7. GTG-banded karyotype of *P.* cf. *kuhlii*

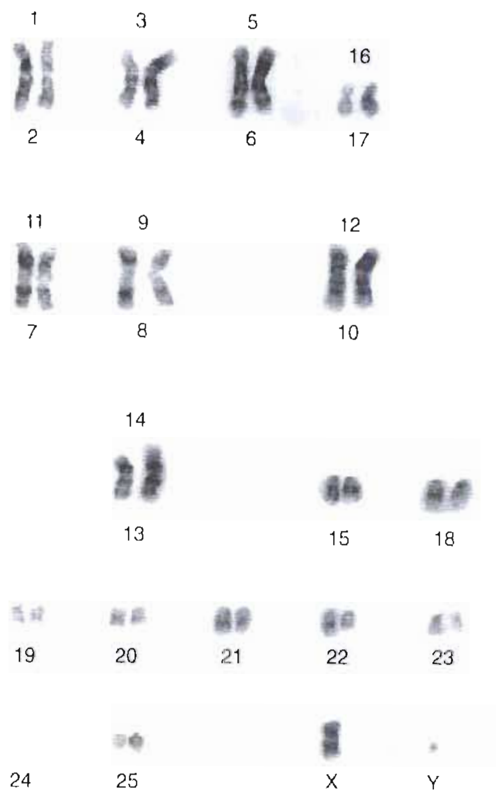

FIG. 8. GTG-banded karyotype of *N. nanus*

Neoromicia capensis shares pairs 7/11, 8/9, 10/12 with *N. nanus*, *N. rendalli*, and *N. zuluensis*, and pair 13/18 with *N. zuluensis* (Fig. 6).

Neoromicia rendalli (2*n* = 38, FN = 50)

The GTG-banded karyotype (Fig. 11) shows seven biarmed, and 11 acrocentric autosomes. The X chromosome is a medium sized metacentric, and the acrocentric Y is as small as the smallest autosomes. GTG-bands show the seven biarmed chromosomes are composed of 1/2, 3/4, 5/6, 16/17, 7/11, 8/9, 10/12. All pairs are shared with *N. nanus*, *N. zuluensis* and *N. capensis* (Fig. 6).

Cladistic Analysis of Chromosomes

Analysis of the chromosome data (Appendix III) resulted in one most parsimonious tree (length (S) = 8; consistency index (CI) = 100; retention index (RI) = 100) (Fig. 12). The tree is not fully resolved. A trichotomy at the base is made up of the outgroup *Myotis tricolor*, forming one of the branches, *E. hottentotus* forms the second branch, while the rest of the species form the third branch.

The third branch of the trichotomy forms two clades. *Pipistrellus rusticus* and *P.* cf. *kuhlii* form one clade supported by a single synapomorphy (fusion of chromosomes 11 and 12), while *N. nanus, N. rendalli, N. zuluensis*, and *N. capensis* form the other clade, as a result of four synapomorphies (fusions of chromosome 7 and 11, 8 and 4, 10 and 12, and state II of chromosome 11). The relationship between these species is not fully resolved as they form a trichotomy. However, *N. zuluensis* and *N. capensis* form the terminal clade separated

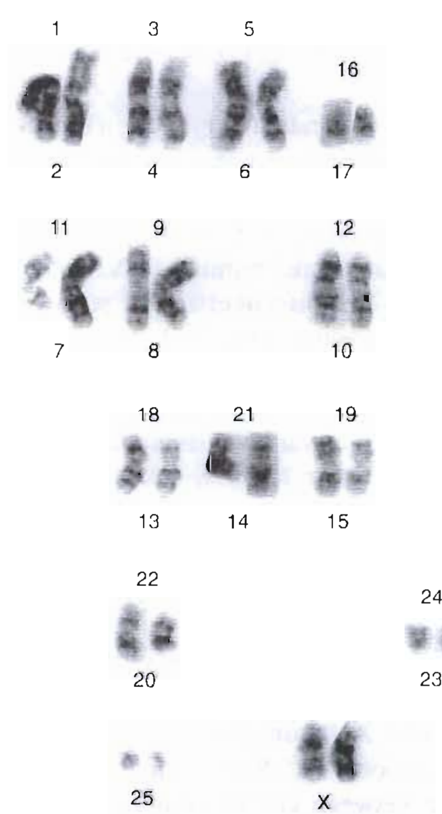

FIG. 9. GTG-banded karyotype of *N. zuluensis*

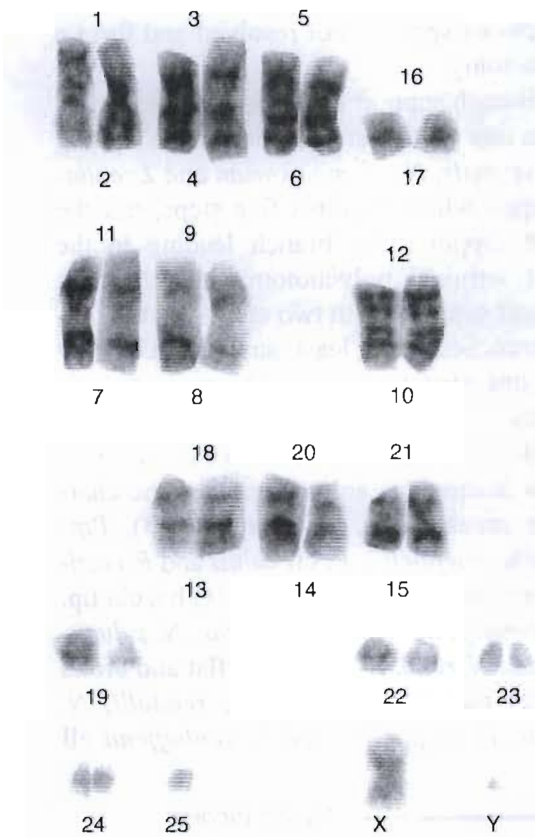

FIG. 10. GTG-banded karyotype of *N. capensis*

from *N. nanus* and *N. rendalli* due to the fusion of chromosomes 13 and 18.

As reflected by CI and RI values of 100, the steps at each node are unique and unreversed synapomorphies, and there is no homoplasy. Branch support is highest (four) for the branch linking the trichotomy, while all the other branches have the same, lower support (one).

Bacular Morphology

Although differences in bacular morphology are slight between certain species, there is considerable variation in the bacular morphology of all the species represented (Fig. 1). These variations in bacular morphology provided characters (see Appendices II and IV) for cladistic analysis.

Cladistic Analysis of Bacula

Analysis of bacular characters (Appendix IV) produced nine most parsimonious trees (S = 12; CI = 100; RI = 100). These cladograms give different alternatives for the resolution of the more terminal polychotomies.

The Nelsen consensus cladogram is not fully resolved (Fig. 13), with polychotomies in three places. The root is an unresolved polychotomy. The outgroup *M. tricolor* forms one branch, *E. hottentotus* another branch, *S. dinganii* yet another branch, while the rest of the species united by a single synapomorphy, bacula shape being medium to large, elongated and 'stick-like' (BS/1), form the forth branch.

A single synapomorphy, the tip not being distinct from the rest of the bacula (TD/1), separates *N. schlieffenii* from the next unresolved polychotomy. In the polychotomy *P. rueppellii* (Fischer, 1829) forms one branch. *Pipistrellus* cf. *kuhlii* and

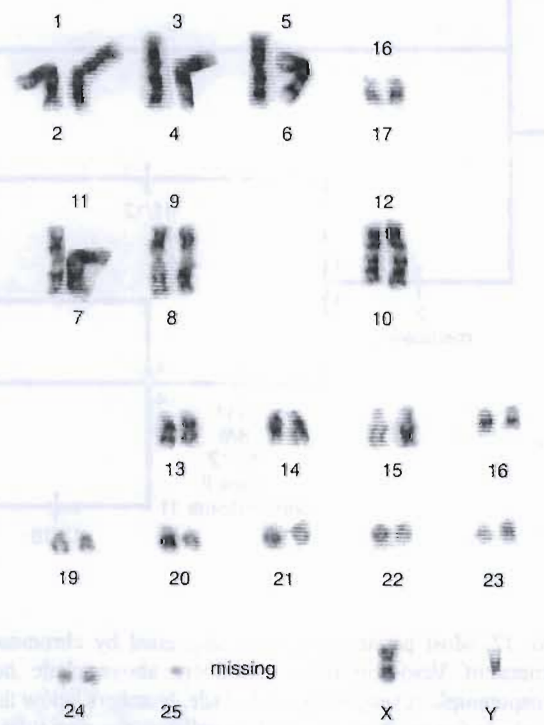

FIG. 11. GTG-banded karyotype of *N. rendalli*

P. rusticus as sister taxa separated by two synapomorphies, unique basal lobe shape (BL/4), and more than 50% of the bacula being deflected (PBD/1), form the second branch. *Neoromicia nanus* forms the third branch; while the rest of the taxa (*H. anchietae*, *N. zuluensis*, *N. rendalli*, *N. capensis*, *N.* cf. *melckorum*, and *Laephotis* spp.) form the forth branch, united by a single synapomorphy, the bacula base being narrower than the tip (TB/1). *Hypsugo anchietae*, *N. zuluensis*, *N. rendalli*, *N. capensis*, *N.* cf. *melckorum*, and *Laephotis* spp. form the third polychotomy. *Hypsugo anchietae*, *N. zuluensis*, and *N. rendalli* each form a branch, while *N. capensis*, *N.* cf. *melckorum*, and *Laephotis* spp. united by three synapomorphies, a unique tip and basal shape (TS/3 and BL/2), and a ventrally deflected tip (AT), form the forth branch. *Neoromicia capensis*, *N.* cf. *melckorum*, and *Laephotis* spp. are not resolved and form a trichotomy.

Branch support of different nodes varies from one to five steps. The branch uniting *N. capensis*, *N.* cf. *melckorum* and *Laephotis* spp., which requires five steps, has the most support. The branch leading to the most terminal polychotomy has the next highest support, with two steps. All the other branches have least support, requiring just one step to collapse the tree at those points.

Both multistate characters (TS and BL) show homoplasy among some of the character states (TS/1, TS/2, and BL/3). *Pipistrellus rueppellii, P.* cf. *kuhlii* and *P. rusticus* all have a 'V' shaped (TS/1) bacula tip. *Neoromicia nanus*, *H. anchietae*, *N. zuluensis*, and *N. rendalli* all have a flat and broad (TS/2) bacula tip. While *N. rendalli*, *N. nanus*, *P. rueppellii*, and *N. schlieffenii* all

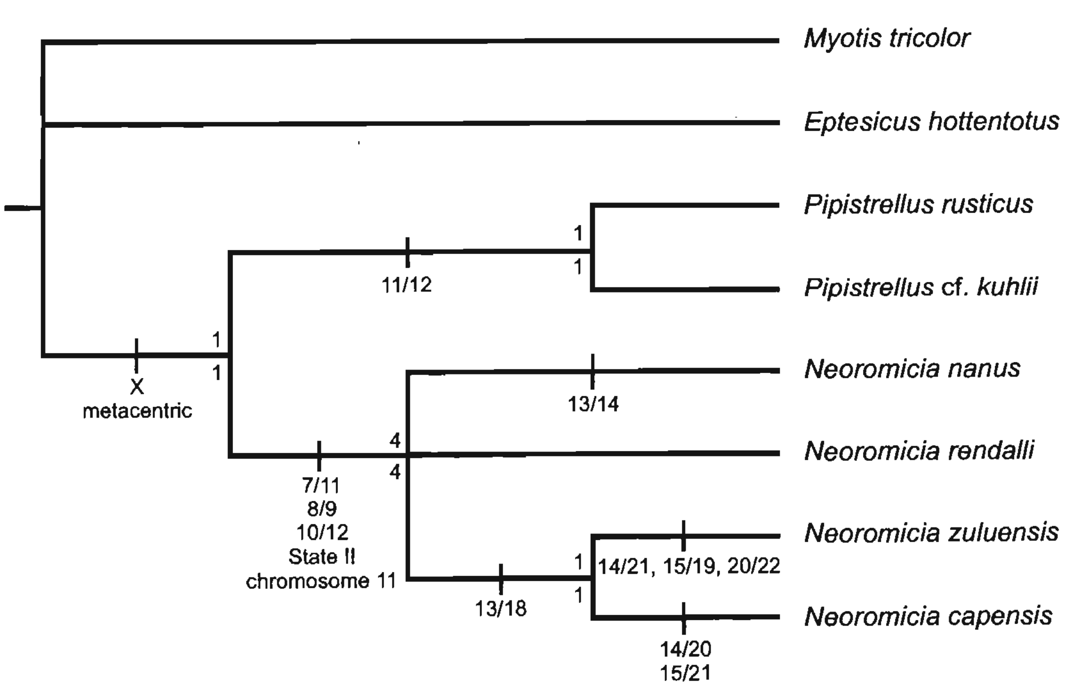

FIG. 12. Most parsimonious tree suggested by chromosome GTG-band characters, for seven taxa, of four genera of Vespertilioninae. Numbers above clade nodes are the number of unique and unreversed synapomorphies supporting each clade. Numbers below the clade nodes are branch support values (which is the number of extra steps required to collapse the particular node). Synapomorphic characters are shown below branches (abbreviations explained in Appendix II)

have evenly wide and 'V' shaped basal lobes (BL/3).

Cladistic Analysis of Combined Chromosome and Bacula Datasets

Only taxa for which there was information about both bacula and chromosomes were included. Analysis of the combined chromosome and bacula data set produced a single most parsimonious tree (S = 20; CI = 100; RI = 100). The cladogram topology (Fig. 14) is almost the same as the single most parsimonious chromosome cladogram. The combination of the two data sets however resolves the more terminal trichotomy present in the chromosome cladogram. The same characters show homoplasies as in the bacula tree. Branch support of the cladogram varies from one to four steps. The most and least supported branches are similar to those in the chromosome cladogram. Both measures of character incongruence due to disparity between

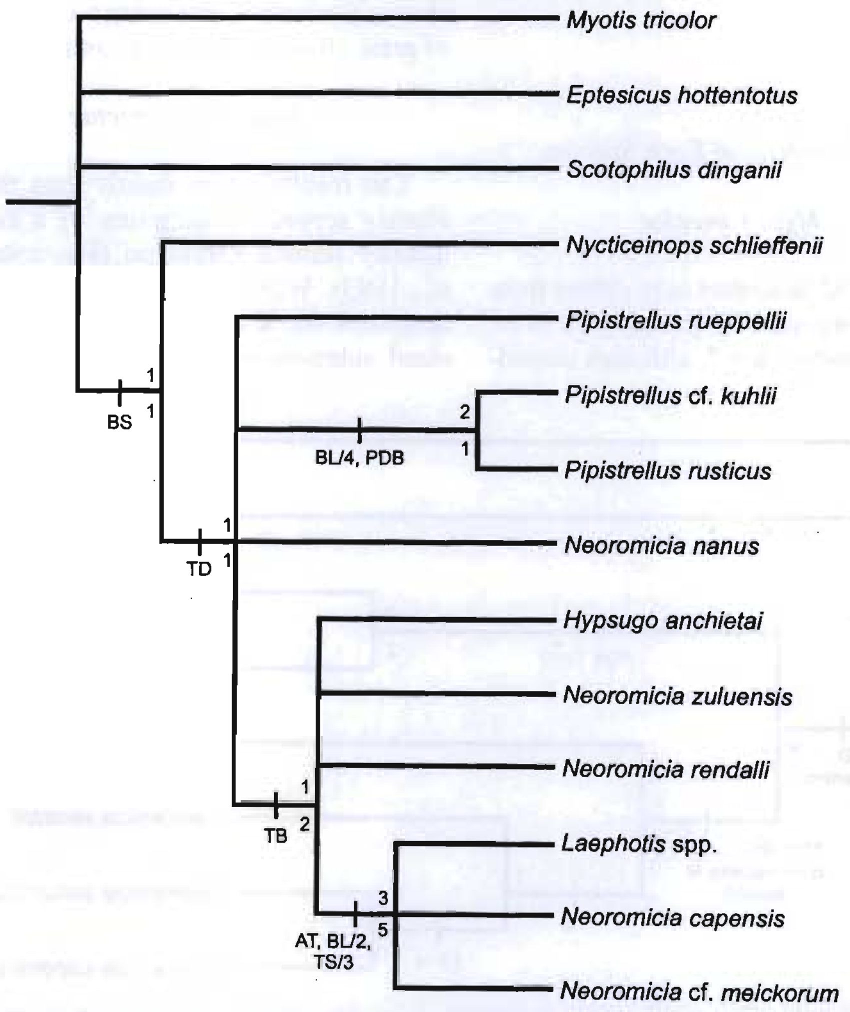

FIG. 13. A Nelsen consensus tree of nine most equally parsimonious trees suggested by bacula characters for fourteen taxa, of eight genera of Vespertilioninae. Numbers above clade nodes are the number of unique and unreversed synapomorphies supporting each clade. Numbers below the clade nodes are branch support values (which is the number of extra steps required to collapse the particular node). Synapomorphic characters are shown below branches (abbreviations explained in Appendix II)

the data sets, the i_{MF} (Kluge, 1989) and the incongruence length difference (Mickevich and Farris, 1981) are zero. As explained by Farris *et al.* (1995) the apparent lack of incongruence between the data sets is due to homoplasy of the entire analysis already being present when the bacula matrix is analysed alone. Thus while some of the characters in the bacula matrix dispute those in the chromosome matrix there are just as many bacula characters that agree with the chromosome matrix, which gives the net effect of zero.

Discussion

Karyological Analysis of Each Species

Myotis tricolor

The FN = 52 described here differs from the FN = 50 reported by Rautenbach *et al.* (1993), as chromosome 7, although considered acrocentric, has a very short arm. This karyotype is close to the proposed ancestral vespertilionid karyotype (e.g., Volleth and Heller, 1994).

Eptesicus hottentotus

The GTG-banded karyotype confirms the previously published conventionally stained karyotype and description (Peterson and Nagorsen, 1975; Rautenbach *et al.*, 1993). FISH experiments by Volleth *et al.* (2001) on other *Eptesicus* species, have shown the single acrocentric chromosome of arms 16 and 17 is due to an inversion.

Hypsugo anchietae

Our results differ slightly from the previously reported description of a conventionally stained karyotype (Rautenbach *et al.*, 1993). While Rautenbach *et al.* (1993) described the X-chromosome as a medium sized submetacentric autosome, we found

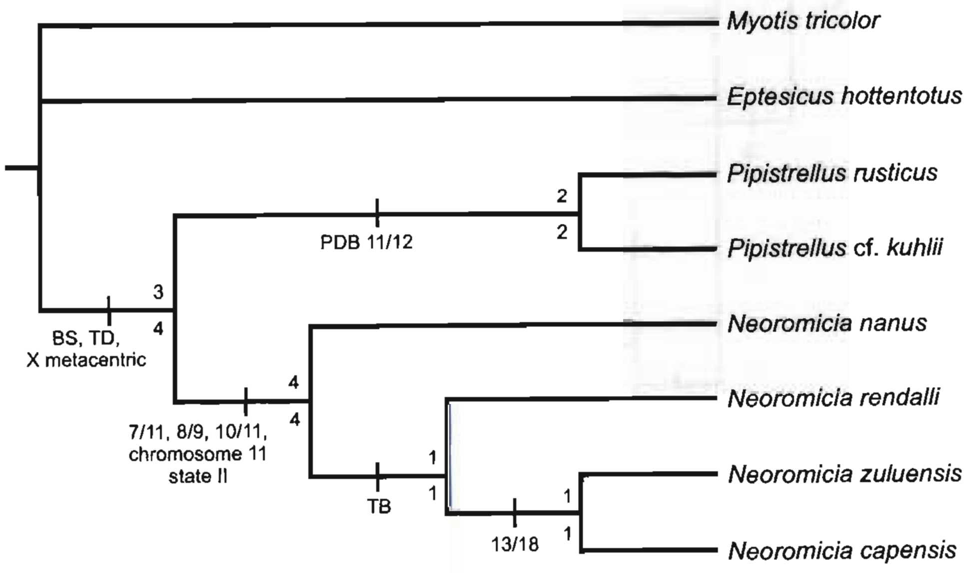

FIG. 14. Most parsimonious tree suggested by bacula and chromosome GTG-band characters for eight taxa, of four genera of Vespertilioninae. Numbers above clade nodes are the number of unique and unreversed synapomorphies supporting each clade. Numbers below the clade nodes are branch support values (which is the number of extra steps required to collapse the particular node). Synapomorphic characters are shown below branches (abbreviations explained in Appendix II)

the X chromosome to be a small metacentric. Due to the highly rearranged karyotype, the GTG-banded chromosomes of *H. anchietae* could not be identified using Bickham's (1979*a*) numbering system. For karyological reasons, a classification of *anchietae* is impossible.

