SYSTEMATIC REVISION OF THE GOLDEN MOLE GENERA

Amblysomus, *Chlorotalpa* and *Calcochloris*

(INSECTIVORA: CHRYSOCHLOROMORPHA; CHRYSOCHLORIDAE)

by

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**Dedicated to the memory of
my mentor, the late Jurgens ("Waldo") Meester,
and my mother, the late Sally Jenkins.**

ABSTRACT

Patterns of variation in hyoid morphology, chromosomal properties and cranio-dental characteristics among ten chrysochlorid species from South Africa were studied to clarify generic relationships among taxa assigned variably to *Amblysomus*, *Chlorotalpa* and *Calcochloris* by previous authors.

Intra-specific variation in hyoid morphology was negligible, but inter-specific differences were marked. Similarly, intra-specific karyotypic variation was negligible, except in *A. hottentotus*, which displayed three cytotypes. These data supported the recognition of *Chlorotalpa*, *Calcochloris* and *Neamblysomus* as taxa distinct from *Amblysomus*.

Only one (presence/absence of M3) of the seven dental traits used by previous authors was consistent enough within species to be taxonomically useful in this work. Dental variability within species appeared to arise from the morphological differences between deciduous and permanent teeth, which may occur together in the same toothrow. Intra-specific craniometric variation in most species involved pronounced sexual size dimorphism, but negligible age-related variation. In the more widespread species, patterns of geographic variation were dominated by divergence in overall size, although subtle differences in cranial shape were also evident. Multivariate analyses confirmed the validity of subspecies in *Chlorotalpa sclateri* and *Calcochloris obtusirostris*, and showed that *A. hottentotus* (as traditionally recognized) includes: four cryptic species; five subspecies (including *A. h. iris*); and several populations that should be relegated to *A. corriae*.

Inter-specific morphometric variation was dominated by overall size. The species fell into two size groups, and eight phena that differed mainly in skull width, palatal shape, rostrum breadth and claw size. Inter-specific relationships suggested by phenetic analyses of metric and mixed-mode data were, however, incongruent owing to discordance between different data suites. Evolutionary relationships inferred by integrating data suites, using either equal or differential weights, indicated that a strong phylogenetic signal was present in the data. Phylogenetic analyses showed that the differentially weighted treatment was more consilient with character-state distributions. A phylogram based on the differential-weights cladogram was used to derive a revised phylogenetic classification for the Chrysochloridae. Unlike previous treatments, this classification affords *Carpitalpa* and *Neamblysomus* generic rank, and assigns *C. leucorhina* from equatorial Africa to *Calcochloris*, rather than to *Chlorotalpa*.

PREFACE

This study was undertaken at the Mammal Department of the Transvaal Museum (Pretoria) from January 1987 to November 1995, during which time I served as a Museum Curator whilst also being registered as a full-time student with the Department of Biology, University of Natal (Durban).

The work presented here was supervised jointly by Dr J. Meester and Dr I. L. Rautenbach. Following the decline in health and death of Dr Meester during the late stages of this project, Prof. J. Cooke and Dr K. Willan kindly served as my academic and editorial supervisors. 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.

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PART I

INTRODUCTION & METHODOLOGY

CHAPTER 1

INTRODUCTION

Linnaeus first documented the existence of golden moles (family Chrysochloridae) nearly 250 years ago, yet current knowledge of these blind, subterranean eutherians is still rudimentary. Systematic relationships among the 18 known species (Meester 1974), and their affinities to other Insectivora, remain obscure despite intensive anatomical study, while information on the ecology and reproduction of most species is limited to the anecdotal notes of collectors. This can be attributed largely to the difficulty of acquiring specimens for study, since most of species are cryptic and trap-shy, and exist in areas that are not easily accessible to collectors.