Pipistrellus rusticus

Our results identified a different X chromosome to that described by Rautenbach *et al.* (1993). We found the X chromosome to be a medium sized metacentric, while Rautenbach *et al.* (1993) described the X chromosome as a medium sized submetacentric.

Pipistrellus cf. *kuhlii*

Our GTG-banded karyotype is identical to the GTG-banded karyogram published by Volleth *et al.* (2001) for a specimen from Madagascar. The results are in agreement with the previously described conventionally stained karyotype (Rautenbach *et al.*, 1993).

Neoromicia nanus

The GTG-banded karyotype confirms the previously published conventionally stained karyotype and description (Peterson and Nagorsen, 1975; Rautenbach *et al.*, 1993).

Neoromicia zuluensis

The GTG-banded karyotype contradicts the previously published description of a conventionally stained karyotype (Rautenbach *et al.*, 1993). Our results show 12 biarmed and one acrocentric autosome, whereas Rautenbach *et al.* (1993) found 11 biarmed and two acrocentric autosomes.

Neoromicia capensis

The GTG-banded karyotype is much the same as the GTG-banded karyogram published by Volleth *et al.* (2001) for specimens from South Africa. GTG-bands in this study could not however verify a rearrangement identified by Volleth *et al.* (2001) on chromosome 1/2 in *N. capensis*. Nor was the polymorphic feature of chromosome pair 24 or 25 described by Volleth *et al.* (2001) found in any of the specimens we examined.

Neoromicia rendalli

Our results identified a different X chromosome to that described by McBee *et al.* (1987) and Rautenbach and Fenton (1992). The GTG-banded karyotype shows the X chromosome is a medium sized metacentric, whereas McBee *et al.* (1987) and Rautenbach and Fenton (1992), from a female and a male specimen respectively, reported a large submetacentric as the X chromosome. Pair 16/17 appears to be rearranged as it does not entirely match the ancestral banding pattern, since there are no bands around the centromere. Surprisingly the short arms are consistently faintly stained, compared to the other darker stained chromosomal arms. Pale short arms can also been seen in the equivalent chromosomes in the conventionally stained karyotype by McBee *et al.* (1987). It also appears as if the short arm of the 16/17 pair in *N. rendalli* could be polymorphic. Of the male and female studied, the short arms in the male are two sizes, whereas both arms in the female are the same size. Besides the possibility that this indicates a polymorphism in the population concerning the size of the short arm, it could also indicate that chromosome pair 16/17 is forming a 'new' chromosome via pericentric inversion. In which case the male might have both the 'old' and the 'new' version of the chromosome. However, in the absence of better metaphase GTG-band spreads and CBG-bands, we can provide no definitive solution to this variation.

Karyological Analysis of All Species

Bickham (1979*b*) and Baker and Bickham (1980) described three types of vespertilionid chromosomal evolution, all three of which are represented by the species examined in this study. *Myotis tricolor* and *E. hottentotus* represent conservative taxa. *Myotis tricolor* like the rest of the *Myotis*-group has a karyotypically primitive karyotype, characterised by a high diploid number and many acrocentric chromosomes. *Eptesicus hottentotus* as a member of the *Eptesicus*-group has also retained a primitive karyotype which is thought to have evolved from the *Myotis*-like karyotype by centric fissions and a pericentric inversion, resulting in a karyotype with acrocentric autosomes only.

Pipistrellus rusticus, *P.* cf. *kuhlii*, *N. nanus*, *N. zuluensis*, *N. rendalli* and *N. capensis* have all undergone karyotypic specialisation, or orthoselection, due to centric fusions, which have produced karyotypes with reduced diploid numbers. *Hypsugo anchietae* has undergone a radical reorganisation of the genome, called 'karyotypic megaevolution' by Baker and Bickham (1980), whereby the diploid chromosome number has been greatly reduced and the GTG-banding pattern totally altered.

Volleth and Heller (1994) found several chromosome fusion products have evolved more than once (in more than one genus or species). The 13/18 chromosome pair found in *N. zuluensis* has also been found in two unrelated lineages, in the Plecotini (*Barbastella, Plecotus)* and in *Rhogeesa alleni* (Volleth and Heller, 1994). The 10/12 chromosome fusion pair shared by *N. capensis*, *N. zuluensis, N. rendalli* and *N. nanus* has also been found in three Asian *Pipistrellus* species (Volleth and Heller, 1994).

On the basis of chromosome GTG-bands, *P.* cf. *kuhlii* and *P. rusticus* are identical. Their bacula are also very similar, to the extent that they cannot always be accurately assigned to either species. However, they are recognised as separate species on the basis of fur length, palatal area, skull length and forehead shape (Meester *et al.*, 1986). We support the suggestion by Volleth *et al.* (2001) to recognise specimens of *P.* cf. *kuhlii* with a reduced chromosome diploid number ($2n$ = 42), due to a fusion of chromosome 11 and 12, as a separate species from *P. kuhlii* ($2n$ = 44) which occurs in North Africa and Europe.

GTG-banded chromosomes confirm that *N. capensis*, *N. rendalli* and *N. zuluensis* share very little with *E. hottentotus*, all have biarmed chromosome pairs 1/2, 3/4, 5/6 and 16/17, unlike *E. hottentotus*. *Neoromicia capensis*, *N. rendalli* and *N. zuluensis* have three Robertsonian fusions in common with *N. nanus* (7/11, 8/9, 10/12), and all show state II of chromosome 11. The latter feature makes them members of the tribe Vespertilionini rather than Pipistrellini (Volleth and Heller, 1994). Unfortunately without R-banding results we cannot assess the state of chromosome 23, which is the other character used for identifying members of the tribes Vespertilionini and Pipistrellini. On bacular morphology, Hill and Harrison (1987) identified the subgenus *P.* (*Neoromicia)* was closely related to *P.* (*Hypsugo*), the subgenus in which they included *N. nanus*. GTG-banded chromosomes now indicate an even closer relationship of *nanus* to *Neoromicia* than Hill and Harrison (1987) suggested, since we propose to transfer *nanus* to the genus *Neoromicia*. On karyological reasons, the following species now are members of the genus *Neoromicia*: *N. nanus, N. capensis*, *N. rendalli* and *N. zuluensis*.

From bacular morphology and diploid chromosome number we know *N. somalicus* and *N.* cf. *melckorum* do not belong to the genus *Eptesicus* (Hill and Harrison, 1987; McBee *et al.*, 1987). Allozyme analysis (Morales *et al.,* 1991) has also shown that *N.* cf. *melckorum* is closely allied with *N. capensis* and does not form part of the *E. hottentotus* group. Unfortunately, we do not yet have GTG-banded karyograms for these species and thus do not know whether they share the same Robertsonian fusion products as *N. capensis*, *N. zuluensis*, *N. rendalli* and *N. nanus*.

Bacular Analysis

As suggested by GTG-banded chromosomes, the bacular cladogram (Fig. 13) also indicates the separation of *E. hottentotus* from the *Neoromicia* species. Heller and Volleth (1984) and Hill and Harrison's (1987) suggestion that *E. hottentotus* is the only true *Eptesicus* of the southern African species assigned to the genus *Eptesicus*, has been validated by GTG-band chromosomes and cladistic analyses of chromosome and bacular characters.

Inclusion of several species in the bacular analysis for which we do not have GTG-banded karyotypes introduced some differences to the relationships suggested by GTG-band chromosome characters. In the bacular cladogram *N. nanus* is not in the same group as the other species sharing three common Robertsonian fusion chromosomes, while *H. anchietae* and *Laephotis* spp. cluster with the other *Neoromicia* species, which includes *N.* cf. *melckorum* for which we do not yet have GTG-banded karyotypes.

It is not surprising that bacular morphology does not support the genus *Neoromicia*, as identified by three common Robertsonian fusion chromosomes, since each of the four species (*N. nanus*, *N. rendalli, N. zuluensis* and *N. capensis*) have a different bacular morphology (Fig. 1). While all are elongated and stick-like, they have different bacular tip shapes, cover three different basal lobe morphologies, and both tip relative to the base categories (Appendix IV). Volleth and Heller (1994) found several instances when mapping overall bacular shape and size onto a chromosome cladogram of Vespertilionidae, where they had to assume independent reductions.

Bacular morphology indicates it is not just the generic relationship between *Eptesicus* and *Pipistrellus* species that requires revision, but also the generic boundary of *Laephotis*. Further analyses using alternative characters would be required to confirm this suggestion. However, *Laephotis* has previously been distinguished as a distinct genus on the basis of morphological characters (Meester *et al.*, 1986).

Many advocate the combination of all data in a single analysis, believing that all data potentially contributes to a phylogenetic analysis, and that a species phylogeny makes less sense considering data sets separately, even if one data set swamps another (Doyle, 1992; Honeycutt and Adkins, 1993; Shaffer *et al.*, 1997). However, there are instances when incongruence between data sets indicates different rates or modes of evolution, or even different underlying phylogenetic histories, and these would be important arguments against combining data sets (Graham *et al.*, 1998; Normark and Lanteri, 1998; Wiens, 1998). Incongruence can also result from sampling error, especially with small numbers of characters (Cannatella *et al.*, 1998; Graham *et al.*, 1998), characters not being independent of one another (Doyle, 1992), errors in polarity assessment (Baker *et al.*, 1989; Patterson *et al.*, 1993), and/or homoplasy (Baker *et al*, 1989; Shaffer *et al.*, 1991).

It is possible that several homoplasies have occurred in the evolution of certain bacula shapes and sizes in Vespertilioninae, as sexual selection might directly be acting on these features (Eberhard, 1996). If so, bacula characters used in an analysis without additional characters that accurately reflect phylogenetic history, would cause convergent taxa to cluster together. Possibly when combined with a larger data set from different sources, bacula morphology will provide useful characters.

The possibility also exists that bacula should be represented by just a single character, as the numerous characters we derived might not be independent (Doyle, 1992). Hill's and Harrison's (1987) bacular arrangements have been criticised for the lack of discussion of character transformational polarity (Frost and Timm, 1992; Bogdanowicz *et al.*, 1998). In this study besides using the outgroup to indicate polarity, for characters which have multiple states there is little basis on which to suggest a pattern of transformation, without becoming trapped in circular reasoning. Our lack of understanding of bacular morphology transformation might mean we have used plesiomorphic characters, which have confused the phylogenetic relationships. However, it appears bacular morphology is not entirely useful for resolving relationships between taxa at the generic level. Certainly, bacular morphology is useful for identifying species.

Interestingly, Frost and Timm (1992) in trying to recover the phylogenetic history of plecotine vespertilionid bats, also found disagreement between bacula morphology and other lines of evidence including karyology, osteology and dental evidence. They suggested certain bacula shapes could be plesiomorphic within vespertilionids, in which case similarities would be phylogenetically uninformative. As a result they dismissed bacula as a morphological system whose application seemed to be at a considerably lower level than the generic, subgeneric and group level at which Hill and Harrison (1987) applied it. Our findings also support Frost's and Timm's (1992) criticism of Hill's and Harrison's (1987) analysis for being subjective, as bacula which appear from their illustrations to be similar are not always found in the same taxonomic groups. Clearly a wider revision of the family Vespertilionidae incorporating more taxa, GTG-banded karyotypes and other techniques and characters will be required to test the relationships suggested above.

GTG-banded chromosomes support the close relationship of *N. rendalli*, *N. capensis* and *N. zuluensis*. Banding data further suggest transferring *nanus* to the genus *Neoromicia*. We support the generic rank of *Neoromicia* as defined by three Robertsonian fusion products (7/11, 8/9, 10/12). It still remains to be shown whether *Neoromicia* can be defined by additional characters. Possibly, analyses of skull morphology by traditional morphometrics and geometric morphometrics, which are still to be completed, might provide additional characters for the genus *Neoromicia*.

While gross bacular morphology differences (small, triangular or medium to large, and elongated) support the separation of *N. rendalli*, *N. capensis*, *N. zuluensis* and *N.* cf. *melckorum* from *Eptesicus*, the generic relationships of taxa with medium to large, elongated bacula are poorly resolved by bacular characters. Bacular morphological characters are useful for species identification, but appear less suitable for phylogeny estimation in the above genera.

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APPENDIX I

Specimens examined for chromosome and bacula analyses. Acronyms: DM – Durban Natural Science Museum, Durban; MM – MacGregor Museum, Kimberley; TM – Transvaal Museum, Pretoria; ZM – South African Museum, Cape Town.

Chromosomes

Eptesicus hottentotus: Algeria, Cederberg, Western Cape, South Africa (32°22'S, 19°03'E): ZM41419, ♀. Kliphuis, Cederberg, Western Cape, South Africa (32°08'S, 19°00'E): ZM41416, ♀ (Fig. 3).

Neoromicia capensis: Messina, Northern Province, South Africa (22°23'S, 30°02'E): DM5398, ♀. Itala Game Reserve, Northern Zululand, KwaZulu-Natal, South Africa (27°30'S, 31°12'E): DM5903, ♂ (Fig. 11). Vrolijkheid, Western Cape, South Africa (33°54'S, 19°53'E): DM7194, ♂. Kersefontein, Western Cape, South Africa (32°54'S, 18°20'E): DM7193, ♀.

N. rendalli: Bonamanzi Game Reserve, Zululand, KwaZulu-Natal, South Africa (28°06'S, 32°18'E): DM5877, ♂ (Fig. 12); DM5878, ♀.

N. zuluensis: Messina, Northern Province, South Africa (22°23'S, 30°02'E): DM5375, ♀ (Fig. 10).

N. nanus: Itala Game Reserve, Northern Zululand, KwaZulu-Natal, South Africa (27°32'S, 31°22'E): DM5901, ♂. Stainbank, Yellowwood Park, Durban, KwaZulu-Natal, South Africa (29°54'S, 30°56'E): DM5870, ♂, (Fig. 9); DM5871, ♂.

Pipistrellus cf. *kuhlii*: Harold Johnson Nature Reserve, South Africa (29°07'S, 31°15'E): DM5369, ♂. Dlinza forest, Eshowe, South Africa (28°54'S, 31°27'E): DM5406, ♀. Cowies Hill, Durban, KwaZulu-Natal, South Africa (29°50'S, 30°53'E): DM7201, ♂. Stainbank, Yellowwood Park, Durban, KwaZulu-Natal, South Africa (29°54'S, 30°56'E): DM5868, ♂ (Fig. 8).

P. rusticus: Messina Nature Reserve, Messina, Northern Province, South Africa (22°23'S, 30°02'E): DM5379, ♂ (Fig. 6); DM5389, ♂; DM5391, ♂; DM5867, ♀.

Hypsugo anchietae: Game Valley Estate, Hella-Hella, 17.5 km SWW Richmond, KwaZulu-Natal, South Africa (29°54'S, 30°05'E): DM5362, ♀ (Fig. 5). Empisini Nature Reserve, 1.5 km NWW Umkomaas, KwaZulu-Natal, South Africa (30°12'S, 30°48'E): DM5377, ♀.

Myotis tricolor: Itala Game Reserve, Northern Zululand, KwaZulu-Natal, South Africa (27°30'S, 31°12'E): DM5897, ♀ (Fig. 2).

Bacula

Eptesicus hottentotus: Itala Game Reserve, South Africa (Doornkraal Farm), 10 km NW Louwsburg, Northern Zululand, KwaZulu-Natal, South Africa (27°31'S, 31°12'E): TM31756. Algeria Forest Station, Clanwilliam, Western Cape, South Africa (32°22'S, 19°15'E): TM38412, ZM41418.

Neoromicia zuluensis: 1.5 km NW dense woodland of western reservoir, Skukuza, Kruger National Park, Mpumalanga, South Africa (24°59'S, 31°35'E): TM39761. 2 km E confluence Letaba and Olifants Rivers, Kruger National Park, Mpumalanga, South Africa (23°59'S, 31°50'E): TM39697.

Neoromicia capensis: Itala Game Reserve, Northern Zululand, KwaZulu-Natal, South Africa (27°30'S, 31°12'E): DM5894, DM5899, DM5902. Mkuzi Game Reserve, 15 km E Mkuze village, Zululand, KwaZulu-Natal, South Africa (27°38'S, 32°16'E): DM5380, DM5400. Loteni Nature Reserve, Drakensberg, KwaZulu-Natal, South Africa (29°27'S, 29°32'E): DM1912, DM1947. Royal Natal National Park, Drakensberg, KwaZulu-Natal (28°41'S, 28°56'E): DM2389. Clifton School, Nottingham Road, Natal Midlands, KwaZulu-Natal, South Africa (29°21'S, 30°00'E): DM5873. Merrivale, Natal Midlands, KwaZulu-Natal, South Africa (29°30'S, 30°15'E): DM5387. Epping Crescent, Forest Hills, Durban, KwaZulu-Natal, South Africa (29°45'S, 30°49'E): DM7017. 22 Ashley Road, Westriding, Durban, KwaZulu-Natal, South Africa (29°47'S, 30°46'E): DM7018. 14 Marion Rd., Westriding, Durban, KwaZulu-Natal, South Africa (29°47'S, 30°46'E): DM5881. Game Valley Estate, Hella-Hella, 17.5 km SWW Richmond, KwaZulu-Natal, South Africa (29°54'S, 30°05'E): DM6894. Ganyesa, North West Province, South Africa (26°32'S, 24°07'E): MM7061. Wonderwerk Cave Farm B, 58 km S Kuruman, Northern Cape, South Africa (27°49'S, 23°35'E): MM7064, MM7066, MM7067. Kersefontein Farm, 16 km N Hopefield, Western Cape, South Africa (32°54'S, 18°20'E): DM7196. Algeria, Cederberg, Western Cape, South Africa (32°22'S, 19°03'E): ZM41452. Kliphuis, Cederberg, Western Cape, South Africa (32°08'S, 19°00'E): ZM41457. Vrolijkheid Nature Reserve, 15 km SW Robertson, Western Cape, South Africa (33°54'S, 19°53'E): DM7194, DM7197.

N. rendalli: Bonamanzi Game Reserve, 5 km S Hluhluwe Village, Zululand, KwaZulu-Natal, South Africa (28°06'S, 32°18'E): DM5370, DM5361, DM5877.

N. nanus: Chingamwe Estates, 15 km SE Juliesdale, Eastern Highlands, Zimbabwe (18°27'S, 32°45'E): DM 5366. Rusito Forest, along Rusito River, Zimbabwe (20°02'S, 32°59'E): TM34782. 10 km N Simunye, Swaziland (26°07'S, 31°57'E): DM5879, DM5880. Itala Game Reserve, Northern Zululand, KwaZulu-Natal, South Africa (27°32'S, 31°22'E): DM5900, DM5901. Jozini Dam Wall, N Zululand, KwaZulu-Natal, South Africa (27°25'S, 32°04'E): DM5367. Stainbank, Yellowwood Park, Durban, KwaZulu-Natal, South Africa (29°54'S, 30°56'E): DM5869, DM5870, DM5871. Old Community Health Hall, Renishaw, KwaZulu-Natal, South Africa (30°17'S, 30°44'E): DM5365, DM5402, DM5404.

N. cf. *melckorum:* Old picnic site, Pafuri, Kruger National Park, Northern Province, South Africa (22°25'S, 31°18'E): TM39506.

Hypsugo anchietae: Sobhengu Lodge, St Lucia, Zululand, KwaZulu-Natal, South Africa (27°59'S, 32°24'E): DM6885. False Bay Park, St Lucia, Zululand, KwaZulu-Natal, South Africa (27°48'S, 32°23'E): DM2269. Harold Johnson Nature Reserve, 8.5 km S Mandini, Zululand, KwaZulu-Natal, South Africa (29°07'S, 31°15'E): DM5353. Empisini Nature Reserve, 1.5 km NWW Umkomaas, KwaZulu-Natal, South Africa (30°12'S, 30°48'E): DM5358.

Pipistrellus cf. *kuhlii:* Chingamwe Estates, 15 km SE Juliesdale, Eastern Highlands, Zimbabwe (18°27'S, 32°45'E): DM4692. Rhodes Inyanga National Park, Zimbabwe (18°17'S, 32°46'E): TM34757. Harold Johnson Nature Reserve, 8.5 km S Mandini, Zululand, KwaZulu-Natal, South Africa (29°07'S, 31°15'E): DM 5369. Servitude into Dlinza Forest, Eshowe, Zululand, KwaZulu-Natal, South Africa (28°54'S, 31°27'E): DM 5360, 5374, 5397, 5356. Twin Streams Farm, Mtunzini, KwaZulu-Natal, South Africa (28°57'S, 31°30'E): DM5872. Sugar Research Association Estate, Mount Edgcombe, KwaZulu-Natal, South Africa (29°42'S, 31°04'E): DM7143. Kloof Falls Road/Bridle Road picnic site, Kranskloof Nature Reserve, Kloof, KwaZulu-Natal, South Africa (29°46'S, 30°49'E): DM5876, DM6219. 26 Hathaway, Wishart Road, Hillcrest, KwaZulu-Natal, South Africa (29°47'S, 30°46'E): DM7016. Cowies Hill, Pinetown, KwaZulu-Natal (29°50'S, 30°53'E): DM7201. Hillary School, Durban, KwaZulu-Natal, South Africa (29°53'S, 30°56'E): DM6150. 183 Sarnia Road, Rossburgh, Durban, KwaZulu-Natal, South Africa (29°54'S, 30°58'E): DM5378. Yellowwood Park, Durban, KwaZulu-Natal, South Africa (29°54'S, 30°56'E): DM5868. North Park Nature Reserve, Durban, KwaZulu-Natal, South Africa (29°52'S, 30°52'E): DM5403. Pigeon Valley Park, Durban, KwaZulu-Natal, South Africa (29°52'S, 30°59'E): DM5384, DM5385.

P. rusticus: Farm Klipfontein, 30 km NE Vaalwater, Waterberg-Ellisras, South Africa (24°08'S, 28°18'E): TM39887, TM39885. Messina Nature Reserve, Messina, Northern Province, South Africa (22°23'S, 30°02'E): DM5379, DM5318, DM5390, DM5389, DM5391.

P. rueppellii: Anthrax Camp, Pafuri, Kruger National Park, Northern Province, South Africa (22°25'S, 31°15'E): TM36609, TM37908.

Myotis tricolor: American Cave, Uitkomst, Krugersdorp District, South Africa (25°55'S, 27°45'E): TM19210. Uitkyk, Krugersdorp, South Africa (26°05'S, 27°46'E): TM9058.

Laephotis cf. *wintoni*: Game Valley Estate, Hella-Hella, 17.5 km SWW Richmond, KwaZulu-Natal, South Africa (29°54'S, 30°05'E): DM5351, DM6899. Algeria, Cederberg, Western Cape, South Africa (32°22'S, 19°03'E): ZM41415, ZM41417.

Laephotis bostwanae: Manditobe Dam, Mahogony Drive, Punda Maria (22°41'S, 31°02'E): TM38123, TM38155. Farm Klipfontein, 30 km NE Vaalwater, Ellisras District, Northern Province, South Africa (24°08'S, 28°18'E): TM39946.

Laephotis namibensis: Klein Aus 8,3 km W Aus, Lüderitz, Namibia (26°39'S, 16°13'E): TM37547.

Nycticeinops schlieffenii: Mkuzi Game Reserve, 15 km E Mkuze Village, Zuluand, KwaZulu-Natal, South Africa (27°38'S, 32°16'E): DM5401.

Scotophilus dinganii: Kloof Falls Road/ Bridle Road picnic site, Kranskloof Nature Reserve, Kloof, KwaZulu-Natal, South Africa (29°46'S, 30°49'E): DM5874, DM5875.

Appendix II

Descriptions of chromosomal and bacular characters

Chromosomes: Chromosome fusion 7/11: absent (0), present (1); — Chromosome fusion 8/9: absent (0), present (1); — Chromosome fusion 10/12: absent (0), present (1); — Chromosome fusion 11/12: absent (0), present (1); — Chromosome fusion 13/18: absent (0), present (1); — State of chromosome 11: (0) GTG-negative band close to the centromere (state I), (1) or found more terminally (state II); — State of X chromosome: (0) submetacentric, (1) metacentric, (2) subtelocentric.

Baculum characters: Baculum shape (BS): (0) small, triangular, (1) medium to large, elongate, 'stick-like'; — Tip not distinct from shaft (TD): (0) yes, (1) no; — Tip shape (TS): (0) rounded, (1) 'V' shaped, (2) flat and broad, (3) triangular; — Tip relative to the base (TB): (0) tip narrower, (1) base narrower; — Percent of bacula length deflected (PBD): (0) ≤ 35%, (1) > 50%; — Angle of tip relative to shaft (AT): (0) same plane, (1) ventrally deflected; — Basal lobe shape (BL): (0) 'V' shaped, small and rounded, (1) 'V' shaped, short, broad, with wider ends, (2) semi-circular, skirt-like, with a 'W' shaped edge, (3) 'V' shaped, longer, evenly wide, (4) triangular.

Appendix III

Matrix of chromosome characters used for Vespertilioninae species. Acronyms: MTR, *Myotis tricolor*; EHO, *Eptesicus hottentotus*; NCA, *Neoromicia capensis*; NZU, *N. zuluensis*; NRE, *N. rendalli*; NNA, *N. nanus*; PRU, *Pipistrellus rusticus*; PcK, *P.* cf. *kuhlii*. Explanations of the characters are given in Appendix II

Character	MTR	EHO	NCA	NZU	NRE	NNA	PRU	PcK
Fusion 7/11	0	0	1	1	1	1	0	0
Fusion 8/9	0	0	1	1	1	1	0	0
Fusion 10/12	0	0	1	1	1	1	0	0
Fusion 11/12	0	0	0	0	0	0	1	1
Fusion 13/18	0	0	1	1	0	0	0	0
State 11	0	0	1	1	1	1	0	0
State X	0	0	1	2	1	1	1	1

APPENDIX IV

Matrix of bacular characters used for Vespertilioninae species. Acronyms: MTR, *Myotis tricolor*; EHO, *Eptesicus hottentotus*; NCA, *Neoromicia capensis*; NZU, *N. zuluensis*; NRE, *N. rendalli*; NNA, *N. nanus*; NcM, *N.* cf. *melckorum*; PRU, *Pipistrellus rusticus*; PcK, *P.* cf. *kuhlii*; PRP, *P. rueppellii*; HAN, *Hypsugo anchietae*; NYS, *Nycticeinops schlieffenii*; LAE, *Laephotis wintoni*; SDI, *Scotophilus dinganii*. Character explanations are provided in Appendix II

Character	MTR	EHO	NCA	NZU	NRE	NNA	NcM	PRU	PcK	PRP	HAN	NYS	LAE	SDI
Baculum shape	0	0	1	1	1	1	1	1	1	1	1	1	1	0
Tip not distinct from shaft	0	0	1	1	1	1	1	1	1	1	1	0	1	0
Tip shape	0	0	3	2	2	2	3	1	1	1	2	0	3	0
Tip relative to the base	0	0	1	1	1	0	1	0	0	0	1	0	1	0
% baculum length deflected	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Angle of tip relative to shaft	0	0	1	0	0	0	1	0	0	0	0	0	1	0
Basal lobe shape	0	0	2	1	3	3	2	4	4	3	1	3	2	0

New distribution records of bats in KwaZulu-Natal

T. KEARNEY[1] & P. J. TAYLOR[2]

[1]Biology Department, University of Natal, P.O. Box 18091, Dalbridge 4014, South Africa; e-mail: kearneyt@biology.und.ac.za

[2]Durban Natural Science Museum, P.O. Box 4085, Durban 4000, South Africa; e-mail: taylorpe@cis.co.za

Summary

Kearney, T. & Taylor, P.J. 1997. New distribution records of bats in KwaZulu-Natal. *Durban Museum Novitates* 22: 53—56. New distribution records are documented for four species of Microchiroptera, including two which are new to South Africa (*Scotoecus albofuscus* (Thomas 1890) and *Eptesicus rendalli* (Thomas 1889)), one which is new to KwaZulu-Natal (*Laephotis cf. wintoni* Thomas 1901), and one which represents a significant range extension within KwaZulu-Natal (*Pipistrellus anchietai* (Seabra 1900)).

KEYWORDS: Eptesicus rendalli, Laephotis cf. wintoni, Scotoecus albofuscus, Pipistrellus anchietai, *KwaZulu-Natal, Chiroptera, distribution.*

Introduction

In comparison with other mammals, chiropteran distributions have been poorly documented, both in KwaZulu-Natal (Bourquin 1988; Rowe-Rowe & Taylor 1996) and in South Africa as a whole (Gelderblom *et al.* 1995). Between 1990 and 1994, three species of bats were reported for the first time in KwaZulu-Natal: *Rhinolophus swinnyi* Gough 1908 (Bronner 1990), *Myotis welwitschii* (Gray 1866) (Taylor 1991), and *Cloeotis percivali* Thomas 1901 (Taylor *et al.* 1994).

The formation of the Durban Bat Interest Group (affiliated to the Durban Natural Science Museum) in 1994 has led to greater public awareness, higher reporting rates from members of the public, and intensified collecting efforts relevant to bats. As a result, two species — *Scotoecus albofuscus* (Thomas 1890) and *Eptesicus rendalli* (Thomas 1889) — were recorded for the first time in KwaZulu-Natal and South Africa, while another two species were captured at localities in KwaZulu-Natal which represented significant range extensions: *Laephotis cf. wintoni* Thomas, 1901 and *Pipistrellus anchietai* (Seabra 1900). Details of these new records are outlined below.

Methods

Standard micro-mistnets, a harp trap modified from Tidemann & Woodside (1978), and a hand net were used for capturing bats.

Where chromosomal analyses were performed, an *in vitro* bone-marrow method modified from Green *et al.* (1980) was used. Bacula were examined following Hill & Harrison (1987). All specimens are accessioned in the Durban Natural Science Museum mammal collection. Cranial measurements were taken with Mitutoyo Digimatic 500-321 calipers. Multivariate analysis (principal component analysis) was performed using subroutines of NT-SYS 1.5 (Rohlf 1989; see Blackith & Reyment 1971, and Pimentel 1979 for explanation of multivariate statistical methods). The following cranial measurements were used (see DeBlase & Martin 1981, Freeman 1981 and Kitchener *et al.* 1993 for full descriptions of measurements): greatest skull length (GSL), condylo-canine length (CCL), zygomatic width (ZW), mastoid breadth (MW), width across outer edges of M^3 (M^3-M^3), least interorbital width (LIW), braincase width (BCW), braincase height (BCH), width across outer edge of canines (C^1-C^1), and maxillary toothrow from anterior surface of C^1 to posterior surface of M^3 (C^1-M^3).

Unless stated otherwise, the keys in Meester *et al.* (1986) were used to identify specimens.

Results and discussion

1. Thomas' house bat *Scotoecus albofuscus* (Thomas, 1890)

This species was previously known from a few scattered localities in Africa, from West Africa to East Africa and southwards to Mozambique (Hill 1974; Skinner & Smithers 1990). Hill (1974) and Meester *et al.* (1986) recognised two subspecies: *S. a. albofuscus* from West Africa; and *S. a. woodii* Thomas 1917 from southeastern Zaire extending into Kenya, Tanzania, Malawi and southwards to the Zinave National Park in southern Mozambique (Smithers & Tello 1976).

A pregnant female (which gave birth to twins just before it died) was found at the Perna Perna Resort in St Lucia Village (28°17'S; 32°25'E), on 30 November 1995, in Dune Forest (Type 1c: Acocks 1988), extending the known distribution some 800 km southwards, and making this the first known record of the species in South Africa, and only the second known locality for southern Africa (after Zinave National Park in Mozambique).

Specimen details, and body and cranial measurements are given in Table 1. The individual is relatively large in size, with a forearm length of 31 mm, equal to the maximum forearm length recorded by Hill (1974) for a series of nine *S. albofuscus*, and with cranial measurements usually exceeding the range given by Hill (1974) (e.g. condylo-canine length of the St Lucia specimen was 14.37 mm, compared to a range of 12.8—13.7 mm given for seven specimens of *S. albofuscus* by Hill 1974). The two subspecies overlap broadly in body and cranial size, based on measurements given by Hill (1974), with *S. a. albofuscus* having a broader rostrum than *S. a. woodi*. However, on geographical grounds, and assuming the validity of the two subspecies, the new specimen is referable to the southerly distributed *S. a. woodi.*

Second upper premolars were absent in the St Lucia specimen. This tiny tooth is usually present in the dark-winged species, *S. hindei* Thomas 1901 and *S. hirundo* (de Winton 1899) (Hill 1974).

This extension in the known range is not surprising, given the distribution of many other species from the subtropical coastal plain of Mozambique down the east coast of the Zululand "subtropical species subtraction zone" (Poynton, 1961), and the distribution of at least two other Vespertilionidae, *Kerivoula argentata* and *Chalinolobis variegatus*, which extend into northern Zululand from Mozambique (Meester *et al.* 1986).

2. Rendall's serotine bat *Eptesicus rendalli* (Thomas, 1889)

Previous records of this species in southern Africa are from northern Botswana, the Tete district south of the Zambezi in Mozambique (Meester *et al.*, 1986), and Mana Pools National Park in Zimbabwe (Rautenbach and Fenton, 1992). Extralimitally, the species occurs throughout West, East and Central Africa (Skinner & Smithers 1990).

Two adult males were mist-netted at Lalapanzi Pan, Bonamanzi Nature Reserve (28°06'S; 32°18'E), on 18 April 1995, in Zululand Palm Veld (1b: Acocks, 1988). Prior to being caught at dusk, these bats, with their distinctively pale wings, were observed fluttering around the net, low to the ground, as described in Skinner & Smithers (1990). Body and cranial measurements are given in Table 1. Karyotype analysis of both individuals revealed a diploid number of 2n=38, in accordance with the findings of McBee *et al.* (1987) and Rautenbach & Fenton (1992).

This being the first record of the species in South Africa, it significantly extends the previously known range by some 1300 km to the south of the Tete district of Mozambique. As for the previous species, the presence of *E. rendalli* in the coastal region of Zululand is not surprising given its occurrence on the coastal plain of northeastern Mozambique (Skinner & Smithers 1990).

3. Anchieta's pipistrelle *Pipistrellus anchietai* (Seabra, 1900)

Known from scattered localities in Angola, Zambia and southern Zaire (Koopman 1993), the first record in South Africa, a specimen collected at Skukuza water reservoir in the Kruger National Park (Rautenbach *et al.* 1985), represented a considerable extension of the known range. Records of *P. anchietai* from four localities in Zimbabwe (Cotterill 1996) provide an intermediate distributional link to the above range. Transvaal Museum records indicate an extension of known distribution within South Africa to the southeast and southwest, with specimens collected subsequently from two other localities; Ngome Forest Reserve in northern KwaZulu-Natal (27°50'S; 31°24'E; TM40205 & TM40206), and the Farm Klipfontein in the Waterberg-Ellisras area of the Northern Province (24°08'S; 28°18'E; TM40287 & TM40291).

The following new distribution records further extend the known range of *P. anchietai* both to the east and south in KwaZulu-Natal. An adult male (DM5353) was mist-netted on 8 January 1996, in the camp site at Harold Johnson Nature Reserve (29°07'S; 31°15'E), on the south bank of the Tugela River, Zululand, in thornveld with patches of coastal forest (Type 1a: Acocks 1988). Two adult females (DM5357 & DM5364) in non-breeding condition were subsequently mistnetted in the same place on 26 April 1996. Another adult female (DM5362) in non-breeding condition was netted on 15 May 1996, beside the bridge over the Umkomaas River, at Game Valley Estates (29°32'S; 30°03'E) in the Hella-Hella area, near Richmond, in Valley Bushveld (northern variation, Type 23a: Acocks 1988). On 12 November 1996, a pregnant female (DM5377) with two foetuses (16 mm total length each), and an adult male (DM5358) were caught at Empisini Nature Reserve (30°07'S; 30°27'E), near Umkomaas, in a harp trap placed across a path in coastal forest (Type 1a: Acocks 1988). Body and cranial measurements are given in Table 1.

Pipistrellus anchietai is very similar cranially (Rautenbach *et al.* 1985) and in overall body size (Skinner & Smithers 1990) to *P. kuhlii* (Kuhl 1819), while J.E. Hill (in Rautenbach *et al.* 1985) points out subtle cranial distinctions between the two species. Identification of the above specimens was based primarily on karyotype number (2n=26), which agreed with that reported by Rautenbach *et al.* (1993) for *P. anchietai*. In the case of DM5353, a male from Harold Johnson Nature Reserve, bacula morphology (Hill and Harrison 1987) further confirms the identification as *P. anchietai*.

Using the key in Meester *et al.* (1986), which is taken from Koopman (1966), all the specimens identified above as *P. anchietai* key out as *P. kuhlii*. The key gives three criteria to separate *P. kuhlii* and *P. anchietai*: height of the posterior incisor, shape and height of the anterior upper premolar, and maxillary toothrow length. Of the above specimens, maxillary toothrow length (c^1-m^3) was never less than 4.5 mm (see Table 1), as is required in the key for *P. anchietai*. It would appear the characters in the key relating to tooth shape and height are a manifestation of tooth wear rather than species differences. Indeed, individuals with flat-crowned anterior premolars (DM5364, DM5362, and one premolar in DM5358) had toothwear classes D, C, and B respectively (following Rautenbach 1986), whilst specimens with pointed anterior premolars (DM5357, DM5353, DM5377, and one premolar in DM5358) had toothwear classes of AB, AB, B, and B respectively. Comparisons in the height of the second incisor relative to the first incisor between *P. kuhlii* and *P. anchietai* showed negligible differences between the species.

Cotterill (1996) used bacula morphology (following Hill & Harrison 1987) to confirm the identity of *P. anchietai* recorded for the first time from four localities in Zimbabwe. Given this fact, and the difficulties mentioned above in keying out *P. anchietai* using conventional morphological characters, it is likely that *P. anchietai* has in the past been collected at more localities, but misidentified as *P. kuhlii*. *Pipistrellus anchietai* could therefore have a more widespread distribution in southern African than previously indicated.

The need for a better key that distinguishes between *P. kuhlii* and *P. anchietai* reinforces previous calls for a revision of the genus *Pipistrellus* (Meester *et al.* 1986, Rautenbach *et al.* 1993, Cotterill 1996).

4. Winton's long-eared bat *Laephotis cf. wintoni* Thomas, 1901

An adult male (DM5351) was netted along a road, in Valley Bushveld (northern variation Type 23a: Acocks 1988), at Game Valley Estates (29°32'S; 30°03'E), Hella-Hella, near Richmond, on 14 May 1996.

The karyotype number (2n=34) of this species agrees with that reported by Rautenbach *et al.* (1993), confirming the genus as *Laephotis* Thomas, 1901. *Laephotis botswanae* Setzer, 1971, *L. namibensis* Setzer, 1971 and *L. wintoni* all share this karyotype number.

To assist with the accurate species identification of DM5351, principal component analysis was employed using the same measurements used by Rautenbach & Nel (1978) and Watson (1990a) (see Table 1). The first three components of the principle component analysis, calculated from a product moment correlation matrix (using standardized values), represented 95.8% of the phenetic variation in eight *Laephotis* samples (individuals and population means). Comparison of the first two axes from the principle component analysis (Fig.

Table 1. Specimen details, and body and cranial measurements for new specimens of bats from KwaZulu-Natal.