1.1 DISTRIBUTION AND ECOLOGY

Golden moles are endemic to subSaharan Africa, where the 18 known species (Table 1.1) inhabit a wide altitudinal, climatic and vegetational spectrum of subterrestrial habitats. Unlike other Insectivora, they have a markedly southern African centre of diversity, with only three species occurring outside this region: *Chlorotalpa leucorhina* in equatorial forest and woodlands of central Africa; *Chrysochloris stuhlmanni* in montane forests of east and central Africa; and *Chlorotalpa tytonis*, which is known from only a single specimen collected in Somalian woodland (Fig. 1.1; Meester 1974; Simonetta 1968). In southern Africa, the 15 known species fall into two broad ecological groups: a xerotherous group of five species which occurs in semi-desert (*Eremitalpa granti*, *Cryptochloris zyli* and *C. wintoni*), karroid (*Chrysochloris visagiei*) or moister fynbos habitats (*Chrysochloris asiatica*) along the south-west coast; and 10 mesic-adapted species which inhabit forests, savanna woodland and temperate grasslands in the eastern part of the subregion (*Chrysospalax*, *Chlorotalpa*, *Calcochloris* and *Amblysomus*). Only two species - *Amblysomus hottentotus* and *Chrysochloris asiatica* - are widespread. Some species, such as *Chrysochloris stuhlmanni* and *Amblysomus julianae*, are known from only scattered localities which are situated hundreds of kilometres apart, but connected by continuous favourable habitat. These may be more widespread than is indicated by the scant distribution data currently available. Other species, such as *Chlorotalpa sclateri*, probably have more restricted

Table 1.1

Classification of the Chrysochloridae, according to Meester (1974) and Meester *et al.* (1986). Asterisks denote type species.

Genus & Species	Colloquial Name	Subspecies
Genus: *Amblysomus* Pomel, 1848		
gunningi (Broom, 1908)	Gunning's golden mole	(monotypic)
hottentotus (A. Smith, 1829)*	Hottentot golden mole	*A. h. hottentotus*; *A. h. marleyi* Roberts, 1931; *A. h. devilliersi* Roberts, 1946.
iris Thomas & Schwann, 1905	Zulu golden mole	*A. i. iris*; *A. i. corriae* Thomas, 1905; *A. i. septentrionalis* Roberts, 1913.
julianae Meester, 1972	Juliana's golden mole	(monotypic)
Genus *Chlorotalpa* Roberts, 1924		
arendsi Lundholm, 1955	Arend's golden mole	(monotypic)
duthieae (Broom, 1907)*	Duthie's golden mole	(monotypic)
sclateri (Broom, 1907)	Sclater's golden mole	*C. s. sclateri*; *C. s. montana* Roberts, 1924; *C. s. guillarmodi* Roberts, 1936; *C. s. shortridgei* Broom, 1950.
leucorhina (Huet, 1885)	Congo golden mole	*C. l. leucorhina*; *C. l. cahni* (Schwarz & Mertens, 1922).
tytonis	Somali golden mole	(known only from holotype)
Genus *Calcochloris* Mivart, 1867		
obtusirostris (Peters, 1851)*	Yellow golden mole	*C. o. obtusirostris*; *C. o. chrysillus* (Thomas & Schwann, 1905); *C. o. limpopoensis* (Roberts, 1946).
Genus *Chrysochloris* Lacèpéde, 1799		
asiatica (Linnaeus, 1758)*	Cape golden mole	(monotypic)
stuhlmanni Matschie, 1894	Stuhlmann's golden mole	*C. s. stuhlmanni*; *C. s. fosteri* (St. Leger, 1931); *C. s. tropicalis* (Allen & Loveridge, 1927).
visagiei Broom, 1950	Visagie's golden mole	(known only from holotype)
Genus *Chrysospalax* Gill, 1883		
trevelyani (Günther, 1875)*	Giant golden mole	(monotypic)
villosus (A. Smith, 1833)	Rough-haired golden mole	*C. v. villosus*; *C. v. transvaalensis* (Broom, 1913); *C. v. leschae* (Broom, 1918); *C. v. dobsoni* (Broom, 1918); *C. v. rufopallidus* (Roberts, 1924); *C. v. rufus* (Meester, 1953).
Genus *Eremitalpa* Roberts, 1924		
granti (Broom, 1907)*	Grant's golden mole	*E. g. granti*; *E. g. namibensis* Bauer & Niethammer, 1959.
Genus *Cryptochloris* Shortridge & Carter, 1938		
zyli Shortridge & Carter, 1938*	Van Zyl's golden mole	(monotypic)
wintoni (Broom, 1907)	De Winton's golden mole	(monotypic)