Mus. no.	Species	Sex	Locality	TB	T	HF	E	FA	Mass	GSL	CCL
DM4885	*S. albofuscus*	F	St Lucia	85	32	8*cu*	9	31.0	-	-	14.37
DM5361	*E. rendalli*	M	Bonamanzi	92	37	6*su*	11	35.9	7.93*	14.17	13.30
DM5370	*E. rendalli*	M	Bonamanzi	94	38	7*su*	11	34.3	8.53*	13.84	12.65
DM5353	*P. anchietai*	M	Harold Johnson	79	34	6/7	10	29.0	4.32	13.15	12.02
DM5357	*P. anchietai*	F	Harold Johnson	83	35	5/6	11	32.0	5.03	13.34	12.17
DM5364	*P. anchietai*	F	Harold Johnson	87	38	5/6	11	31.7	5.61	13.74	12.50
DM5362	*P. anchietai*	F	Hella-Hella	78	32	6/7	11	30.3	4.42	13.74	12.50
DM5377	*P. anchietai*	F	Empisini	84	39	5/6	13	31.7	5.37	13.42	12.25
DM5358	*P. anchietai*	M	Empisini	80	34	6/6	11	30.5	4.23	13.02	11.78
DM5351	*L. wintoni*	M	Hella-Hella	94	43	6/7	19	37.0	6.63	15.03	-

Mus. no.	Species	Sex	Locality	ZW	MW	M^3-M^3	C^1-M^3	LIW	BCW	BCH	C^1-C^1
DM4885	*S. albofuscus*	F	St Lucia	10.25	8.84	7.25	5.24	4.58	9.55	-	5.17
DM5361	*E. rendalli*	M	Bonamanzi	9.42	8.19	6.19	5.09	-	-	-	-
DM5370	*E. rendalli*	M	Bonamanzi	9.77	8.54	6.51	4.94	-	-	-	-
DM5353	*P. anchietai*	M	Harold Johnson	8.16	6.87	5.31	4.63	-	-	-	-
DM5357	*P. anchietai*	F	Harold Johnson	8.60	7.29	5.36	4.76	-	-	-	-
DM5364	*P. anchietai*	F	Harold Johnson	8.90	7.55	5.53	4.83	-	-	-	-
DM5362	*P. anchietai*	F	Hella-Hella	8.90	7.55	5.53	4.83	-	-	-	-
DM5377	*P. anchietai*	F	Empisini	8.48	7.23	5.36	4.73	-	-	-	-
DM5358	*P. anchietai*	M	Empisini	8.40	7.22	5.44	4.61	-	-	-	-
DM5351	*L. wintoni*	M	Hella-Hella	8.67	-	5.63	4.91	3.69	7.51	5.21	4.35

(* bats in captivity for four weeks)

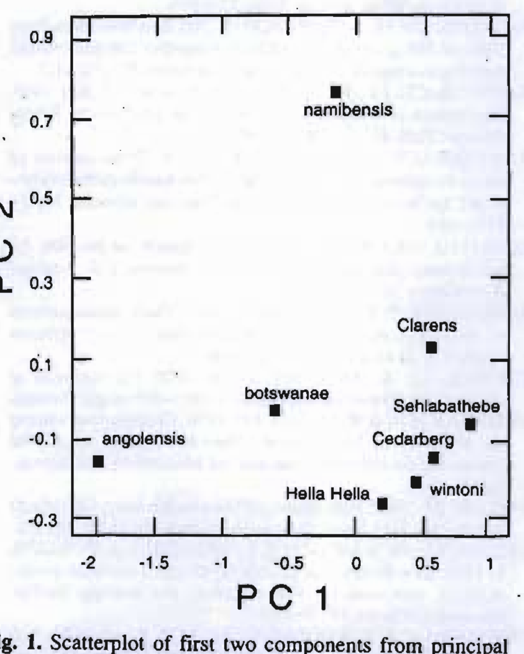

Fig. 1. Scatterplot of first two components from principal component analysis (PCA) of *Laephotis* specimens from southern Africa (data obtained from Watson 1990, and Table 1). The first two components explained 79.6% and 10.7% respectively of the total variation. Samples sizes for the taxa and populations are as follows: *L. namibensis* (n=2), *L. angolensis* (n=1), *L. botswanae* (n=12), *L. wintoni* (n=7), Cedarberg (n=1), Sehlabathebe (n=5), Clarens (n=2) and Hella Hella (n=1).

1) showed a clear separation along the first axis between *L. angolensis*, *L. botswanae*, and *L. wintoni* (including DM5351 from Hella Hella). *Laephotis namibensis* plotted between *L. botswanae* and *L. wintoni*. Variation along the first component (which explained 79.6% of the total variation) reflected overall variation in size, as indicated by high eigenvectors loadings of similar magnitude and sign (Table 2). There is some overlap between *L. wintoni*, *L. angolensis* and *L. botswanae* along the second axis, while *L. namibensis* separated well from the others. The second component (which explained 10.7% of the total variation) was interpreted as being a shape vector contrasting skull length and width, with skull length (greatest skull length; positive coefficient) and width (least interorbital width and C^1-C^1 width; negative coefficients) loading most heavily (Table 2).

From the PCA it was concluded the specimen from Hella-Hella is phenetically closest to *L. wintoni*. However the validity of *L. wintoni* in South Africa still remains ambiguous. Watson (1990a) found specimens from Lesotho and the Free State province that are phenetically closest to the two specimens from the Cape identified by Rautenbach & Nel (1978) as closest to *L. wintoni*, although the geographic locality of these specimens was closest to *L. namibensis* and furthest from the type locality of *L. wintoni*. Skinner & Smithers (1990) withdrew *L. wintoni* on the suggestion of I.L. Rautenbach (personal communication) that the specimens from the Western Cape Province called *L. wintoni* are more appropriately placed with *L. namibensis*. Small sample sizes (due to limited material in collections) used in the above calculations for *L. angolensis* (n=1), *L. botswanae* (n=2-12), and *L. namibensis* (n=1-2), may have confounded the problem. A review of the genus in Africa, considering all the material that has been acquired since 1978 might well clarify some of the uncertainty.

Table 2. Eigenvector coefficients for the first three eigenvectors from principal component analysis (PCA) of *Laephotis* specimens (data obtained from Watson 1990a, and Table 1). Variable abbreviations are defined in the Methods.

Variable abbreviation	Eigenvectors 1	2	3
FA	0.950	0.262	0.070
GLS	0.862	0.395	0.270
LIW	0.812	-0.549	0.134
ZYW	0.918	0.256	-0.055
BCW	0.959	0.217	-0.082
BCH	0.795	-0.061	-0.566
C^1-C^1	0.811	-0.507	0.187
M^3-M^3	0.927	-0.238	-0.119
C^1-M^3	0.975	0.096	0.134
% variation	79.6	10.7	5.5

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Correction of a montane (Drakensberg) record of lesser yellow house bat *Scotophilus viridis* (Chiroptera: Vespertilionidae)

T.C. KEARNEY[1] & E.C.J. SEAMARK[2]

[1]Vertebrate Department, Transvaal Museum, P.O. Box 413, Pretoria 0001, South Africa
E-mail: kearney@nfi.co.za
[2]507 San Martino, 199 Troye Street, Muckleneuk, Pretoria 0002, South Africa.

Whilst checking the collection of *Scotophilus viridis* (Peters, 1852), previously known as *Scotophilus borbonicus* (E. Geoffroy, 1803) (Koopman, 1993; Taylor, 2000) in the Durban Natural Science Museum, to confirm our identification of specimens caught at Mkuze Game Reserve, we noticed skins of DM1887 and DM1888 appeared different to other *Scotophilus* skins. We have been working on a field key for vesper bats, which includes hair colour, our observations of individuals we have caught and museum study skins (Durban Natural Science Museum and Transvaal Museum collections), and have found that vesper species apparently have three different patterns of colour along individual hairs. Some species have hair that is a single colour from base to tip (unicoloured), a few species have two distinct colours along the length of the hair (bicoloured), and yet others have three different colours along the hair length (tricoloured). Our observations indicate that *Scotophilus* have a single colour along the length of the hair both dorsally and ventrally (unicoloured), whereas the skins of DM1887 and DM1888 have bicoloured hair.

Furthermore, while *Scotophilus* have a single upper incisor, examination of the skulls of DM1887 and DM1888 revealed minute, flat-crowned second upper incisors, well below the cingulum of the first incisor, which had previously not been observed as dried flesh was removed to reveal their presence. Comparison of skulls DM1887 and DM1888, with other skulls of *S. dinganii* and *S. viridis* in the Durban Natural Science Museum collection identified several differences. The muzzle region of DM1887 and DM1888 was longer than that in *Scotophilus*, the squamosal bones of DM1887 and DM1888 were not as broad as those of the *Scotophilus*, and neither DM1887 nor DM1888 had the distinct sagittal crest along the posterior portion of the cranium observed in the *Scotophilus* specimens. Based on hair colour, number of upper incisors, overall body size, forearm length and ear length we identified DM1887 and DM1888 as *Eptesicus hottentotus* (A. Smith, 1833).

A principal component analysis (PCA), based on six cranial and mandible measurements of 105 *S. viridis* and 48 *E. hottentotus* (see Appendix 1 for specimen details), as well as DM1887 and DM1888, was computed using NT-SYS 2.01h (Rohlf, 1997). The following cranial and mandible measurements were made with Mitutoyo Digimatic 500-321 calipers: condylo-incisor skull length (CIL); greatest brain case breadth (BB); maxillary toothrow length, from anterior surface of C^1 to the posterior surface of M^3 (MTR); width across outer edge of upper canines (C^1-C^1); width across outer edge of upper M^3 (M^3-M^3); and dentary length (DENL) (see Table 1 for mean measurements and ranges). Comparison of the first two principle components (Fig. 1) showed a clear separation between the two species, with DM1887 and DM1888 falling within the range of *E. hottentotus*.

Both *S. viridis* and *E. hottentotus* have been recorded from savanna woodlands and riverine habitats (Skinner and Smithers 1990; Taylor, 2000), however their habitat preferences appear to differ with *E. hottentotus* also being associated with drier, mountainous or craggy regions (Skinner and Smithers 1990; Taylor, 2000), whereas *S. viridis* is generally associated with areas having a mean annual rainfall in excess of 500 mm (Skinner and Smithers, 1990).

Although *E. hottentotus* had been reported in KwaZulu-Natal from three localities, Ithala Game Reserve, Kranskloof

Table 1. The mean and range of cranial (condylo-incisor skull length (CIL); greatest brain case breadth (BB)), mandibular (maxillary toothrow length, from anterior surface of C^1 to the posterior surface of M^3 (MTR); width across outer edge of upper canines (C^1-C^1); width across outer edge of upper M^3 (M^3-M^3); and dentary length (DENL)) and forearm length (FA) measurements of *Scotophilus viridis* and *Eptesicus hottentotus* (males and females are combined, total sample sizes are given in parentheses), as well as measurements for DM1887 and DM1888.

Taxon	CIL	BB	MTR	C^1-C^1	M^3-M^3	DENL	FA
S. viridis	16.82	8.9	6.15	6.15	8.21	13.15	48.24
	15.83-17.83	8.47-9.45	5.79-6.48	5.57-6.48	7.53-9.03	12.26-13.93	44.25-50.78
	(105)	(105)	(105)	(105)	(105)	(105)	(105)
E. hottentotus	18.98	9.01	7.15	6.25	8.37	14.65	49.46
	16.99-20.07	8.42-9.82	6.28-7.59	5.46-7.12	7.43-9.18	12.99-16.06	46.63-52.63
	(48)	(48)	(48)	(48)	(48)	(48)	(48)
DM1887	18.71	9.28	6.93	6.15	7.94	14.37	49.3
DM1888	19.36	9.28	7.09	6.13	8.22	14.84	49.9

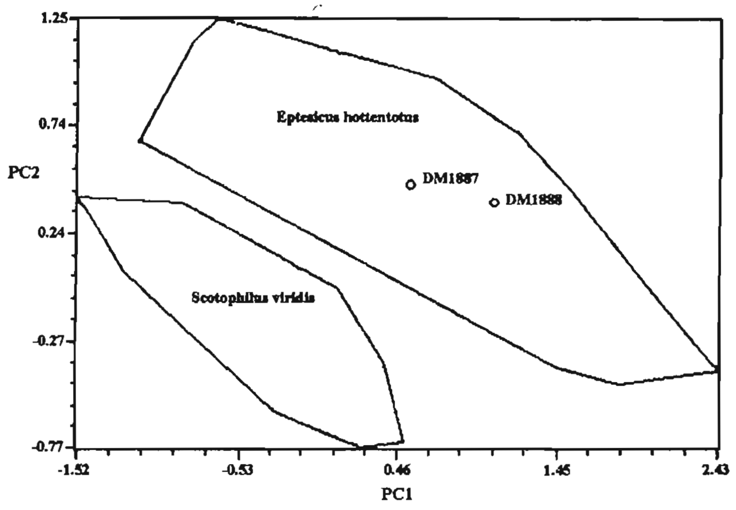

Fig. 1. A plot of the first two components of a principal component analysis (PCA) of 105 specimens of *Scotophilus viridis*, 48 specimens of *Eptesicus hottentotus*, DM1887 and DM1888, based on the six cranial and mandibular measurements. Polygons outline the maximum scatter of each taxon.

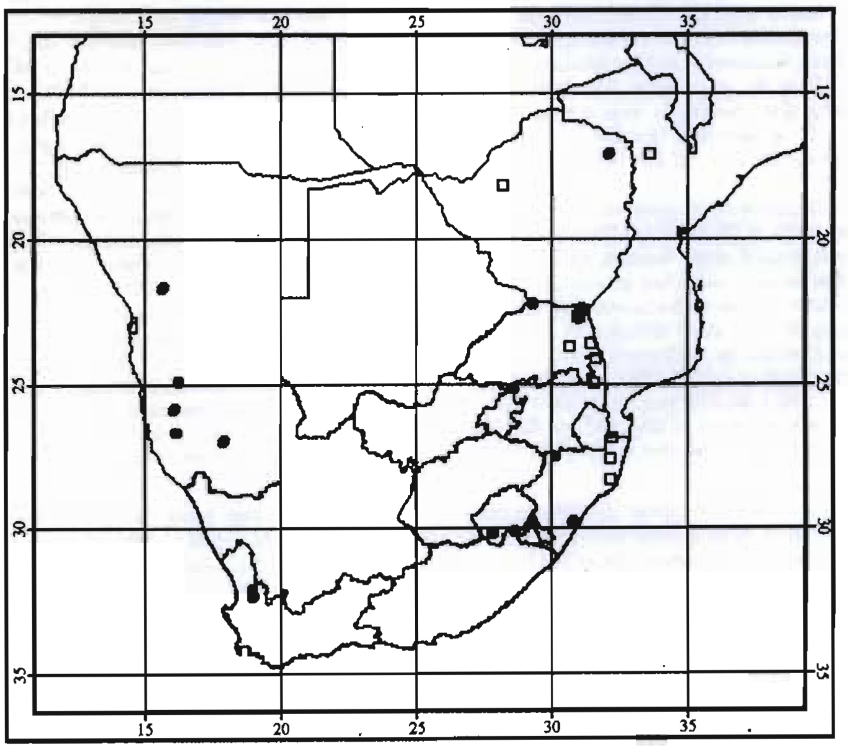

Fig. 2. Southern African distribution of 48 specimens of *Eptesicus hottentotus* (●) and 105 specimens of *Scotophilus viridis* (□) used in the principal component analysis, together with the locality of DM1887 and DM1888 (▲).

Nature Reserve and Ukuhlambe-Drakensberg World Heritage Site (formerly the Natal Drakensberg) (Taylor 1998), the record from the Ukuhlambe-Drakensberg World Heritage Site (reported by Sclater 1901) could not be substantiated, as the whereabouts of the specimen remains unknown (Taylor 1998). Our re-identification of DM1887 and DM1888 collected in 1992 at Garden Castle Nature Reserve (29°45'S; 29°13'E) as *E. hottentotus*, which was previously identified as *S. borbonicus* by Taylor *et al.* (1994), confirms the occurrence of *E. hottentotus* in the Ukuhlambe-Drakensberg World Heritage Site. This re-identification of DM1887 and DM1888 also changes the habitat association of montane grassland attributed to *S. viridis* by Taylor (1998, 2000).

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Appendix 1. Additional specimens examined.

Eptesicus hottentotus (A. Smith 1833) (48 specimens)
SOUTH AFRICA: Western Cape: Cederberg, Algeria State Forest 32°24'S; 19°08'E (TM35150, 35150, 38411, 38411, 38412, 41419, 40630, 40631, SAM41418); Cederberg, Kliphuis Campsite 32°08'S; 18°57'E (SAM41416). KwaZulu-Natal: Kranskloof Nature Reserve 29°47'S; 30°48'E (TM40017); 9 km NE of Louwsburg, Ithala Game Reserve: 27°30'S; 30°12'E (Tm31756). Limpopo Province: 67 km W of Messina, Farm Greefswald 37, Shashi-Limpopo confluence 22°13'S; 29°22'E (TM41421); Kruger National Park (KNP) - Punda Milia 22°33'S; 31°04'E (TM36780); KNP- Levuhu Hippo Pool, 4 km W of bridge 22°26'S; 31°11'E (TM34239); KNP- Pafuri 22°25'S; 31°11'E (TM36879, 38167). **LESOTHO**: Kofa, Quacha's Nek 30°07'S; 28°41'E (NMB8343); Quthing, Mt Morosi 30°11'S; 27°52'E (NMB8176). **NAMIBIA**: 3 km W of Aus, Farm Klein Aus 8 26°39'S; 16°13'E (TM37555, 37553, 37551, 37540, 37552, 37554, 37560); 70 km W of Maltahohe, Farm Zwartmodder 101 24°54'S; 16°17'E (TM32695,37588, 37624); Ombu, Eronga Mountain 21°35'S; 15°43'E (TM9493, 9482, 9482, 9484-9486, 9488, 9489, 9491); Farm Kanaan 25°52'S; 16°07'E (TM27418, 32565); 35 km SSW of Keetmanshoop, Farm Rheinsvels 26°57'S; 17°56'E (TM32566). **ZIMBABWE**: Nyapfunde School, Nyashato dam 17°08'S; 32°08'E (NMZ32571-32580).

Scotophilus viridis (Peters 1852) (105 specimens)
SOUTH AFRICA: Limpopo Provice: KNP-Letaba Camp 23°59'S; 31°50'E (Tm39571, 39575); KNP- Levuhu Hippo pools, 4 km W of bridge 22°26'S; 31°11'E (TM30488, 30510, 30511, 30524, 30528-30530, 30551, 30552, 34166, 34168, 34169, 34193, 34228-34231, 3451-34260, 39482); KNP- Punda Maria 22°41'S; 31°02'E (TM39481, 30599-30600, 30605-30607, 30617-30623, 30631, 30632); KNP- Shashanga Windmill 22°40'S; 30°59'E (TM30665, 30667); 30 km NE of Letsitele, Hans Merensky Nature Reserve 23°40'S; 30°41'E (TM24555); Mpumalanga: KNP- Skukuza camp, Sabie River 24°57'S; 31°38'E (TM42087, 42088, 42090, 42091); KNP- 2km SE of Roodevaal Private Camp 24°08'S; 31°36'E (TM39679, 39677). KwaZulu-Natal: Dukuduku Forest 28°24'S; 32°20'E (TM40354, 40385, 40387, 40388); Mkuzi Game Reserve 27°47'S; 32°12'E (TM35250-35254, 35256-35260, 35274, 35276, 35277, 35318-35320, 35329-35332); Ndumu Game Reserve 26°53'S; 32°16'E (TM35218, 35219, 35235, 35236, 35238). **MOZAMBIQUE**: Beira 19°50'S; 34°55'E (TM35238); Tete District 17°09'S; 33°38'E (TM1093, 14703). **ZIMBABWE**: Sengwa Wildlife Research Station 18°10'S; 28°13'E (TM34893, 34894, 34896-34899, 34902-34904, 34952-34957, 34976, 34977).

Morphometric analysis of cranial and external characters of *Laephotis* Thomas, 1901 (Mammalia: Chiroptera: Vespertilionidae) from southern Africa

Teresa C. Kearney[1,2*] and Ernest C. J. Seamark[1]
[1]Vertebrate Department, Transvaal Museum, NFI, P.O. Box 413, Pretoria, 0001 South Africa
[2]School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban, 4041 South Africa

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Morphometric analyses, which included palatal and post-palatal measurements, allow the distinction of *Laephotis botswanae* and *L.* cf. *angolensis* from other *Laephotis* species, and suggest the assignment of specimens from KwaZulu-Natal in South Africa previously identified as *L.* cf. *wintoni* to *L. botswanae*. The distinction between *L. wintoni* and *L. namibensis*, however, was not confirmed and still remains to be clarified. It is suggested that until the species distinction is further clarified by additional characters or other systematic techniques, the current species assignments be retained. Morphometric analyses based on cranial characters, which excluded palatal and post-palatal measurements, show some separation of the *Laephotis* species in the principal component analysis, but not in the cluster analysis. Analyses based on external characters only were not useful for the separation of the *Laephotis* species.

Keywords: *Laephotis*, Species Identification, Cranial and External Measurements, Multivariate Morphometrics.

INTRODUCTION

Although the genus *Laephotis* Thomas, 1901, is poorly known due to the paucity of specimens (Kock and Howell, [1988]; Stanley and Kock, 2004), four species are currently recognized (Koopman, 1993): *L. angolensis* Monard, 1935, *L. botswanae* Setzer, 1971, *L. namibensis* Setzer, 1971, and *L. wintoni* Thomas, 1901. The accurate species identification of individuals of the genus *Laephotis* found in the southwestern (Rautenbach and Nel, 1978) and southeastern (Kearney and Taylor, 1997; Watson, 1990) parts of southern Africa has proved contentious and complicated. The initial identification of a specimen from the Western Cape Province, South Africa as *L. wintoni* (Rautenbach and Nel, 1978) was made on the basis of a multivariate morphometric analysis of nine measurements using mean values calculated for each of the *Laephotis* species from measurements in Hill (1974). This identification was contrary to an assumption of the species' identity as *L. namibensis* based on the closer geographic proximity of the Western Cape locality to localities of *L. namibensis*, whereas the Western Cape locality is much further from localities of the type and other specimens of *L. wintoni*. Rautenbach and Nel (1978) cautioned that their analysis indicated the taxonomic status of species in the genus *Laephotis* was not satisfactorily resolved, and would require further specimens to remedy the problem. Neither Honacki *et al.* (1982) nor Corbet and Hill (1991) followed the contentious identification by Rautenbach and Nel (1978), instead they both referred the specimen from the Western Cape to *L. namibensis*. Later, Koopman (1994) indicated *L. namibensis* was only definitely known from Namibia, and that the Western Cape specimen apparently belonged to *L. wintoni*. However, the species account for *L. wintoni* was withdrawn from the accounts in 'Mammals of the Southern African Subregion' (Skinner and Smithers, 1990:107) as 'further investigation in progress by I.L. Rautenbach and D.A. Schlitter reveal that this specimen is placed more appropriately with *L. namibensis* (I.L. Rautenbach, pers. comm.), with which it is provisionally placed'. Using the same morphometric analysis and measurements as Rautenbach and Nel (1978), subsequent records of *Laephotis* from the Free State, Lesotho (Watson, 1990) and KwaZulu-Natal (Kearney and Taylor, 1997) were also identified as *L. wintoni* and *L.* cf. *wintoni*. Of the currently recognized *Laephotis* species, only *L. wintoni* and *L. botswanae* were assessed in the latest Red Data Book of the Mammals of South Africa (Friedmann and Daly, 2004), since the taxonomic emendation in Skinner and Smithers (1990) recognizing the specimens from the Western Cape as *L. namibensis* was not taken into account.

The measurement suite of nine standard morphometric measurements, one forearm and eight

*Author for correspondence. E-mail: kearney@nfi.co.za

cranial and dental measurements, used in previous multivariate analyses to identify specimens of South African *Laephotis* (Rautenbach and Nel, 1978; Watson, 1990; Kearney and Taylor, 1997) did not incorporate Hill's (1974) six palatal and post-palatal measurements. Stanley and Kock (2004) confirmed palatal and post-palatal measurements as characteristic and useful for the separation of at least two of the *Laephotis* species, *L. wintoni* and *L. botswanae*. Hill (1974) identified that in *L. wintoni* the post-palatal measurement of the distance from a line across the rear margins of M^3 to the anterior edge of the mesopterygoid fossa is longer than the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars. In *L. botswanae* and *L. angolensis*, however, the post-palatal measurement of the distance from a line across the rear margins of M^3 to the anterior edge of the mesopterygoid fossa is shorter than the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars (Hill, 1974). The aim of this study was to revisit as many of the specimens of southern African *Laephotis* as possible to assess their identification with reference to palatal and post-palatal measurements (Hill, 1974; Stanley and Kock, 2004) and to include these measurements in a morphometric analysis to evaluate whether they support earlier morphometric identifications.

MATERIAL AND METHODS

Eighteen cranial and mandibular measurements (Table 1, Fig. 1) were taken with digital callipers from 36 specimens of *Laephotis* variously ascribed to the species *botswanae, namibensis,* cf. *wintoni* and *wintoni* (see Appendix I for specimen details). Where appropriate, the same measurement abbreviations used by Stanley and Kock (2004) have been followed. Measurements were made of the same eight cranial and dental lengths included in previous analyses of specimens from South Africa: greatest skull length, from anterior-most point of I^1 to posterior-most point of occipital (Cnr inc); condylocanine length (Cdl); zygomatic width (Zyg); least postorbital breadth (Por); braincase breadth (Bcw); braincase depth, from basioccipital bone to top of braincase (Bcd); greatest breadth across outer edge of upper canines (C–C); width across outer edge of upper third molars (M^3–M^3); maxillary tooth row from anterior surface of canine to posterior surface of upper third molar (C–M^3). An additional four cranial, mandibular and dental measurements were added: skull breadth at mastoids (Mast); length from anterior surface of first upper incisor to posterior surface of upper third molar (I^1–M^3); mandible length (Mand); length from anterior surface of canine to posterior surface of lower third molar (C–M_3). The six palatal measurements described by Hill (1974) included: palatal length from the anterior edge of incisors to anterior edge of mesopterygoid fossa (Palat); length from the rear of pre-palatal emargination to anterior edge of mesopterygoid fossa (Lpp–mesop); length from rear of pre-palatal emargination to line across posterior faces of M^{3-3} (Lpp–M^3); length from line across posterior faces of M^3–M^3 to anterior edge of mesopterygoid fossa (LM^3–mesop); length from anterior edge of mesopterygoid fossa to tip of pterygoid hamulars (Lmesop–ham); length from line across posterior faces of M^{3-3} to tip of pterygoid hamulars (LM^3–ham).

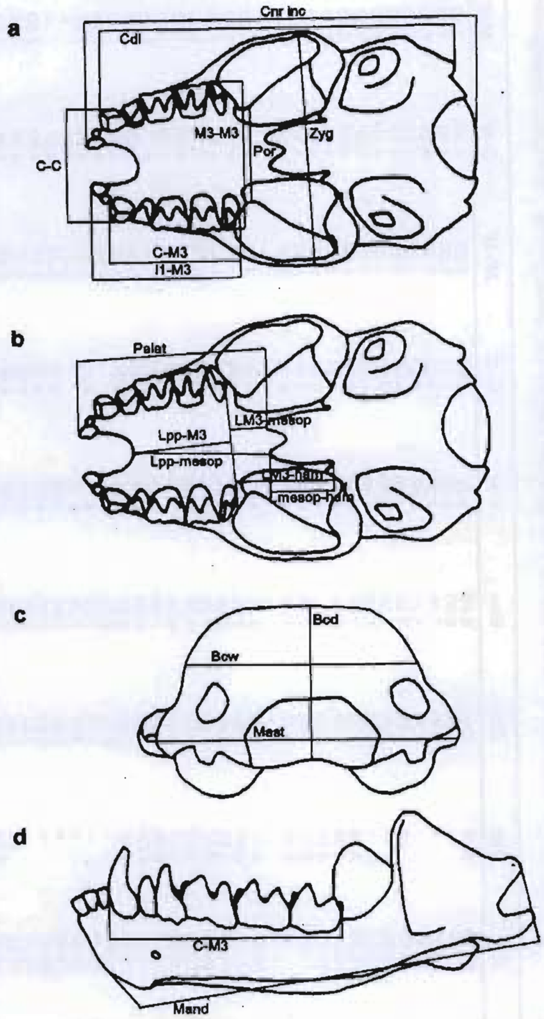

Fig. 1

Diagrams showing the position of measurements on the ventral (**a** and **b**) and posterior (**c**) skull, and lateral mandible (**d**). See material and methods for a description of measurement abbreviations.

Five external measurements (Table 2) were noted

Table 1

Cranial measurements of various *Laephotis* species used in this analysis taken from the literature (L1 = Hill, 1974; L2 = Stanley and Kock, 2004; L3 = Setzer, 1971; L4 = Kock and Howell, [1988]; L5 = Bauer, 1992) or measured (M) by one of the authors (TK). Species identification (Id) records information from the most recent literature and, where unpublished, follows museum records for the specimen: L.cf.a = *L.* cf. *angolensis*; L.b = *L. botswanae*; L.cf.w = *L.* cf. *wintoni*; L.n = *L. namibensis*; L.w = *L. wintoni*. Holotypes are denoted by *, paratypes by '. See text of material and methods for descriptions of measurement abbreviations.

Code	Accession	Source	Id	Cnr inc	Cdl	Zyg	Por	Bcw	Bcd	C–C	M^3–M^3	C–M^3	Mast
ca1	BM57.435	L1	L.cf.a	13.80	13.10	8.10	3.40	6.80	4.50	3.80	5.20	4.30	7.40
ca2	BM57.437	L1	L.cf.a	13.70	12.90	–	3.50	6.80	4.30	3.70	5.00	4.30	7.40
b1	MRAC26.402	L1	L.b	14.50	13.60	–	3.70	7.40	4.60	4.00	5.40	4.50	7.90
b2	MRAC26.403	L1	L.b	14.30	13.50	–	3.70	7.30	4.60	4.00	5.40	4.60	7.60
b3	MRAC26.404	L1	L.b	14.60	13.70	–	3.50	7.10	4.60	4.00	5.40	4.50	7.80
b4	MRAC26.405	L1	L.b	14.30	13.60	–	3.60	7.20	4.70	3.80	5.20	4.50	7.80
b5	BM55.1135	L1	L.b	14.30	13.50	–	3.60	7.10	4.50	4.00	5.50	4.60	7.50
b6	HZM1.2533	L1	L.b	15.00	14.30	8.80	3.70	7.40	4.60	4.30	5.80	4.80	8.40
b7	FMNH84120	L2	L.b	14.90	13.65	8.73	3.70	7.06	4.84	4.37	5.56	4.68	7.63
b8	FMNH83605	L2	L.b	14.52	13.27	8.59	3.65	–	4.75	3.93	5.45	4.52	7.28
b9	FMNH152728	L2	L.b	14.50	13.40	8.50	3.46	7.19	4.84	4.10	5.50	4.58	7.58
b10*	USNM425349*	L3	L.b	14.50	–	8.30	3.40	7.00	4.70	4.40	5.40	4.70	–
b11	NMW19823	L5	L.b	–	–	–	–	–	–	–	–	–	–
b12	TM44544	M	L.b	15.50	14.85	8.75	3.60	7.30	4.91	4.45	5.55	4.90	8.20
b13	TM38153	M	L.b	–	–	8.60	3.65	7.05	5.03	4.20	5.40	4.70	7.90
b14	TM38154	M	L.b	15.05	14.50	8.60	3.60	7.05	4.81	4.20	5.45	4.80	7.80
b15	TM40107	M	L.b	14.90	14.50	8.35	3.60	7.05	–	4.15	5.40	4.75	8.20
b16	TM39946	M	L.b	14.65	13.90	8.00	3.75	7.15	4.58	4.20	5.50	4.70	7.60
b17	TM38123	M	L.b	14.45	13.90	8.25	3.65	6.90	–	4.10	5.50	4.70	7.70
b18	TM38155	M	L.b	14.90	14.25	8.70	3.65	7.30	4.72	4.25	5.55	4.70	8.05
b19	TM39796	M	L.b	14.75	14.35	8.00	3.55	6.95	4.76	4.05	5.30	4.60	7.85
b20	TM34964	M	L.b	14.40	13.80	8.05	3.60	8.85	5.04	4.00	5.20	4.50	7.60
b21	NM29992	M	L.b	14.67	13.81	–	3.75	7.22	4.61	–	5.59	4.66	7.96
b22	NM29592	M	L.b	14.89	14.23	–	3.76	7.26	4.75	4.22	5.37	4.90	7.87
b23	NM30030	M	L.b	14.73	13.47	–	3.57	7.30	4.76	–	5.21	4.55	–
b24	NM58131	M	L.b	14.55	13.43	–	3.63	7.05	4.53	4.10	5.39	4.67	–
b25	NM59330	M	L.b	14.50	13.41	–	3.53	7.13	4.71	4.12	5.38	4.80	7.60
b26	NM63201	M	L.b	14.14	13.12	–	3.64	6.97	4.60	3.92	5.17	4.59	7.64
b27	NM63202	M	L.b	14.60	13.55	–	3.63	6.96	4.57	4.08	5.53	4.94	7.63
cw1	DM6898	M	L.cf.w	15.22	14.27	8.73	3.75	7.43	4.45	4.47	5.65	4.86	8.26
cw2	DM5351	M	L.cf.w	14.99	13.97	8.66	3.72	7.36	4.86	4.35	5.53	4.91	8.14
cw3	DM6899	M	L.cf.w	15.00	13.95	8.46	3.64	7.19	4.76	4.41	5.33	4.82	8.03
n1*	USNM342152*	L3	L.n	16.50	–	9.00	3.20	7.50	4.70	4.00	5.20	4.90	–
n2'	USNM342153'	L3	L.n	16.50	–	–	3.60	7.60	4.90	4.00	5.40	5.00	–
n3	TM37548	M	L.n	16.30	15.40	8.85	3.65	7.95	5.12	4.30	5.50	4.85	8.15
n4	TM37586	M	L.n	16.90	16.20	9.00	3.60	7.70	4.92	4.30	5.45	5.15	8.20
n5	TM37547	M	L.n	16.10	15.40	8.55	3.65	7.95	4.87	4.15	5.10	4.75	7.95
n6	TM33472	M	L.n	16.25	15.25	8.40	3.45	7.40	4.82	3.95	5.20	4.90	7.80
n7	TM37608	M	L.n	16.10	15.25	8.95	3.75	7.80	4.89	4.15	5.20	5.00	8.10
n8	TM37609	M	L.n	16.05	15.45	8.75	3.65	7.65	4.77	4.10	5.30	4.90	8.00
n9	TM28316	M	L.n	16.25	15.65	8.85	3.80	7.60	5.00	4.30	5.55	5.20	8.40
n10	TM38426	M	L.n	17.00	16.70	9.15	3.90	7.95	5.32	4.35	5.55	5.35	8.60
n11	ZM41415	M	L.n	16.66	15.26	9.15	3.85	7.95	5.13	4.46	5.44	5.24	8.68
n12	ZM41417	M	L.n	16.61	15.28	9.00	3.64	7.68	5.05	4.33	5.46	5.18	8.58
w1	NMB6698	M	L.w	15.97	15.31	9.19	4.14	7.96	5.17	4.64	5.72	5.33	8.54
w2	NMB6687	M	L.w	15.90	15.18	9.22	3.95	8.05	5.12	4.45	5.79	5.16	–
w3	NMB6688	M	L.w	–	15.17	9.00	3.97	7.87	–	4.40	5.63	5.22	8.70
w4	NMB6686	M	L.w	15.94	15.12	–	3.94	7.77	5.06	4.61	5.69	5.25	8.59
w5	NMB6697	M	L.w	15.98	15.33	9.03	3.84	7.87	4.94	4.47	–	5.25	8.50
w6	NMB6379	M	L.w	15.58	14.93	8.99	3.92	7.86	4.97	4.39	5.42	5.11	8.26
w7	NMB6378	M	L.w	15.78	15.23	8.76	3.94	7.82	4.98	4.38	5.62	5.18	8.48
w8	BM72.4398	L1	L.w	16.30	15.50	9.40	3.90	7.50	4.70	4.60	5.90	5.20	8.50
w9	BM72.4397	L1	L.w	16.30	15.60	8.90	3.70	7.40	4.80	4.50	5.60	5.20	8.30
w10*	BM1.5.6.5*	L1	L.w	15.80	15.20	–	3.70	7.40	4.80	4.30	5.50	5.00	8.50
w11	BM72.4399	L1	L.w	16.20	15.80	9.10	3.70	7.60	4.80	4.50	5.50	5.00	8.50
w12	SMF66961	L4	L.w	15.80	14.80	9.00	3.90	7.70	–	–	5.90	5.20	8.20
w13	FMNH171300	L2	L.w	16.20	14.92	9.50	3.87	7.61	5.04	4.52	5.87	5.16	8.21

Table 1 (*continued*)

Code	Accession	Source	Id	I^1–M^3	Mand	C–M_3	Palat	Lpp–mesop	Lpp–M^3	LM^3–mesop	Lmesop–ham	LM^3–ham
ca1	BM57.435	L1	L.cf.a	–	8.80	4.80	6.20	4.80	3.60	1.20	2.00	3.20
ca2	BM57.437	L1	L.cf.a	–	8.90	4.70	6.10	4.80	3.50	1.30	1.90	3.20
b1	MRAC26.402	L1	L.b	–	9.40	4.90	6.60	5.20	3.70	1.50	2.00	3.50
b2	MRAC26.403	L1	L.b	–	9.10	4.90	6.60	5.20	3.70	1.50	1.90	3.40
b3	MRAC26.404	L1	L.b	–	9.50	5.00	6.40	5.20	3.80	1.40	1.90	3.30
b4	MRAC26.405	L1	L.b	–	9.20	5.00	6.50	5.30	3.80	1.50	1.90	3.40
b5	BM55.1135	L1	L.b	–	9.20	4.90	6.40	5.20	3.70	1.50	1.90	3.40
b6	HZM1.2533	L1	L.b	–	9.90	5.20	7.10	5.60	4.10	1.50	2.00	3.50
b7	FMNH84120	L2	L.b	–	9.85	5.15	7.29	5.26	3.92	1.34	1.90	3.24
b8	FMNH83605	L2	L.b	–	–	–	6.31	–	–	1.22	2.22	–
b9	FMNH152728	L2	L.b	–	9.45	4.94	6.16	4.90	3.96	0.94	2.24	3.28
b10*	USNM425349*	L3	L.b	–	–	–	–	–	–	–	–	–
b11	NMW19823	L5	L.b	–	–	–	6.60	5.20	3.80	1.50	1.90	3.40
b12	TM44544	M	L.b	5.65	10.35	5.15	7.15	5.63	4.18	1.45	2.18	3.45
b13	TM38153	M	L.b	–	9.95	4.80	6.70	5.47	3.87	1.58	1.68	3.16
b14	TM38154	M	L.b	5.45	10.25	5.20	6.78	5.56	4.17	1.45	2.05	3.15
b15	TM40107	M	L.b	5.50	10.05	5.10	6.73	5.21	4.02	1.40	2.26	3.41
b16	TM39946	M	L.b	5.47	9.99	5.18	6.64	5.19	3.85	1.47	1.89	3.08
b17	TM38123	M	L.b	5.48	10.01	5.16	6.85	5.45	4.18	1.47	1.95	3.07
b18	TM38155	M	L.b	5.45	10.05	5.10	–	–	3.68	–	–	2.64
b19	TM39796	M	L.b	5.35	10.00	4.90	6.97	5.54	4.01	1.65	1.64	3.33
b20	TM34964	M	L.b	5.20	9.70	4.80	–	–	4.02	–	–	3.37
b21	NM29992	M	L.b	5.34	10.00	5.06	6.51	5.10	3.91	1.49	2.14	3.44
b22	NM29592	M	L.b	5.42	10.24	5.17	6.76	5.29	3.84	1.49	2.26	3.62
b23	NM30030	M	L.b	5.20	–	4.78	6.40	4.99	3.79	1.31	–	–
b24	NM58131	M	L.b	5.34	–	4.97	6.43	4.93	3.67	1.45	–	–
b25	NM59330	M	L.b	5.46	–	5.16		–	–	–	–	–
b26	NM63201	M	L.b	5.29	–	4.84	–	–	–	–	–	–
b27	NM63202	M	L.b	5.37	9.94	5.03	–	5.03	3.67		2.09	3.60
cw1	DM6898	M	L.cf.w	5.63	10.41	5.26	7.03	5.49	3.99	1.57	2.30	3.70
cw2	DM5351	M	L.cf.w	5.63	10.17	5.20	6.94	5.40	4.31	1.54	2.13	3.29
cw3	DM6899	M	L.cf.w	5.61	10.20	5.06	6.94	5.60	4.25	1.69	2.01	3.53
n1*	USNM342152*	L3	L.n	–	–	–	–	–	–	–	–	–
n2*	USNM342153*	L3	L.n	–	–	–	–	–	–	–	–	–
n3	TM37548	M	L.n	5.70	10.85	5.75	7.93	6.37	4.61	2.30	2.13	4.18
n4	TM37586	M	L.n	5.95	11.50	5.40	8.20	6.74	4.53	2.34	2.00	4.32
n5	TM37547	M	L.n	5.64	11.21	5.10	7.63	6.23	4.42	2.19	–	–
n6	TM33472	M	L.n	5.60	10.35	5.05	7.59	6.39	4.24	1.86	–	–
n7	TM37608	M	L.n	5.77	10.80	5.28	7.81	6.13	4.36	2.16	2.00	3.94
n8	TM37609	M	L.n	5.60	10.65	5.10	7.75	6.11	4.24	2.21	2.01	4.01
n9	TM28316	M	L.n	6.10	11.15	5.40	8.24	6.47	4.62	1.96	–	–
n10	TM38426	M	L.n	6.30	11.50	5.50	8.72	6.78	4.68	2.47	2.61	4.54
n11	ZM41415	M	L.n	6.22	10.95	5.45	8.24	6.39	4.69	2.18	2.50	4.31
n12	ZM41417	M	L.n	6.14	11.13	5.53	7.97	6.39	4.62	2.08	2.49	4.27
w1	NMB6698	M	L.w	6.18	11.56	5.62	8.18	6.68	4.58	2.11	2.22	3.93
w2	NMB6687	M	L.w	6.09	11.46	5.45	8.13	6.74	4.63	2.03	2.25	4.17
w3	NMB6688	M	L.w	6.15	11.29	5.53	8.13	6.90	4.86	2.13	2.47	4.41
w4	NMB6686	M	L.w	6.22	–	5.46	8.23	6.57	4.50	2.04	2.46	4.34
w5	NMB6697	M	L.w	6.11	11.25	5.46	8.16	6.75	4.43	2.10	2.43	4.48
w6	NMB6379	M	L.w	6.04	10.88	5.44	7.90	6.43	4.40	1.97	2.18	4.03
w7	NMB6378	M	L.w	5.99	11.17	5.40	7.91	6.47	4.52	2.15	–	–
w8	BM72.4398	L1	L.w	–	10.70	5.50	8.20	6.40	4.20	2.20	2.00	4.20
w9	BM72.4397	L1	L.w	–	10.80	5.60	8.10	6.80	4.40	2.40	1.80	4.20
w10*	BM1.5.6.5*	L1	L.w	–	10.60	5.50	7.90	6.50	4.40	2.10	1.90	4.00
w11	BM72.4399	L1	L.w	–	–	5.50	8.50	6.80	4.30	2.50	1.90	4.40
w12	SMF66961	L4	L.w	–	10.90	5.40	–	–	–	–	–	–
w13	FMNH171300	L2	L.w	–	10.49	5.55	8.01	6.47	4.20	2.20	1.92	4.07

Table 2

External measurements used in this analysis (Source) taken from the literature (L1 = Hill, 1974; L2 = Stanley and Kock, 2004; L3 = Setzer, 1971; L4 = Kock and Howell, [1988]; L5 = Bauer, 1992), specimen labels (S), measured on dry skins (M) by one of the authors (TK), and calculated (C) (see material and methods for explanation). Species identification (Id) records information from the most recent literature and, where unpublished, follows museum records for the specimen: L.cf.a = *Laephotis* cf. *angolensis*; L.b = *L. botswanae*; L.cf.w = *L.* cf. *wintoni*; L.n = *L. namibensis*; L.w = *L. wintoni*. Holotypes are denoted by '*', paratypes by '+'. See materials and methods for a description of measurement abbreviations.