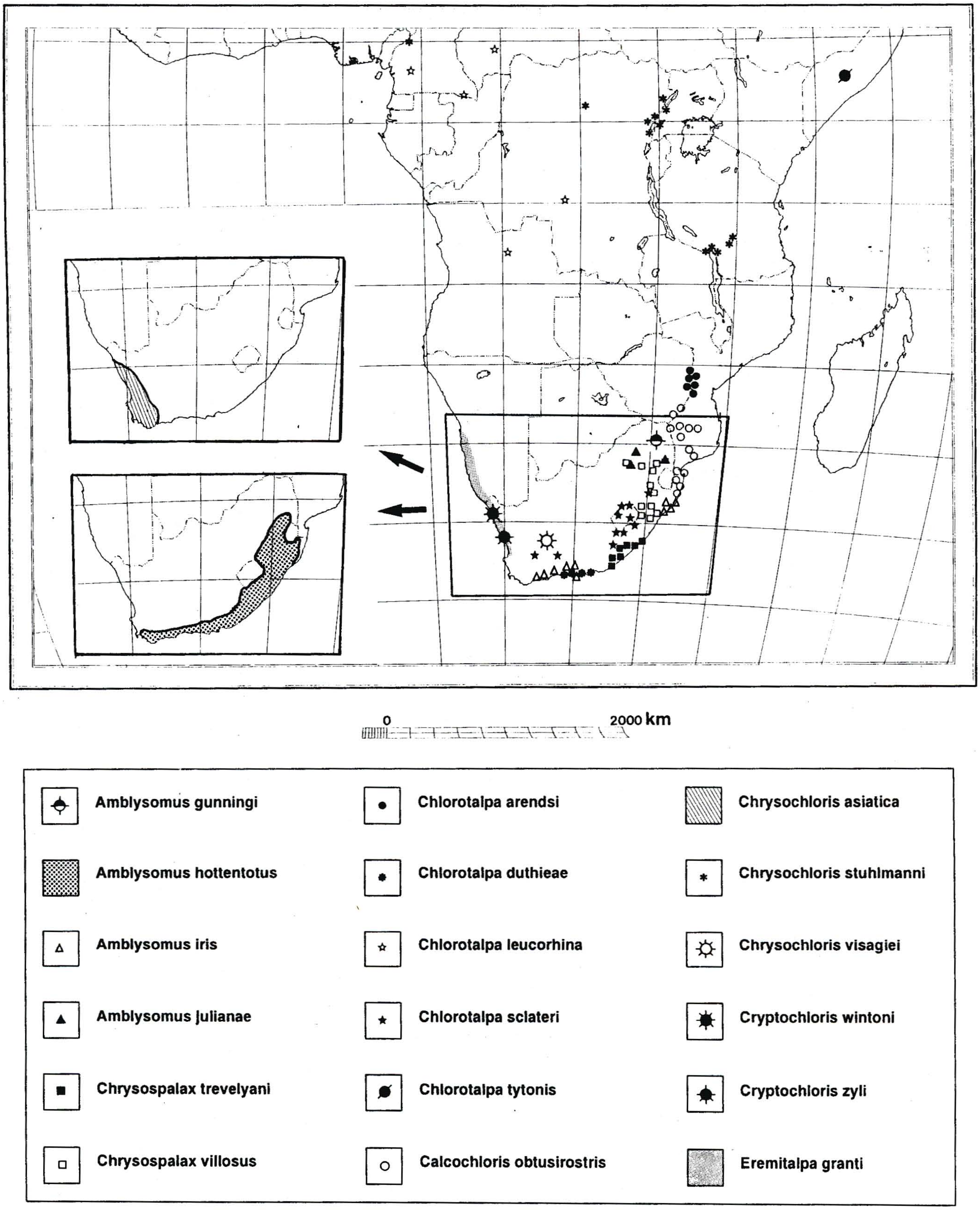


Fig. 1.1 The distribution of golden moles in subSaharan Africa, as indicated by range maps (shading) or quarter-degree square records (symbols).

ranges than general texts (Meester *et al.* 1986; Skinner and Smithers 1990) indicate, since the few populations known to exist occur at localities separated by wide expanses of seemingly inhospitable habitat. Geographical continuity between them seems unlikely.