Code	Accession no.	Source	Id	TL	T	HF	E	FA
ca1	BM57.435	L1	L.cf.a	–	–	–	16.0	35.5
ca2	BM57.437	L1	L.cf.a	–	–	–	15.9	34.3
b1	MRAC26.402	L1	L.b	–	–	–	16.5	37.8
b2	MRAC26.403	L1	L.b	–	–	–	16.3	35.8
b3	MRAC26.404	L1	L.b	–	–	–	16.8	37.0
b4	MRAC26.405	L1	L.b	–	–	–	17.9	36.4
b5	BM55.1135	L1	L.b	–	–	–	–	35.3
b6	HZM1.2533	L1	L.b	–	–	–	–	37.0
b7	FMNH84120	L2	L.b	100.0	45.0	6.0	19.0	37.5
b8	FMNH83605	L2	L.b	96.0	44.0	6.5	19.0	37.0
b9	FMNH152728	L2	L.b	99.0	43.0	6.0	18.0	34.8
b10*	USNM425349*	L3	L.b	96.0	41.0	8.0	21.0	37.3
b11	NMW19823	L5	L.b	–	39.5	7.5	16.0	35.3
b12	TM44544	M	L.b	–	–	–	18.1^{C}	37.5
b13	TM38153	M	L.b	–	–	–	18.6^{C}	37.6
b14	TM38154	M	L.b	–	–	–	17.1^{C}	36.5
b15	TM40107	S	L.b	95.0	40.0	7.0	19.0	35.6
b16	TM39946	M	L.b	–	–	–	18.6^{C}	35.5
b17	TM38123	M	L.b	–	–	–	17.1^{C}	–
b18	TM38155	M	L.b	–	–	–	18.6^{C}	35.5
b19	TM39796	S	L.b	98.0	44.0	–	16.5	35.0
b20	TM34964	M	L.b	94.0	40.0	7.0	17.0	34.2
b21	NM29992	S	L.b	–	–	–	–	35.4
b22	NM29592	S	L.b	94.5	43.5	8.0	20.5	37.0
b23	NM30030	S	L.b	90.2	43.6	–	18.9	36.4
b24	NM58131	S	L.b	92.6	46.0	6.3	17.8	34.2
b25	NM59330	S	L.b	90.0	44.0	8.0	19.0	36.0
b26	NM63201	S	L.b	90.0	40.0	8.0	21.0	33.0
b27	NM63202	S	L.b	100.0	46.0	8.0	20.0	36.0
cw1	DM6898	M	L.cf.w	113.0	45.0	7.8	19.6	38.1
cw2	DM5351	M	L.cf.w	94.0	43.0	7.0	19.0	37.0
cw3	DM6899	M	L.cf.w	109.0	42.5	8.0	20.0	36.9
n1*	USNM342152*	L3	L.n	106.0	47.0	8.0	25.0	38.2
n2*	USNM342153+	L3	L.n	104.0	46.0	8.0	24.0	38.6
n3	TM37548	M	L.n	–	–	–	23.1^{C}	38.0
n4	TM37586	M	L.n	–	–	–	23.1^{C}	37.2
n5	TM37547	M	L.n	–	–	–	22.6^{C}	36.2
n6	TM33472	S	L.n	91.0	38.0	8.0	24.0	39.0
n7	TM37608	M	L.n	–	–	–	22.6^{C}	35.9
n8	TM37609	M	L.n	–	–	–	23.1^{C}	36.6
n9	TM28316	S	L.n	111.0	46.0	–	22.0	38.9
n10	TM38426	M	L.n	–	–	–	-	39.5
n11	ZM41415	M	L.n	96.0	47.0	8.0	20.0	37.4
n12	ZM41417	M	L.n	103.0	47.0	9.0	25.0	39.0
w1	NMB6698	S	L.w	108.0	47.0	9.0	21.0	40.0
w2	NMB6687	S	L.w	107.0	50.0	9.0	23.0	40.0
w3	NMB6688	S	L.w	106.0	49.0	9.0	21.0	39.0
w4	NMB6686	S	L.w	107.0	47.0	9.0	21.0	40.0
w5	NMB6697	S	L.w	111.0	47.0	9.0	24.0	40.0
w6	NMB6379	S	L.w	102.0	46.0	9.0	23.0	39.0
w7	NMB6378	S	L.w	91.0	38.0	8.5	23.0	40.0
w8	BM72.4398	L1	L.w	–	–	–	21.1	40.2
w9	BM72.4397	L1	L.w	–	–	–	21.4	40.7
w10*	BM1.5.6.5*	L1	L.w	–	–	–	–	37.2
w11	BM72.4399	L1	L.w	–	–	–	21.5	40.2
w12	SMF66961	L4	L.w	–	44.5	6.3	21.2	39.0
w13	FMNH171300	L2	L.w	96.0	42.0	8.0	23.0	39.0

from specimen records, or recorded from dry museum specimens: total length (TL), tail length (T), hind foot length (HF), ear length (E), and forearm length (FA). Ear length was measured from dry skins of 11 specimens that lacked records of external measurements. In order to account for shrinkage due to the dried nature of the specimens, a mean shrinkage value of 3.13 mm was calculated from four specimens by subtracting the measurement of ear length made on the dried specimen from the measurement recorded in the museum records. The calculated shrinkage value was added to measurements made from dried specimens.

Cranial (Table 1) and external (Table 2) measurements for an additional 21 specimens of *Laephotis* were added from the literature (Setzer, 1971; Hill, 1974; Kock and Howell, [1988]; Stanley and Kock, 2004). These specimens were largely records from localities extra-limital to the range of the southern African specimens measured for this analysis. Unfortunately most of the cranial measurements for a new specimen of *L. botswanae* from Tanzania (Bauer, 1992) could not be included as the cranial measurements presented were ambiguous. Palatal measurements and some external measurements from this specimen were, however, included in this analysis. Measurements from the literature included information for the holotype of *L. wintoni* (Hill, 1974) (BM 1.5.6.5), the holotype of *L. botswanae* (Setzer, 1971) (USNM 425349), and the holotype and a paratype of *L. namibensis* (Setzer, 1971) (USNM 342152 and USNM 342153, respectively). Unfortunately, the *L. botswanae* and *L. namibensis* type specimens lacked post-palatal measurements. The species identifications used in the text and tables follow what is most recently published in the literature, and where unpublished, follow the identification in museum records for the specimen. Cranial measurements of two new *L. wintoni* specimens from Ethiopia (Lavrenchenko *et al.*, 2004) were not included as these were given as a mean for the specimens and did not include all the measurements used in this analysis. These specimens were, however, included in the distribution map (Fig. 1) and in calculations of vegetation biome associations.

The statistical package NTSYS-pc, version 2.01h (Rohlf, 1997) was used for principal component analyses (PCA) using correlation matrices based on standardized measurements, and unweighted pair group method using arithmetic averages (UPGMA) cluster analyses based on distance matrices of standardized measurements. PCA and UPGMA analyses were based on five different data suites to allow the analysis of external and cranial measurements together and separately, as well as compensate for specimens with missing variables. The measurements and number of specimens included in each of analyses were as follows:

1. six palatal measurements (Palat, Lpp–mesop, Lpp–M^3, LM^3–mesop, Lmesop–ham, LM^3–ham), introduced by Hill (1974), from 40 specimens;
2. 17 cranial measurements (Cnr inc, Cdl, Por, Bcw, Bcd, Mast, C–C, M^3–M^3, C^1–M^3, Mand, C–M_3, Palat, Lpp–mesop, Lpp–M^3, LM^3–mesop, Lmesop–ham, LM^3–ham) from 31 specimens;
3. two external (E, FA) and 14 cranial measurements (Cnr inc, Por, Bcw, Mast, C–C, M^3–M^3, C^1–M^3, C–M_3, Palat, Lpp–mesop, Lpp–M^3, LM^3–mesop, Lmesop–ham, LM^3–ham) from 31 specimens;
4. one external (FA) and seven cranial measurements (Cnr inc, Por, Bcw, Bcd, C–C, M^3–M^3, C^1–M^3) from 46 specimens – these measurements were chosen specifically to include literature records of type specimens of *L. botswanae*, *L. namibensis,* and *L. wintoni,* together with as many other specimens as possible;
5. five external measurements (TL, T, HF, E, FA) from 27 specimens.

Only the first, second and third analyses included palatal and post-palatal measurements.

An updated distribution map for the different species was plotted based on museum voucher records. Biomes associated with distributions of each of the species were assessed using Rutherford and Westfall's (1994) biome data for South Africa, Lesotho, Swaziland, Namibia and Botswana (supplied as a GIS shape file data 'SA Biomes (Rutherford)' at the South African National Botanical Institute's website http://www.plantzafrica.com/vegetation/vegmain.htm), and using the eco-region data of Olsen and Dinerstein (2002) for the rest of Africa (supplied as a GIS shape file data at the World Wildlife Foundation Global 200 Eco-regions website http://worldwildlife.org/science/data/terreco.cfm).

RESULTS

Post-palatal measurements of specimens from Hella-Hella in KwaZulu-Natal that were previously identified as *L.* cf. *wintoni* (Table 1) fall within the ranges described by Hill (1974) for *L. botswanae.* Furthermore, as described by Hill (1974) for *L. botswanae,* the distance from a line across the rear margins of both M3 to the anterior edge of the mesopterygoid fossa is less than the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars in specimens from Hella-Hella in KwaZulu-Natal. Hill's (1974) description of palatal and post-palatal measurements did not include *L. namibensis.* Table 1 shows that in specimens of *L. namibensis* from Namibia, as in *L. wintoni,* the distance from a line across the rear margins of M^3 to the anterior edge of the mesopterygoid fossa (LM3–mesop) is longer than the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars. Specimens from the Western Cape and Free State Provinces in South Africa and from Lesotho do not, however, follow the condition noted by Hill (1974) for *L. wintoni* in that the distance from a line across the rear margins of both M^3 to the anterior edge of the mesopterygoid fossa does not exceed the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars. In these specimens measurements from a line across the rear margins of both M^3 to the anterior edge of the mesopterygoid fossa, and from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars (Table 1), are larger than those for *L. botswanae* and *L. angolensis,* being instead more like measurements for *L. wintoni* (Hill, 1974; Stanley and Kock, 2004).

The PCA and UPGMA results of all three analyses that included palatal and post-palatal measurements (Figs 2–4) show a distinction of specimens identified as *L. angolensis* from the other *Laephotis* species, and a clear distinction of specimens identified as *L. botswanae* from specimens identified as *L. wintoni* and *L. namibensis.* As indicated by palatal measurements, specimens from Hella-Hella in KwaZulu-Natal that were previously identified as *L.* cf. *wintoni* are found together with specimens of *L. botswanae* in all three analyses (Figs 2–4). Of the three analyses that included palatal and post-palatal measurements (Figs 2–4), only the PCA, but not the UPGMA, of 17 cranial measurements (Fig. 3a) separates specimens of *L. wintoni* from *L. namibensis* on the second principal component axis. The other PCA and UPGMA results (Figs 2–4) show no clear distinction between specimens identified as *L. wintoni* and *L. namibensis.* Each of the three analyses (Figs 2–4) show slightly different clustering patterns of specimens identified as *L. wintoni* and *L. namibensis.*

Loadings of individual measurements on the first principal component axis (Table 3), of all three principal component analyses that included palatal and post-palatal measurements, indicate the same measurements are most important in distinguishing between species. All loadings on the first principal component axis are positive. The highest positive loading in each case is always palatal length and the least positive loading is always length from anterior edge of mesopterygoid fossa to tip of pterygoid hamulars. Table 4 shows that in palatal length and length from anterior edge of mesopterygoid fossa to tip of pterygoid hamulars the ranges for *L.* cf. *angolensis* and *L. botswanae* overlap, as do those for *L. namibensis* and *L. wintoni,* although there is no overlap in the ranges of *L.* cf. *angolensis* / *L. botswanae* and *L. namibensis* / *L. wintoni.* Other measurements that are important to the separation on the first principal component axis and are common to more than one analysis are: maxillary tooth row from anterior surface of canine to posterior surface of upper third molar; greatest skull length; and length from the rear of pre-palatal emargination to anterior edge of mesopteygoid fossa (Table 3). Table 4 shows that for each of these measurements the ranges for *L.* cf. *angolensis* and *L. botswanae* do not overlap. The ranges for the different species of greatest skull length and length from the rear of pre-palatal emargination to anterior edge of mesopteygoid fossa also separate *L. botswanae* from *L. namibensis* and *L. wintoni,* but do not separate *L. namibensis* from *L. wintoni* (Table 4). For maxillary tooth row length the ranges for the different species separate *L. botswanae* from *L. wintoni* but not *L. namibensis,* while *L. namibensis* and *L. wintoni* overlap (Table 4).

On the second principal component axis, length from a line across posterior faces of M^{3-3} to anterior edge of mesopterygoid fossa is most important in distinguishing between species in two of the three analyses that included palatal and post-palatal measurements (Table 3). Table 4 shows that ranges of measurements of length from a line across posterior faces of M^{3-3} to anterior edge of mesopterygoid fossa in *L.* cf. *angolensis* and *L. botswanae* do not overlap the ranges for *L. namibensis* and *L. wintoni.* Other important measurements on the second principal component, which are also common to more than one analysis, are length from a line across posterior faces of M^{3-3} to tip of pterygoid hamulars and width across outer edge of upper third molars (Table 3). Table 4 shows that ranges of measurements of length from a line across posterior faces of M^{3-3} to tip of pterygoid hamulars in *L.* cf. *angolensis* and *L. botswanae* do not overlap the ranges for *L. namibensis* and *L. wintoni.* In width across the outer edge of upper third molars, the range of measurements for *L.* cf. *angolensis* do not overlap the range of measurements for *L. wintoni,* whereas the ranges for the other species overlap (Table 4).

In all three UPGMA cluster analyses that included palatal and post-palatal measurements, specimens of *L. botswanae* split into three different clusters (Figs 2b–4b). A specimen from Hwange National Park in Zimbabwe (FMNH152728) separated from the rest of the specimens, and the remaining specimens split into two major clusters. What separates the majority of the *L. botswanae* specimens into two clusters is not clear, although geographic locality appears to have some influence since all specimens from the Democratic Republic of Congo cluster together.

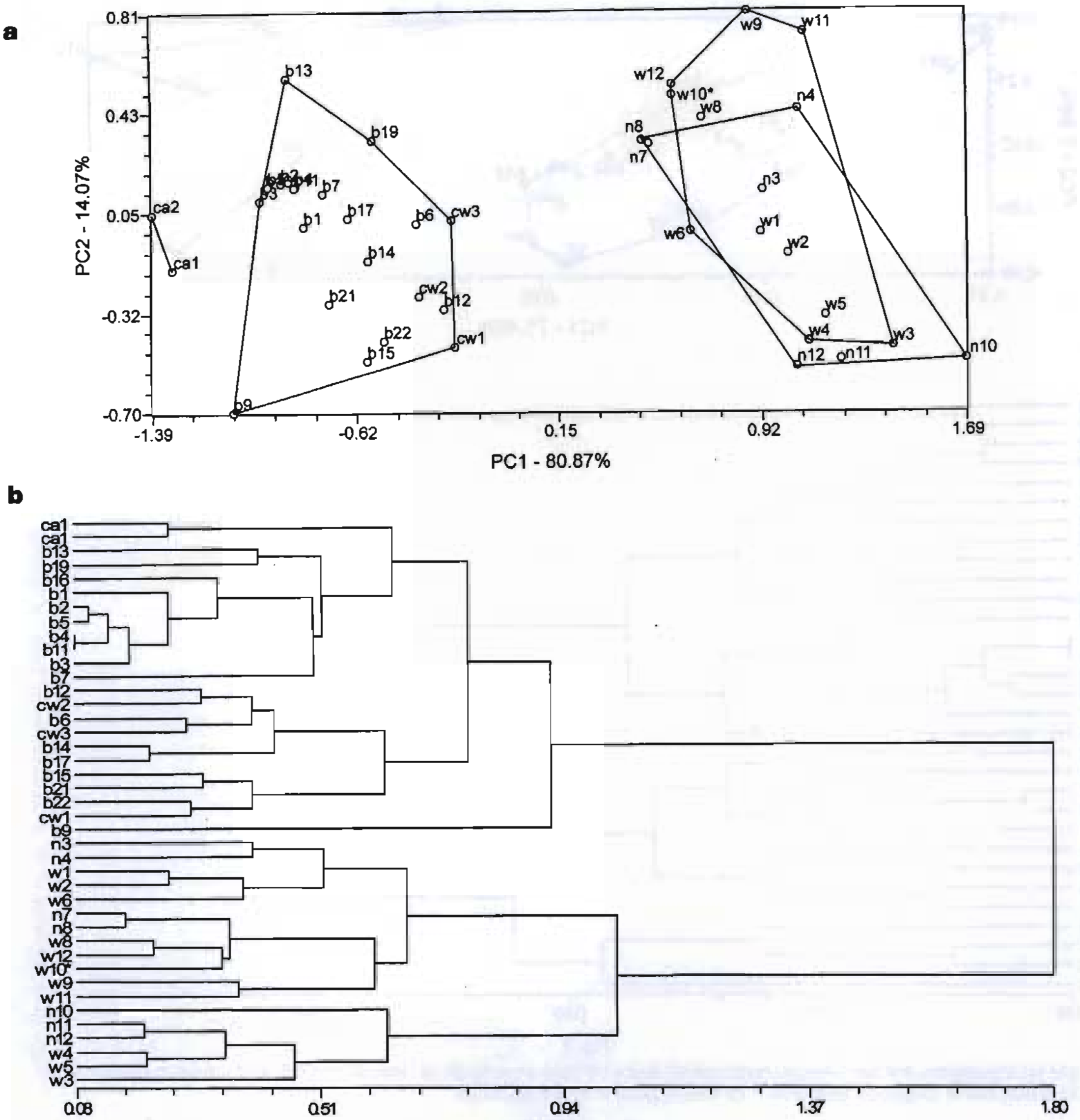

Fig. 2

PCA plot (a) showing the first two principal components, and a UPGMA phenogram (b) from analysis 1 of six palatal measurements from 41 specimens of *Laephotis*. See Table 1 for identification of specimen codes.