Populations of golden moles are often restricted to patches of suitable habitat with friable soils and abundant invertebrate prey, so that the distribution of demes is clumped, even within the more widespread taxa (Roberts 1951). Consequently, different species seldom coexist and compete for resources, even though their distribution may appear to be broadly sympatric (Fig. 1.1). If two species occur in the same area they tend to occupy different microhabitats, probably as a result of ecological displacement. Thus, for example, the Hottentot golden mole (*A. hottentotus*) and Cape golden mole (*C. asiatica*) occur together at Stellenbosch but inhabit different soil types (Broom 1907a). Similarly, at Wakkerstroom *A. hottentotus* is found only in vleis and grassland, whereas *Chlorotalpa sclateri* is restricted to montane kloofs and scrub (Roberts 1951).

Like most other subterranean mammals, chrysochlorids are stenoeocious with low vagility, and have specialized K-selected life history strategies (Nevo 1979). Their natural history was recently reviewed in detail by Hickman (1990). The limited data available show that all species are opportunistic insectivores which feed primarily on earthworms, termites and/or millipedes, although their diet may vary in relation to the abundance of other prey items in specific habitats. Most are solitary and subterrestrial, and construct semi-permanent tunnel systems comprising two tiers: an upper level of subsurface burrows used for foraging, and a lower level with chambers and interconnecting tunnels used for resting and raising young (Kuyper 1985; Roberts 1951). An exception to this pattern is found in the "Shark of the Dunes" - the small Namib golden mole (*Eremitalpa granti namibensis*). This subspecies does not construct a permanent tunnel system but "swims" through the desert sands, often emerging to forage on the surface (Fielden *et al.* 1990a). The giant golden mole (*Chrysospalax trevelyani*) is also a surface forager found in indigenous forests, and is the only species which shows any indication of sociality (Maddock 1986). Roberts (1951) reported a similar lifestyle for the rough-haired golden mole (*Chrysospalax villosus*), a vlei-specialist whose biology remains obscure since only two individuals have been caught in the last 15 years (Nicoll and Rathbun 1990).

1.2 PHYSIOLOGY AND REPRODUCTION

Physiologically, chrysochlorids are unique amongst African Insectivora in displaying daily and seasonal torpor (Korn 1986; Kuyper 1985; Withers 1978) or almost complete thermolability (Fielden *et al.* 1990b). The scant reproductive data available suggest that they breed throughout the year and may be polyoestrous (Bernard *et al.* 1994). Although these are r-selected characters, other facets of their breeding biology (small litter sizes and extended post-natal development; Bronner 1992) are more typical of a specialized, K-selected reproductive strategy (Pianka 1970).

1.3 MORPHOLOGY AND SYSTEMATICS

1.3.1. Higher taxonomy

Morphologically, the 18 known golden mole species display a high degree of structural conformity comprising both primitive and highly specialized mammalian characters (Broom 1915, 1916a; Bugge 1974; Butler 1972; Findlay 1944; Roux 1947; see also Hickman 1990). Specialized characters include unique traits such as hyoid-dentary articulation (Bronner *et al.* 1990) and hypertrophied mallei (Forster Cooper 1928). Most of the anatomical specializations shown by extant taxa are also found in fossil species (Broom 1941; Butler and Hopwood 1957; de Graaff 1957), and are so numerous and unusual that chrysochlorids have been described as "spectacularly autapomorphic" and worthy of at least subordinal separation from other Insectivora (MacPhee and Novacek 1993:26). This proposal is by no means novel. Dobson (1882) first noted that while chrysochlorids resemble the Tenrecidae of Madagascar in having zalambdodont molars, golden moles present many important structural differences indicating that they are not closely allied to any other family of extant Insectivora. Broom (1916b) subsequently showed that zalambdodonty has arisen independently several times in mammals, and thus that the common possession of zalambdodont molars in the Chrysochloridae and Tenrecidae is probably due to morphological convergence. On the basis of their unique cranial and nasal morphology, he proposed that chrysochlorids be classified in the distinct order Chrysochloridea (Broom 1915, 1916a), an approach subsequently endorsed by Heim de Balsac and Bourlière (1954), Roberts (1951) and Roux (1947).