The analysis based on one external and seven cranial measurements (which excluded palatal and post-palatal measurements), included measurements from the literature of type specimens of three *Laephotis* species, *L. botswanae*, *L. namibensis*, and *L. wintoni* that were not included in the analyses above as they were lacking palatal and post-palatal measurements. Although the PCA of one external and seven cranial measurements (Fig. 5a) is similar to the analyses above in that there is an oblique separation of the specimens along the first and second PC into three groups which distinguishes specimens of *L.* cf. *angolensis* and *L. botswanae* from those of *L. wintoni* and *L. namibensis*, this PCA places the type specimen of *L. wintoni* closer to the group of specimens that includes the type specimen of *L. botswanae*. Maxillary tooth row length is the most important measurement causing separation on the first principal component axis (Table 3). Maxillary tooth row length is also an important measurement in the separation of species along the first principal component axis in the analyses of 17 cranial measurements and two external, and 14 cranial measurements. Other measurements that

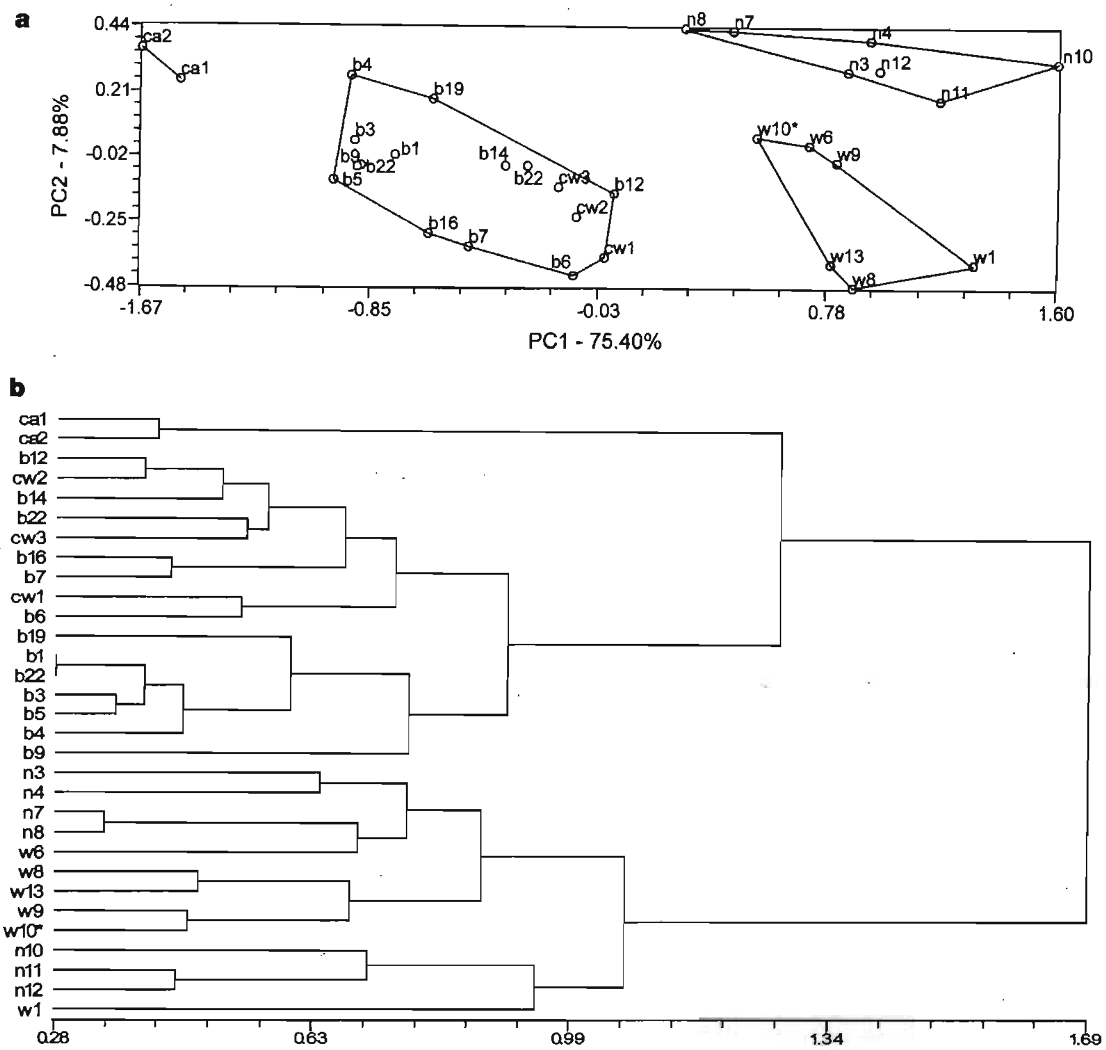

Fig. 3

PCA plot (a) showing the first two principal components, and a UPGMA phenogram (b) from analysis 2 of 17 cranial measurements from 31 specimens of *Laephotis*. See Table 1 for identification of specimen codes.

were important on the first principal component axis are braincase breadth, greatest breadth across outer edge of upper canines, and forearm length (Table 3). The range of braincase breadth for each of the species (Table 4) shows that the measurement for *L.* cf. *angolensis* does not overlap the range of measurements for the other species, which all have overlapping ranges of braincase breadth. Table 4 also shows that the ranges for greatest breadth across outer edge of upper canines in *L.* cf. *angolensis* and *L. botswanae* overlap, but the range of *L.* cf. *angolensis* is different to that for *L. namibensis* and *L. wintoni,* and the ranges of the other species overlap. Forearm lengths of *L.* cf. *angolensis* are smaller than those for *L. wintoni* (Table 4), whereas the ranges for each of the other species overlap. On the second principal component axis the measurements that are most important are greatest skull length, which loads highest, and width across outer edge of upper third molars, which loads lowest (Table 3). Greatest skull length is also important in separation along the first principal component axis, while width across the outer edge of upper third molars is also important in separation along the second principal component axis in analyses of 17 cranial characters and two external and 14 cranial characters.

The UPGMA cluster analysis (Fig. 5b) identified four major clusters that combine specimens contrary to the current species distinctions. Hence,

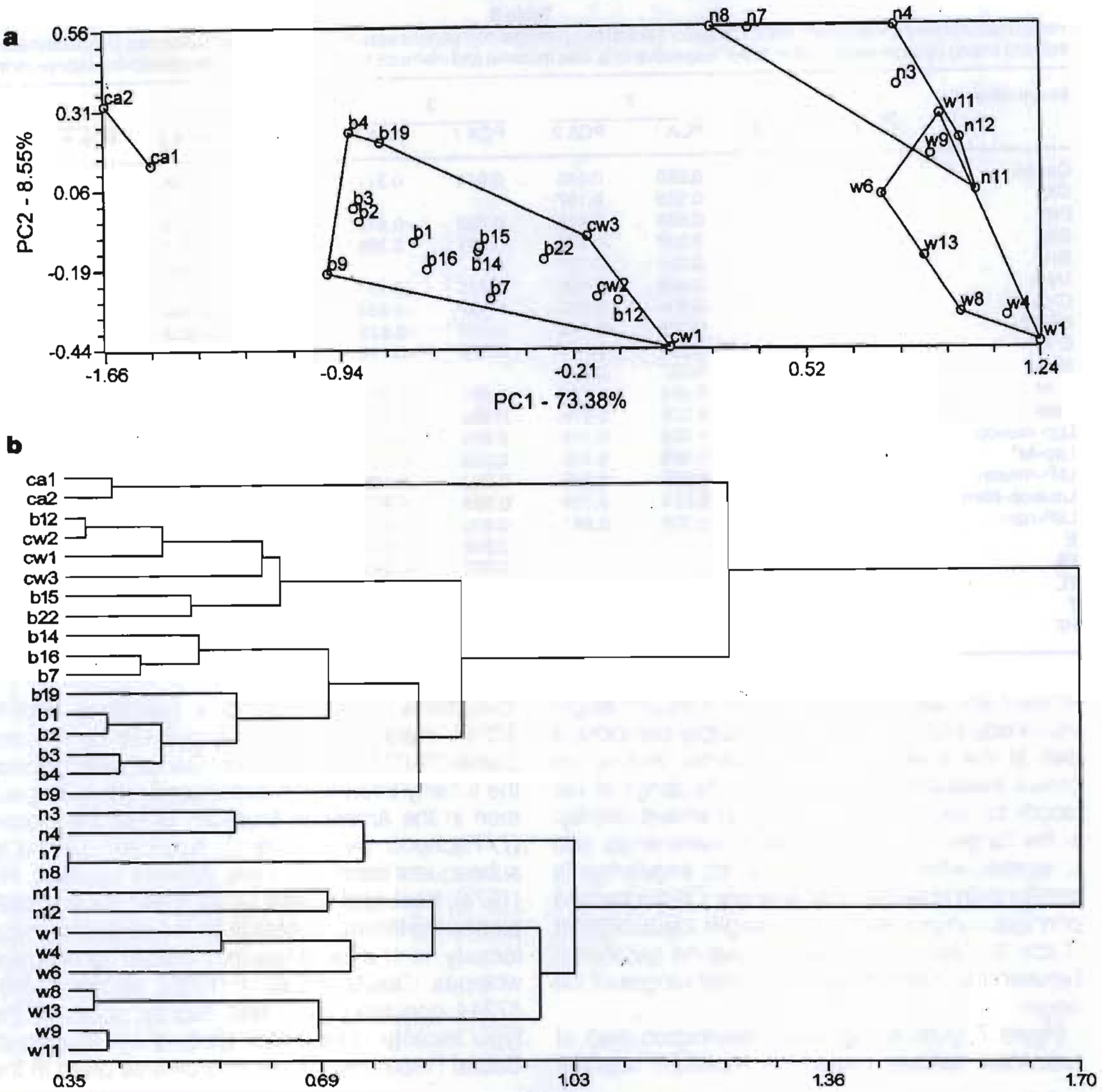

Fig. 4

PCA plot (a) showing the first two principal components, and a UPGMA phenogram (b) from analysis 3 of two external and14 cranial measurements from 31 specimens of *Laephotis*. See Table 1 for identification of specimen codes.

the first cluster contains specimens of *L.* cf. *angolensis* together with specimens of *L. botswanae*. The second cluster contains specimens of *L. botswanae* (including the holotype), the holotype of *L. wintoni*, and specimens from KwaZulu-Natal in South Africa previously assigned to *L.* cf. *wintoni*. The third cluster contains specimens of *L. namibensis* (including the type specimens). The fourth cluster contains specimens of *L. namibensis* together with specimens from the Western Cape Province in South Africa previously assigned to *L. namibensis* and specimens from the Free State Province in South Africa and Lesotho previously assigned to *L. wintoni.*

The PCA based on five external measurements (Fig. 6a) shows no clear separation of specimens into different species groups, and as in the analysis based on one external and seven cranial measurements the UPGMA analysis based on five external measurements (Fig. 6b) also gives results that are contrary to the current species distinctions. Hind foot length is important on both the first and second principal component axes (Table 3). The ranges of hind foot lengths of the different species overlap between *L. botswanae* and *L. wintoni*, and between *L. namibensis* and *L. wintoni*, whereas those for *L. botswanae* and *L. namibensis* form a continuum (Table 4). The other measurements that load highly on the first principal component axis are

Table 3

Factor matrix showing measurement loadings for the first two principal component axes in the five different analyses. Boldface loadings indicate strong variable participation in the respective axis. See material and methods for a description of measurement abbreviations.

Measurement	1		2		3		4		5	
	PCA 1	PCA 2	PCA 1	PCA 2	PCA 1	PCA 2	PCA 1	PCA 2	PCA 1	PCA 2
Cnr inc			0.965	0.145	0.944	0.211	0.830	**0.465**		
Cdl			0.935	0.197						
Por			0.694	−0.418	0.702	−0.412	0.739	−0.371		
Bcw			0.892	0.126	0.881	0.135	**0.853**	0.337		
Bcd			0.821	0.137			0.786	0.331		
Mast			0.906	−0.100	0.915	−0.107				
C–C			0.804	−0.525	0.855	−0.433	0.852	−0.368		
M^3–M^3			0.524	**−0.760**	0.637	**−0.615**	0.688	**−0.626**		
C–M^3			0.968	−0.113	0.959	−0.110	**0.944**	0.086		
Mand			0.957	0.058						
C–M_3			0.926	−0.124	0.940	−0.033				
Palat	**0.976**	0.126	**0.970**	0.078	**0.962**	0.159				
Lpp–mesop	0.974	0.167	0.956	0.110	0.953	0.210				
Lpp–M^3	0.925	−0.137	0.936	0.140	0.899	0.121				
LM^3–mesop	0.930	**0.315**	0.893	0.245	0.882	**0.386**				
Lmesop–ham	**0.555**	**−0.826**	**0.514**	0.124	**0.395**	−0.307				
LM^3–ham	0.960	0.006	0.906	**0.251**	0.910	0.278				
E					0.848	0.281			0.766	−0.515
FA					0.827	−0.249	0.851	0.005	**0.873**	−0.198
TL									0.747	0.517
T									0.637	**0.665**
HF									**0.835**	**−0.291**

forearm and ear lengths (Table 3). Forearm length also loads highly on the first principal component axis in the analysis of one external and seven cranial measurements (Table 3). The range of ear length for each species (Table 4) shows overlap in the ranges of *L. botswanae*, *L. namibensis* and *L. wintoni*, while the range of *L.* cf. *angolensis* is smaller than in all the other species. On the second principal component axis tail length loads highest (Table 3). Table 4, however, shows no separation between the different species in their ranges of tail length.

Figure 7 gives an up-dated distribution map of *Laephotis* species based on museum voucher specimens. The locality of a specimen (AMNH 87244) identified as *L.* cf. *angolensis* by Hill and Carter (1941) from '35 km E of Dande', which is also the locality information associated with the specimen in the American Museum of Natural History (T. Pacheco, pers. comm.), has been plotted in subsequent literature at two different localities. Hill (1974), Kock and Howell ([1988]) and Bauer (1992) plotted the locality of AMNH 87244 north of the type locality in the northeastern corner of Angola, whereas Crawford-Cabral (1989) plotted AMNH 87244 occurring west and slightly south of the type locality. The point plotted by Crawford-Cabral (1989) follows the coordinates given in the

Table 4

Ranges of measurement for each species, *Laephotis* cf. *angolensis*, *L. botswanae* (including specimens previously identified as *L.* cf. *wintoni*), *L. namibensis*, and *L. wintoni*, for cranial and external measurements that were important in distinguishing between species in the different principal component analyses. See materials and methods for a description of measurement abbreviations.

Measurement	*L.* cf. *angolensis*	*L. botswanae*	*L. namibensis*	*L. wintoni*
Palat	6.10–6.20	6.16–7.29	7.59–8.72	7.90–8.50
LM^3–mesop	1.20–1.30	0.94–1.69	1.86–2.47	1.97–2.50
Lmesop–ham	1.90–2.00	1.68–2.30	2.00–2.61	1.80–2.47
Lpp–mesop	4.80	4.90–5.63	6.11–6.78	6.40–6.90
LM^3–ham	3.20	2.64–3.70	3.94–4.54	3.93–4.48
C–M^3	4.30	4.50–4.94	4.75–5.35	5.00–5.33
Cnr inc	13.70–13.80	14.10–15.50	16.05–17.00	15.58–16.30
M^3–M^3	5.00–5.20	5.17–5.80	5.10–5.55	5.42–5.90
BcW	6.80	6.85–7.43	7.40–7.95	7.40–8.05
C–C	3.70–3.80	3.80–4.50	4.00–4.50	4.30–4.60
FA	34.0–36.0	33.0–38.0	36.0–40.0	37.0–41.0
HF	–	6.0–8.0	8.0–9.0	6.3–9.0
T	–	40.0–46.0	38.0–47.0	38.0–50.0
E	15.9–16.0	16.0–21.0	20.0–25.0	21.0–24.0

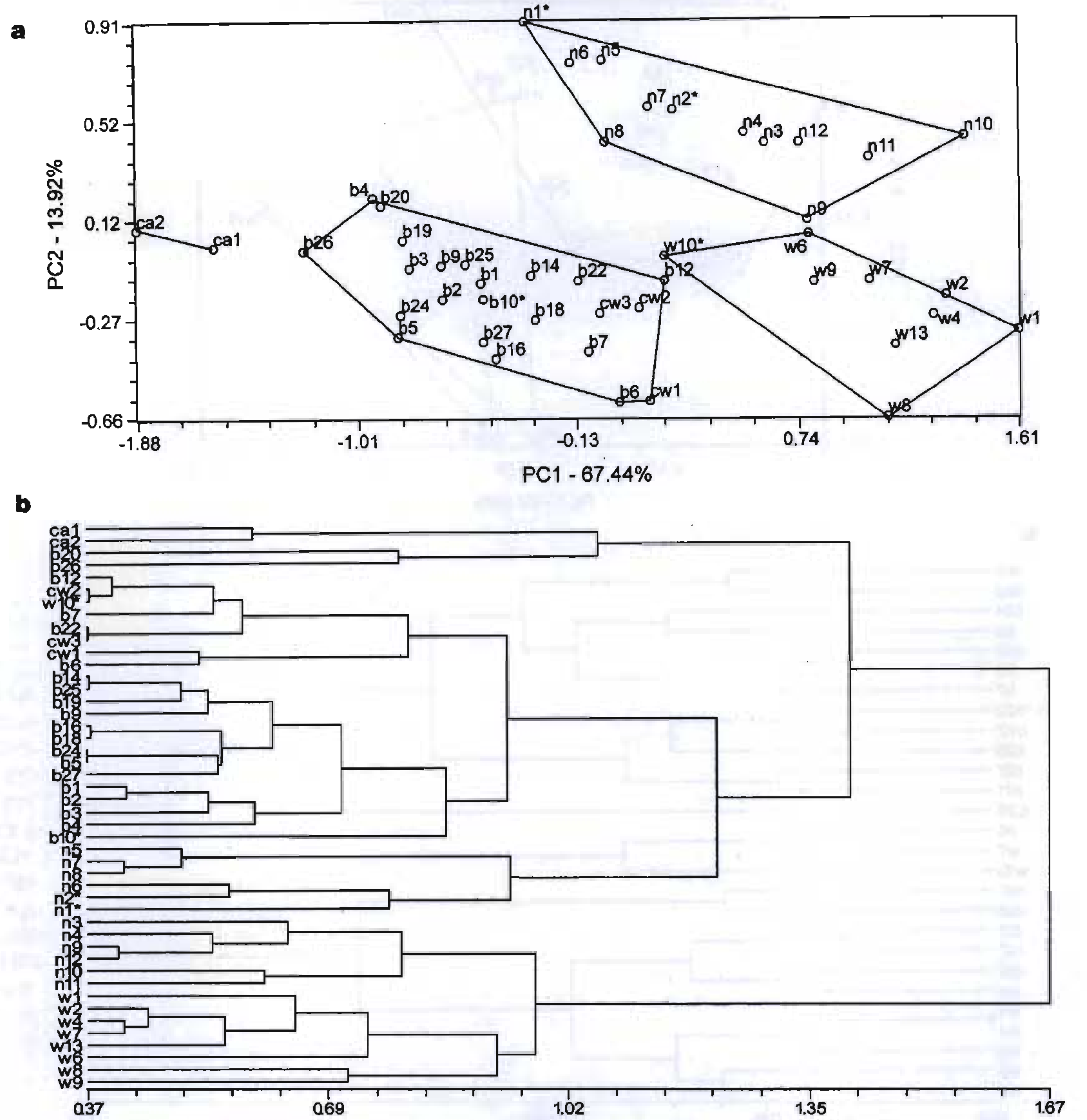

Fig. 5

PCA plot (a) showing the first two principal components, and a UPGMA phenogram (b) from analysis 4 of one external and seven cranial measurements from 46 specimens of *Laephotis*. See Table 1 for identification of specimen codes.

gazetteer of Hill and Carter (1941) for 'Dande (= Dando) 11°10'S, 17°10'E'. It also coincides with the description in the body of the text of Dande being 'nearly 330 kilometers south-west from the type locality' (Hill and Carter, 1941), as the type locality for *L. angolensis* is on the Tyihumbwé (Chiumbe) River, 15 km west of Dala (Monard, 1935). Following the information in Hill and Carter (1941) the locality would be close to the present day town of Dando (*Encarta World Atlas*, 1995–1997; 10th edition of the *Times Atlas of the World*, 1999). A possible explanation for the locality of AMNH 87244 being plotted in the northeast of Angola (Hill, 1974; Kock and Howell, [1988]; Bauer, 1992) is that Dande became confused with the locality Dundo (D. Kock, pers. comm.). Mammal species, including bats, albeit no *Laephotis*, were collected for the Dundo Museum by A. de Barros Machado from in and around Dundo in the Lunda District of northeastern Angola and recorded by Sanborn (1951) and Hayman (1963). The gazetteer in Hayman (1963) gives the coordinates for Dundo as 7°22'S, 20°50'E.