This proposal, however, implied a polyphyletic origin of the Insectivora (= Lipotyphla of some authors, see Butler 1956), and was therefore challenged by some subsequent authors (Bugge 1974; Eisenberg 1981; Van Valen 1967). Simpson (1945:176) conceded that common possession of zalambdodont molars is not sufficient to infer a close phylogenetic relationship between chrysochlorids and tenrecoids, but argued that the ordinal separation proposed by Broom (1916a) was too radical. He instead considered chrysochlorids to represent an aberrant lateral lineage of insectivores worthy of no more than superfamilial distinction (in the Chrysochloroidea) from tenrecs (Tenrecoidea) and shrews (Soricoidea). This was followed by Saban (1954) who, however, erected the suborder Soricomorpha for these three superfamilies.

Butler (1956) maintained that the cranial uniqueness of chrysochlorids is related to their peculiar burrowing habits, and thus that skull differences do not necessarily imply a lack of relationship with other insectivores. He concluded that chrysochlorids possess all but one of the 12 'soricomorph' characters he examined, and that "..their relationship to the Tenrecoidea seems very probable" (Butler 1956:475). But he subsequently changed his opinion, and argued that golden moles should be afforded subordinal status in the Chrysochlorida since the evidence suggesting a close phylogenetic relationship between chrysochlorids and tenrecs is equivocal (Butler 1972). Then, after reviewing characters associated with the tympanic bulla, placentation and the gastro-intestinal tract, he reverted to the view that chrysochlorids and tenrecs are closely allied taxa belonging to the suborder Soricomorpha (Butler 1988).

The higher classification of golden moles has thus been the subject of widely divergent opinion and indecision resulting from the consideration of often conflicting character suites - a dilemma not resolved by palaeontological evidence, since fossil chrysochlorids were already well-specialized, and offer no clues to their ancestral relationships (Butler and Hopwood 1957; de Graaff 1959). MacPhee and Novacek (1993), however, recently made significant progress in resolving the macrotaxonomy of insectivores. By critically analysing traits which Butler (1988) proposed as ancestral for the Insectivora, they demonstrated that extant taxa share only two traits (hindgut simplification and reduction of the pubic symphysis) supporting a monophyletic origin of the order. Character-state distributions relating to the alisphenoid canal, proboscis mobility, jugal reduction and hemichorial placentation do not support the monophyly of the Soricomorpha. They thus argued that chrysochlorids display no resemblance to 'soricomorphs' that cannot be explained as merely primitive retentions or convergences. Since golden moles differ in many important respects from other Insectivora, this ought to be recognized in classification by assigning them to a distinct suborder (Chrysochloromorpha). This is consistent with the findings of Bronner *et al.* (1990).

1.3.2 Generic relationships

The generic taxonomy of golden moles has also been the subject of widely divergent opinions. Dobson (1882) argued against the validity of dental characters for recognizing *Amblysomus* and *Calcochloris*, and assigned all five species then known to *Chrysochloris*. But, Thomas and Schwann (1905) considered *Amblysomus* as distinct from *Chrysochloris* on the basis of cranial and dental differences (lack of temporal fossa and reduction in the number of molars from three to two), and synonymized *Calcochloris* with *Amblysomus*. Broom (1907a,b; 1910) then argued that since dental formula varies within *Chrysochloris asiatica*, the recognition of *Amblysomus* was not warranted. However, he treated *Calcochloris* as a distinct subgenus of *Chrysochloris,* owing to dental differences between this species (P1 molariform) and *Amblysomus* (P1 sectorial).

Roberts (1924) resurrected *Amblysomus* for those species with 36 teeth and molar talonids, and *Chrysotricha* (= *Calcochloris*) for the forms with short, broad skulls having 36 teeth, but lacking molar talonids. He also described two new genera: *Neamblysomus* for *Chrysochloris gunningi* which has peg-like M3 but lacks molar talonids; and *Chlorotalpa* for species having molar talonids and small M3 that are distinctly molariform. This treatment was largely followed by Allen (1939) and Forcart (1942), although these authors afforded *Chrysotricha* only subgeneric status within either *Amblysomus* or *Chrysochloris*, respectively. Forcart (1942) also described the new subgenus *Huetia* for the central African species *Chrysochloris leucorhinus* Huet, 1955, but assigned a specimen from Zaire to the new species *Neamblysomus luluanus* owing to its lack of M3 and molar talonids. Roberts (1951) did not refer to these proposals, and simply followed his earlier classification (Roberts 1924).

Ellerman *et al.* (1953) showed that *Calcochloris* Mivart, 1867 antedates *Chrysotricha* Broom, 1907, and emphasized Broom's (1910) finding that dental formula is not a valid generic character in chrysochlorids, owing to intraspecific variability in both *Neamblysomus gunningi* and *Chrysochloris asiatica*. They synonymized *Neamblysomus*, *Chlorotalpa* and *Calcochloris* with *Amblysomus*, and included *C. leucorhina* in the latter (Table 1.2).

Lundholm (1955) resurrected *Chlorotalpa*, partly on the basis of dental characters, but largely also because of the existence of the enlarged mallei found in some species (Forster Cooper 1928). He allocated these to one of three subgenera: *Chlorotalpa* (head of malleus rounded, but epitympanic recess not sufficiently developed to form a temporal bulla - *C. duthieae*, *C. sclateri*); *Carpitalpa* (head of malleus large and elongated, but temporal bulla not present - *C. arendsi* from Zimbabwe); and *Kilimatalpa* (head of malleus large and elongated, with temporal bulla present - for the species *C. stuhlmanni*, which most other authors referred to *Chrysochloris*). Simonetta (1968) placed even greater emphasis on middle ear characteristics, and elevated *Carpitalpa* to a distinct genus (for *C. arendsi* and *C. stuhlmanni*), but referred *C. stuhlmanni tropicalis* to the distinct species *Chlorotalpa tropicalis*. He also transferred *Chlorotalpa leucorhina* (including *Neamblysomus luluanus*) to *Amblysomus* purely on the basis of malleus morphology, dental characters notwithstanding.

Meester (1974) did not place emphasis on malleus and epitympanic recess characters, although he did regard the presence of a temporal bulla (housing the hypertrophied head of the malleus) as diagnostic for the genus *Chrysochloris*. He thus treated *Calcochloris* and *Chlorotalpa* as discrete genera on the basis of cranial and dental differences, but did not recognize either *Carpitalpa* or *Kilimatalpa* as valid taxa (Table 1.2). Following Ellerman *et al.* (1953), he assigned the central African species *C. stuhlmanni* (including *C. s. tropicalis*) to *Chrysochloris* owing to its possession of a temporal bulla, and included *Neamblysomus* in *Amblysomus*. Meester (1974) also argued that *Amblysomus tytonis*, described by Simonetta (1968) from Somalia, should be assigned to *Chlorotalpa* since it has ten teeth in the lower jaw, and that the type of *Neamblysomus luluanus* is merely an aberrant specimen of the sympatric *Chlorotalpa leucorhina*, thus endorsing Simonetta's (1968) conclusion that these species are synonymous.

Table 1.2.

Schematic summary of the five most recent holistic classifications proposed by previous authors. Asterisks indicate taxa not yet described at the time of revision. Dashes indicate taxa that were not recognized as valid species by previous authors, whereas taxa not included in their revisions are indicated by (NI). Data for *Eremitalpa*, *Cryptochloris* and *Chrysospalax* are excluded since these genera are not examined here.

Roberts (1951)		**Ellerman *et al.* (1953)**		**Simonetta (1968)**		**Petter (1981)**		**Meester (1974)** **Meester *et al.* (1986)**	
Amblysomus	*hottentotus*	*Amblysomus*	*hottentotus*	*Amblysomus*	*hottentotus*	*Amblysomus*	*hottentotus*	*Amblysomus*	*hottentotus*
	iris		--		*iris*		*iris*		*iris*
	marleyi		--						
	corriae		--		*corriae*		--		
	**		**		**		*julianae*		*julianae*
Neamblysomus	*gunningi*		*gunningi*		*gunningi*		*gunningi*		*gunningi*
Chrysotricha *(Calcochloris)*	*obtusirostris*		*obtusirostris*		*obtusirostris*		*obtusirostris*	*Calcochloris*	*obtusirostris*
	chrysilla		--		--		--		--
Chlorotalpa	**		**		*tytonis*		*tytonis*	*Chlorotalpa*	*tytonis*
	NI		*leucorhinus*		*leucorhinus*		*leucorhinus*		*leucorhina*
	duthieae		--	*Chlorotalpa*	*duthieae*		*duthieae*		*duthieae*
	sclateri		*sclateri*		*sclateri*		*sclateri*		*sclateri*
	guillarmodi		--		--		--		--
	montana		--		--		--		--
	**		**	*Carpitalpa*	*arendsi*		*arendsi*		*arendsi*
Chrysochloris	*NI*	*Chrysochloris*	*stuhlmanni*		*stuhlmanni*	*Chrysochloris*	*stuhlmanni*	*Chrysochloris*	*stuhlmanni*
	asiatica		*asiatica*	*Chrysochloris*	*asiatica*		*asiatica*		*asiatica*
	NI		*NI*		*NI*		*visagiei*		*visagiei*