Table 5 lists the biomes associated with each of the species distributions. Two localities, Mazumbai

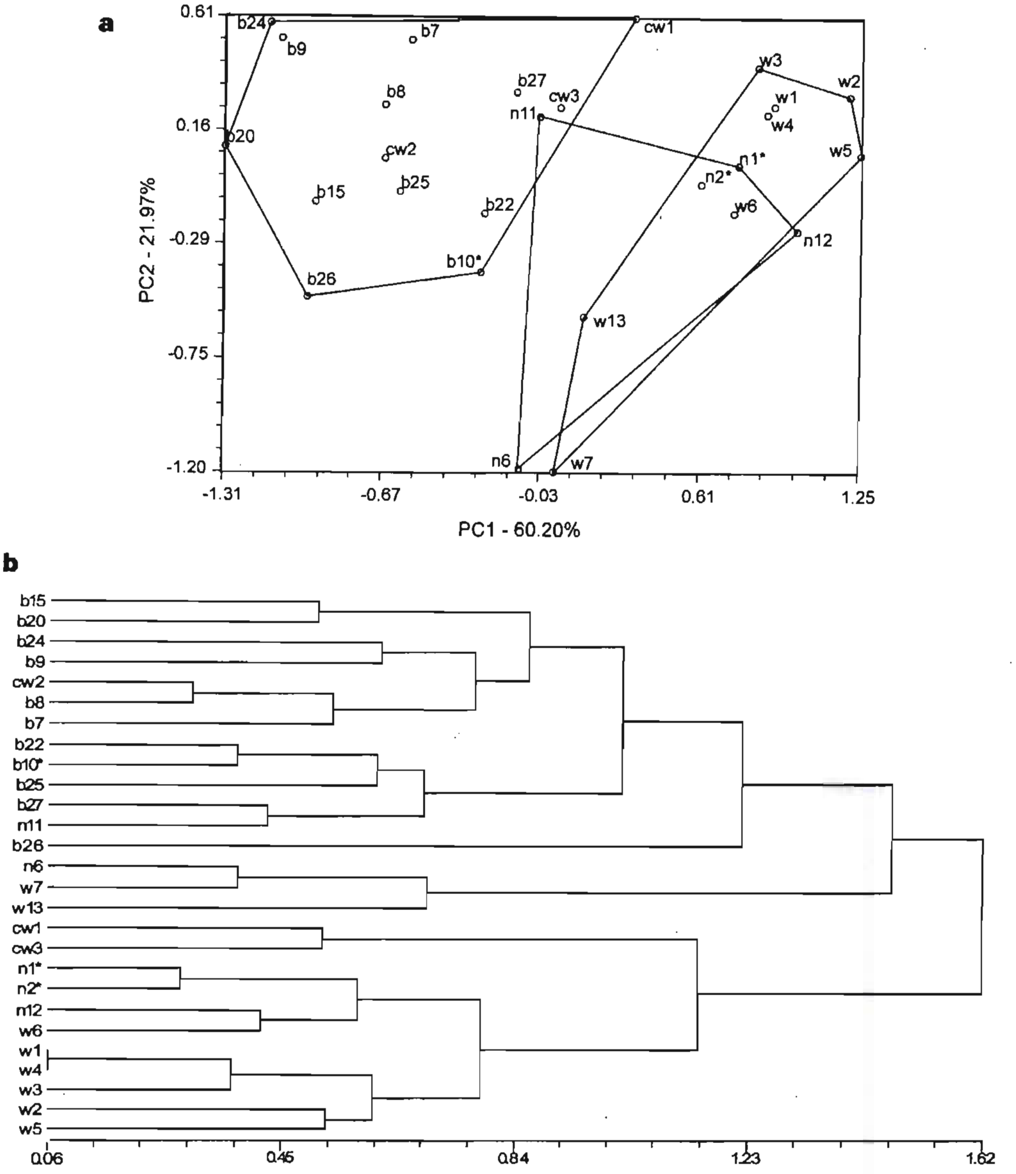

Fig. 6

PCA plot (a) showing the first two principal components, and a UPGMA phenogram (b) from analysis 5 of five external measurements from 27 specimens of *Laephotis*. See Table 1 for identification of specimen codes.

Forest Reserve and Beletta Forest, were identified by the GIS spatial biome data as savanna and grassland respectively. However, since both were known to be near forests (Kock and Howell, [1988]; Lavrenchenko *et al.*, 2004), the assignments indicated by the spatial data were ignored and these localities were assigned to the forest biome. This highlights the problem associated with the GIS information due to spatial and scale errors, which should be borne in mind while interpreting the results. *Laephotis* cf. *angolensis* is entirely confined to the savanna biome. *Laephotis botswanae* was found in both savanna (75%) and grassland (25%) biomes, the latter being in their distribution in Malawi. As was identified by Kock and Howell ([1988]), 62.5% of the distribution of *L. wintoni* in East Africa (Ethiopia, Kenya and Tanzania) was within the forest biome and 37.5% in the savanna, whereas in South Africa and Lesotho, the distribution of *L.* cf. *wintoni* was only within the grassland biome. Of the different *Laephotis* species, *L. namibensis* was associated with the largest number

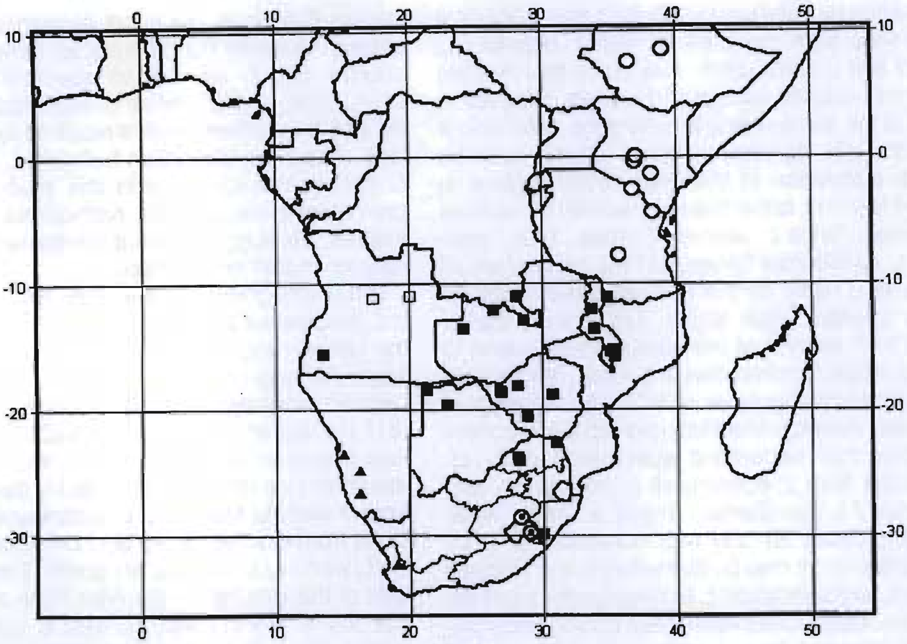

Fig. 7

Distribution of *Laephotis angolensis* (□); *L. botswanae* (■), *L. namibensis* (▲), *L. wintoni* (○), and *L.* cf. *wintoni* (◉) based on museum specimen records (see Appendix 1 for further information).

of different biomes: desert (60%), fynbos (20%) and savanna (20%). In southern Africa, the genus *Laephotis* was absent from two biomes, namely the succulent Karoo and Nama Karoo.

DISCUSSION

This study confirmed Stanley and Kock's (2004) suggestion that Hill's (1974) post-palatal measurements, previously overlooked in the identification of southern African species of *Laephotis*, are useful for the distinction of *L. botswanae* from *L. wintoni*. However, specimens from the Western Cape and Free State Provinces in South Africa identified as *L. namibensis* and specimens from Lesotho identified as *L. wintoni* do not fit Hill's (1974) descriptions for *L. angolensis*, *L. botswanae* or *L. wintoni*, of the distance from a line across the rear margins of both M^3 to the anterior edge of the mesopterygoid fossa relative to the distance from the anterior edge of the mesopterygoid fossa to the tips of the pterygoid hamulars. The keys to the southern African species of *L. botswanae*, *L. namibensis*, and *L. wintoni* in Meester *et al.* (1986) and Taylor (2000) emphasize skull and ear lengths for distinguishing between the different species. The skull and ear length measurements of *Laephotis* specimens presented here indicate these keys are in need of revision as the ranges of ear lengths for *L. namibensis* and *L. wintoni* overlap, and the ranges of skull lengths for *L. botswanae*, *L. namibensis*, and *L. wintoni* are greater than indicated in Meester *et al.* (1986) and Taylor (2000).

These results did not show a clear distinction between *L. namibensis* and *L. wintoni*, instead they suggest *L. namibensis* and *L. wintoni* are different forms of the same species. This supports an earlier

Table 5

Biome associations of the different *Laephotis* species, giving the number of localities each species is currently known from (No. loc), and the number of locations found within each biome.

Species	No. loc	Fynbos	Desert	Savanna	Grassland	Forest
L. angolensis	3	–	–	3	–	–
L. botswanae	28	–	–	21	7 [(1)]	–
L. wintoni	8	–	–	4/(3) [(2)]	1/(0) [(3)]	3/(5) [(2/3)]
L. cf. *wintoni*	2	–	–	–	2	–
L. namibensis	5	1	3	1	–	–

[(1)] All localities are in Malawi (Happold and Happold, 1997); [(2)] the Mazumbai Forest Reserve locality was transferred to the forest biome; [(3)] the Beletta Forest locality was transferred to the forest biome.

suggestion by Peterson (1973: 602) that 'additional specimens from the area of hiatus' between *L. wintoni* and *L. namibensis* 'may prove that they are rather well-marked eastern and western geographic races of the same species', where the paler colour distinction of *L. namibensis* from *L. wintoni* could be a local adaptation to the drier desert regions in which it is found, rather than a character for species distinction. Since *L. wintoni* Thomas, 1901, antedates *L. namibensis* Setzer, 1971, *L. wintoni* would be the valid name for this species. Four measurements (greatest skull length, braincase breadth, length from the rear of pre-palatal emargination to anterior edge of mesopteygoid fossa, length from line across posterior faces of M^{3-3} to tip of pterygoid hamulars) were identified from principal component analyses that separated specimens of *L.* cf. *angolensis* from specimens of *L. botswanae,* and *L. wintoni* / *L. namibensis.* These analyses were, however, based on only two individuals of *L.* cf. *angolensis,* and it may be that with more individuals of both *L. angolensis* and *L. botswanae* the small differences observed between these species may disappear, and as with *L. namibensis* and *L. wintoni* they may be shown to be different forms of the same species. If so, this would support a suggestion previously made by Peterson (1973: 602) that '*L. botswanae* may prove to be a larger, southern race of *L. angolensis*'. Five measurements (greatest skull length, palatal length, length from line across posterior faces of M^{3-3} to anterior edge of mesopterygoid fossa, length from the rear of pre-palatal emargination to anterior edge of mesopteygoid fossa, length from line across posterior faces of M^{3-3} to tip of pterygoid hamulars) were identified from principal component analyses that separated specimens of *L.* cf. *angolensis* and *L. botswanae* from specimens of *L. wintoni* / *L. namibensis*. All measurements that were important in separation of the different species have featured in earlier written descriptions of differences between the different *Laephotis* species (Setzer, 1971; Peterson, 1971, 1973; Hill, 1974).

Further analyses, incorporating other characters and possibly molecular data, are required to clarify the species distinctions between *L. wintoni* and *L. namibensis,* and between *L. angolensis* and *L. botswanae.* This study, being based for the most part on museum specimens comprising dry skins and cleaned skulls, was unable to present detailed information on soft palate and tragus characteristics which have previously been used to characterize different *Laephotis* species (Setzer, 1971; Peterson, 1971, 1973; Hill, 1974; Stanley and Kock, 2004). Baculum morphology, while proving a useful character for species identification of several other vesper species occurring in southern Africa of the genera *Eptesicus, Hypsugo, Neoromicia* and *Pipistrellus,* showed no differences between *L. botswanae* and *L. namibensis* specimens (Kearney *et al.,* 2002). In the interest of nomenclatural stability, pending further studies required to confirm the lack of species distinction between *L. wintoni* and *L. namibensis* identified in this study, it may be premature to reassign all *L. namibensis* to *L. wintoni.* Instead, it is suggested that current species designations should be retained.

The re-assignment of KwaZulu-Natal specimens to *L. botswanae* supported by these results extends the known range of *L. botswanae* 658 km farther south. Although the KwaZulu-Natal, Free State, and Lesotho localities are relatively close to each other (217 km and 91 km from the KwaZulu-Natal to the Free State and Lesotho localities, respectively), the morphometric results clearly identify the specimens from KwaZulu-Natal as *L. botswanae* whereas those from the Free State and Lesotho are part of the *L. wintoni* / *L. namibensis* group. The higher altitude of the localities in the Free State and Lesotho than the locality in KwaZulu-Natal is, however, consistent with earlier descriptions of *L. wintoni* as a montane species found at high altitudes (above 1000 m) in Ethiopia, Kenya and Tanzania (Kock and Howell, [1988]; Stanley and Kock, 2004). An association between the distribution of *L. wintoni* and higher altitudes could explain the disjunct pattern of distribution as well as the differences in biome association seen across the distribution of *L. wintoni.* High altitude localities at higher latitudes (East Africa) are dominated by forests, while at lower latitudes (southern Africa: Malawi and South Africa) high altitude localities fall within the grassland biome. The vegetation association of *L. botswanae* over most of its distribution to the savanna biome, and the association of *L. wintoni* with higher elevations, suggests the identification of the Malawian specimens found in a grassland biome at higher elevations (Happold and Happold, 1997) might be reconfirmed using palatal and post-palatal measurements (Hill, 1974).

CONCLUSION

These results support the re-assignment of specimens from KwaZulu-Natal from *L.* cf. *wintoni* to *L. botswanae.* However, further studies are required to clarify the species distinction between *L. wintoni* and *L. namibensis,* and between *L. angolensis* and *L. botswanae.* Pending this, it is suggested current species designations assigned to specimens should be retained.

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Appendix I

Specimen details of all known voucher specimens of *Laephotis*, incorporating species re-assignments suggested in this analysis.

AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London; DCHC, David C.D. Happold collection; DNSM, Durban Natural Science Museum, Durban; FMNH, Field Museum of Natural History, Chicago; HZM, Harrison Zoological Museum, Sevenoaks; KMMA, Koninklijk Museum voor Midden-Afrika, Tervuren; MHNC, Musée La Chaux-de-Fonds, Neuchâtel; NHMZ, National Museums of Zimbabwe, Bulawayo; NMB, National Museum Bloemfontein, Bloemfontein; NMW, Naturhistorisches Museum, Wien; ROM, Royal Ontario Museum, Toronto; SAMC, Iziko (South African) Museum, Cape Town; SMF, Senckenberg Museum, Frankfurt; TMSA, Transvaal Museum, Pretoria; USNM, United States National Museum, Washington D.C.; ZMMU, Zoological Museum, Moscow University, Moscow.

Laephotis angolensis

ANGOLA: 35 km E Dande (syn. Dando) (11°10'S, 17°10'E): AMNH 87244. 15 km W Dala, Tshiumbe (syn. Tyihumbwe, Tyhumbwe, Chiumbe) river, tributary of Kasai river, (11°02'S 20°04' E): MHNC (holotype).

Laephotis cf. angolensis

DEMOCRATIC REPUBLIC OF CONGO: 68 km E Lubumbashi (= Elisabethville), Musonge (11°07'S, 28°08'E): BM 57.435. 70 km E of Lumbumbashi (= Elisabethville), Mumene, (11°07'S, 28°08'E): BM 57.437.

Laephotis botswanae

ANGOLA: Huila (15°04'S, 13°32'E): FMNH 83605, FMNH 84120.

BOTSWANA: 50 mi W, 12 mi S of Shakawe (18°33'S, 21°18'E): USNM 425349. Kurunxaraga (syn. Xugana Lagoon) (c. 19°40'S, 22°50'E): NHMZ 59310.

DEMOCRATIC REPUBLIC OF CONGO: 70 km E of Lumbumbashi (syn. Elisabethville), Mumene, (11°07'S, 28°08'E): BM 57.436, BM 57.438, KMMA 26.402–26.407, SMF 16868. 68 km E Lubumbashi (= Elisabethville), Musonge (11°07'S, 28°08'E): SMF 16869.

MALAWI: Nkhota-kota Game Reserve, Chipata Camp, 1350 m asl. (13°04'S, 33°56'E): DCHC 2937. Viphya Plateau, Luwawa Dam, 1700 m asl. (12°07'S, 33°44'E): DCHC 2673. 3 km N Namadzi Village, Kapalasa Farm, 1000 m asl. (15°31'S, 35°11'E): DCHC 2972, DCHC 2992. Mt Mulanje, Likabula Mission (15°57'S, 35°24'E): TM 44544. Namadzi, Kapina Estates, Kapino Dam, 1000 m asl. (15°31'S, 35°11'E): DCHC 3040. Thondwe, Mpalanganga Dam, 1100 m asl. (15°27'S, 35°15'E): DCHC 2855. Zomba District, Zomba town, Bone's Garden, 16th Avenue, 800–900 m asl. (15°23'S, 35°19'E): DCHC 2269, DCHC 2456, DCHC 2682. Zomba Plateau, Chagwa Dam, (15°21'S, 35°20'E): DCHC 3012.

SOUTH AFRICA: *Kwazulu-Natal Province*: Hella-Hella, Game Valley Estates (29°54'S, 30°03'E): DNSM 5351, DNSM 6898–6899. *Limpopo Province*: Kruger National Park, 2.5 km NE of Punda Maria, Maditobe Witsand Dam (22°41'S, 31°02'E): TM 38123, TM 38153–38155. Waterberg, 30 km NE Vaalwater, Farm Klipfontein (24°08'S, 28°08'E): TM 39946, TM 40107. Waterberg, 65 km N Vaalwater, Lapalala Wilderness area (23°51'S, 28°09'E): TM 39796.

TANZANIA: Songea District, SE Mbinga, Ugano Plantation, 1 560m asl. (11°06'S, 34°55'E): NMW 19823.

ZAMBIA: Ndola (12°58'S, 28°38'E): HZM 1.2533. NORTH-WEST PROVINCE: Kabompo (syn. Kabompo Boma) (c. 13°38'S, 24°08'E): NHMZ 9111. Solwezi Boma (12°10'S, 26°23'E): BM 55.1134–55.1135. Between Livingstone (17°52'S, 25°51'E) & Lochinvar (15°51'S, 27°14'E): NHMZ 2801.

ZIMBABWE: Hwange National Park (syn. Wankie N.P.), 15 mi E Dett, 3000 ft asl. (18°37'S, 26°52'E): FMNH 152728. Eastern Matopos, Lunare Valley (c. 20°36'S, 28°52'E): NHMZ 29992. Eastern Matopos, Mtshavezi Valley (c. 20°36'S, 28°52'E): NHMZ 29592. 75 km W Gokwe, Sengwa Wildlife area (18°10'S, 28°13'E): NHMZ 30030, NHMZ 63201–63202, TM 34964. Gem Tree Ranch, Sebakwe River (c. 18°55'S, 30°50'E): NHMZ 58131. Hostes Nicoll Research Institute (18°10'S, 28°13'E): NHMZ 59330.

Laephotis namibensis

NAMIBIA: *Lüderitz Region*: 3 km W Aus, Farm: Klein Aus 8 (26°39'S, 16°13'E): TM 37547–37548. Tiras Mountains, Helmeringshausen (26°45'S, 16°15'E): TM 33472. Maltahöhe Region: 70 km W Maltahöhe, Farm Zwartmodder 101 (24°54'S, 16°17'E): TM 37586, TM 37608–37609. *Swakopmund Region*: Gobabeb, Namibia Desert Research Station (syn. DERU) (23°33'S, 15°03'E): USNM 342152–342153.

SOUTH AFRICA: *Western Cape Province*: Cederberg, Algeria State Forest campsite (32°21'S, 19°03'E): SAMC 41415, SAMC 41417, TM 28316, TM 38426.

Laephotis wintoni

ETHIOPIA: 38 km SW Jimma, Beletta Forest, 2050 m asl. (07°32'N, 36°33'E): ZMMU S-165956, ZMMU S-165957. Koka, 1700 m asl. (08°27'N, 39°06'E): BM 72.4397–72.4399.

KENYA: Nyeri, 6000 ft (00°24'S, 36°57'E): HZM 2.3020. Kitui (01°22'S, 38°12'E): BM 1.5.6.5. 37 km W of Mt Kenya, Nanyuki (syn. Nanguki) (00°01'N, 37°04'E): ROM 66245. Kajiado District, Namanga, 4200 ft (02°33'S, 36°48'E): ROM 36368.

TANZANIA: 6 km E Iringa, Kibebe Farms (07°47'S, 35°45'E): FMNH 171300. West Usambara Mountains, Mazumbai Forest Reserve (04°25'S, 38°15'E): SMF 66961.

Laephotis cf. wintoni

LESOTHO: *Qacha's Nek District:* Sehlabathebe National Park, small dam (29°51'S, 29°06'E): NMB 6686–6688, NMB 6697–6698.

SOUTH AFRICA: *Free State Province*: Clarens, Farm Schaapplaas (c. 28°37'S, 28°22'E): NMB 6378–6379.