After reviewing cranial, dental and malleus variation, Petter (1981) concluded that the distinction between *Amblysomus*, *Chlorotalpa* and *Calcochloris* was inconsistent with character-state distributions, and that these taxa are too vaguely defined to warrant their recognition as discrete genera. He thus applied Occam's razor, and followed Ellerman *et al.* (1953) in synonymizing *Calcochloris* and *Chlorotalpa* with *Amblysomus* once again.

The generic taxonomy of golden moles thus remains confused owing to lumping and splitting by successive authors. This can be attributed to the 'omnispective' approach (*sensu* Blackwelder 1964) adopted by previous revisors, whose conclusions were based on intuition or only elementary statistical analyses of relatively few specimens and often contradictory character suites. Such scholarly classifications have a mildly evolutionary basis with a phenetic outlook, and are often quite accurate (Wiley 1983), but have been dismissed as art rather than science (Charig 1982; McNeill 1978) since they cannot be defended on a purely logical basis. As pointed out by Hull (1970), taxonomic disputes arising from conflicting omnispective classifications can be settled only by assuming authority after assessing the experience and stature of the taxonomists concerned. Such classifications thus encourage subjectivity, speculation and confusion.

The most recent taxonomic treatment of chrysochlorids by Meester *et al.* (1986) follows that of Meester (1974), and is the classification currently accepted by most mammalogists (Hutterer 1993). However, Meester *et al.* (1986) emphasized that their classification is tentative, and pointed to the need for further revision (particularly of the genera *Amblysomus*, *Chlorotalpa* and *Calcochloris*) to clarify generic relationships. This was echoed by the IUCN\SSC Insectivore, Tree-Shrew and Elephant Shrew Specialist Group, which considers the resolution of taxonomic relationships within the Chrysochloridae a top priority for the conservation of golden moles, 13 species of which are included in IUCN Threatened Species categories (Nicoll and Rathbun 1990).

1.4 AIMS OF THIS STUDY

This thesis examines systematic relationships among 13 chrysochlorid species traditionally assigned to *Amblysomus*, *Chlorotalpa* and *Calcochloris*, with the aim of producing a polythetic classification which reflects phylogenetic relationships, but is also stable with wide general applicability.

Griffiths (1974), Ghiselin (1975) and Hull (1976) have shown that species have an ontological basis and display the properties of individuals. This philosophy is concordant with the Evolutionary Species Concept which defines a species as "..a single lineage or minimal monophyletic group of lineages of ancestor-descendant populations which maintains its identity from other such lineages or groups of lineages and which has its own evolutionary tendencies and historical fate" (Wiley 1978; modified by Brothers 1985:38). Lidicker (1962:169) similarly maintained that subspecies are real units of evolution rather than arbitrary classificatory constructs, and defined a subspecies as "..a relatively homogeneous and genetically distinct portion of a species which represents a separately evolving, or recently evolved, lineage with its own evolutionary tendencies, inhabits a definite geographic area, and may intergrade gradually, although over a fairly narrow zone, with adjacent subspecies". Furthermore, Brothers (1985:41) argued that a higher taxon can also be regarded as a real entity in evolution if it is "..a single evolutionary species or a monophyletic group of such species which exhibits relative epiphenotypic constancy and distinctness from other such species or groups of species and which has its own evolutionary tendencies and historical fate". The hierarchical arrangement of taxa I shall propose therefore reflects inferred evolutionary relationships amongst ontological units of nature, whether these be subspecies, species or even genera. Such classifications represent scientific hypotheses that can be verified or falsified by subsequent revisions based on other data suites (Bock 1974; Brothers 1985; Griffiths 1974; Hull 1967; Kitts 1977).

The classification I shall derive is phylogenetically natural in that it reflects cladogeny, but it does not satisfy the cladists' credo that sister-groups should be afforded equal categorical rank (see Ashlock 1974; Mayr 1974). Brothers (1978) and Charig (1982) have argued that any worker interested in a branching pattern will find it easier to refer to a cladogram directly rather than to reconstruct the branching pattern from a classification, especially since there are various quite different conventions for translating cladograms into classifications. It is thus simplistic and unnecessary to demand that a classification should mirror a cladogram. Cladistic classifications are often excessively monotypic and asymmetrical (Hull 1970), and characterized by an explosion of taxonomic ranks, with the result that they are often incomprehensible to non-taxonomists, and restrict inductive generalization (Ashlock 1974). Furthermore, cladistic classifications are inherently unstable and monothetic, since the discovery of only one novel character can show that a group thought to be monophyletic is in fact paraphyletic, thus making it invalid despite the fact that it may display a high level of phenetic homogeneity.

Bock (1974) argued that if a classification is to prove useful to all comparative studies in biology, full consideration of all the evolutionary mechanisms and phenomena that have contributed to the development of biological attributes is imperative. Classifications should thus be based on not only cladogeny, but also patristic affinity and ecological success, so that genealogical relationships between monophyletic taxa at similar grades of evolution are conveyed (Brothers 1978). Such phylistic classifications are more robust, but no less objective, than cladistic classifications (Charig 1982; Michener 1970), facilitate the efficient storage and retrieval of information about organisms, and permit the greatest number of inductive generalizations and predictions to be made. Phylistic classifications thus have greater heuristic value than cladistic classifications, and provide a solid but phylogenetically-natural and consilient foundation for all comparative studies in biology (Bock 1974; Mayr 1974).

Regardless of its philosophical leaning, any classification must be polythetic if it is to satisfy the criterion of taxonomic stability. Given that the different character suites afforded priority in previous taxonomic revisions of chrysochlorids are somewhat contradictory, this study uses a multi-faceted approach whereby traditional characters are supplemented with additional data suites pertaining to chromosomal properties and hyoid morphology (Part II). The α-taxonomy of species referred to *Amblysomus*, *Chlorotalpa* and *Calcochloris* by Meester (1974) is then revised, using mainly craniometric evidence (Part III). In Part IV, I attempt to clarify intraspecific and generic relationships by integrating morphometric and cytogenetic data, and derive a new phylistic classification for the Chrysochloridae.

CHAPTER 2

MATERIALS AND METHODS

The materials and general methods described here apply to the various morphometric analyses performed in Chapters 5 - 10. Further methodological details of less general applicability, as well as discussion of qualitative morphological characters used, are provided in the text of each chapter.

2.1 GENERAL

A total of 980 specimens from the following collections (abbreviations used in the text follow each name in parentheses) were examined and measured: Transvaal Museum, Pretoria (TM); Kaffrarian Museum, King Williams Town (KM); Durban Natural Science Museum (DM); Natal Museum, Pietermaritzburg (NM); National Museum, Bloemfontein (NMB); South African Museum, Cape Town (SAM); Port Elizabeth Museum (PEM); National Museum of Natural History, Bulawayo (ZM); The Natural History Museum, London (BM); Carnegie Museum of Natural History, Pittsburgh (CM); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (AKM); Forschungsinstitut Senckenberg, Frankfurt (SM); Koninklijk Museum voor Midden-Afrika, Tervuren (KMT).

When available, three external body measurements (TL = total length, HF = hindfoot length *cum unguis*, and mass) were transcribed from specimen skin labels. Basal claw width (measured directly from skins) and most cranial measurements were taken with Tesa Digit-Cal II callipers to the nearest 0,1 mm. Tooth measurements and the diameter of the external auditory meatus (EAM) were taken to two decimal places using an optical micrometer on a Wild-Heerbrugg M5 stereo microscope.

Williams *et al.* (1993) reported that fluctuations in environmental conditions, especially the relative humidity in which skulls are stored and measured, may alter cranial measurements slightly. They found that while the magnitude of changes in individual measurements is unlikely to affect the results of univariate analyses, differential changes in various measurements may distort patterns of variation in multivariate analyses (such as principal components analyses) which are powerful enough to detect slight differences in shape. However, this conclusion was based on limited and equivocal evidence, and requires independant verification - especially in southern Africa, where seasonal fluctuations in climate are less severe than North America.

2.2 DENTAL CHARACTERS

2.2.1 Cheektooth cusp nomenclature

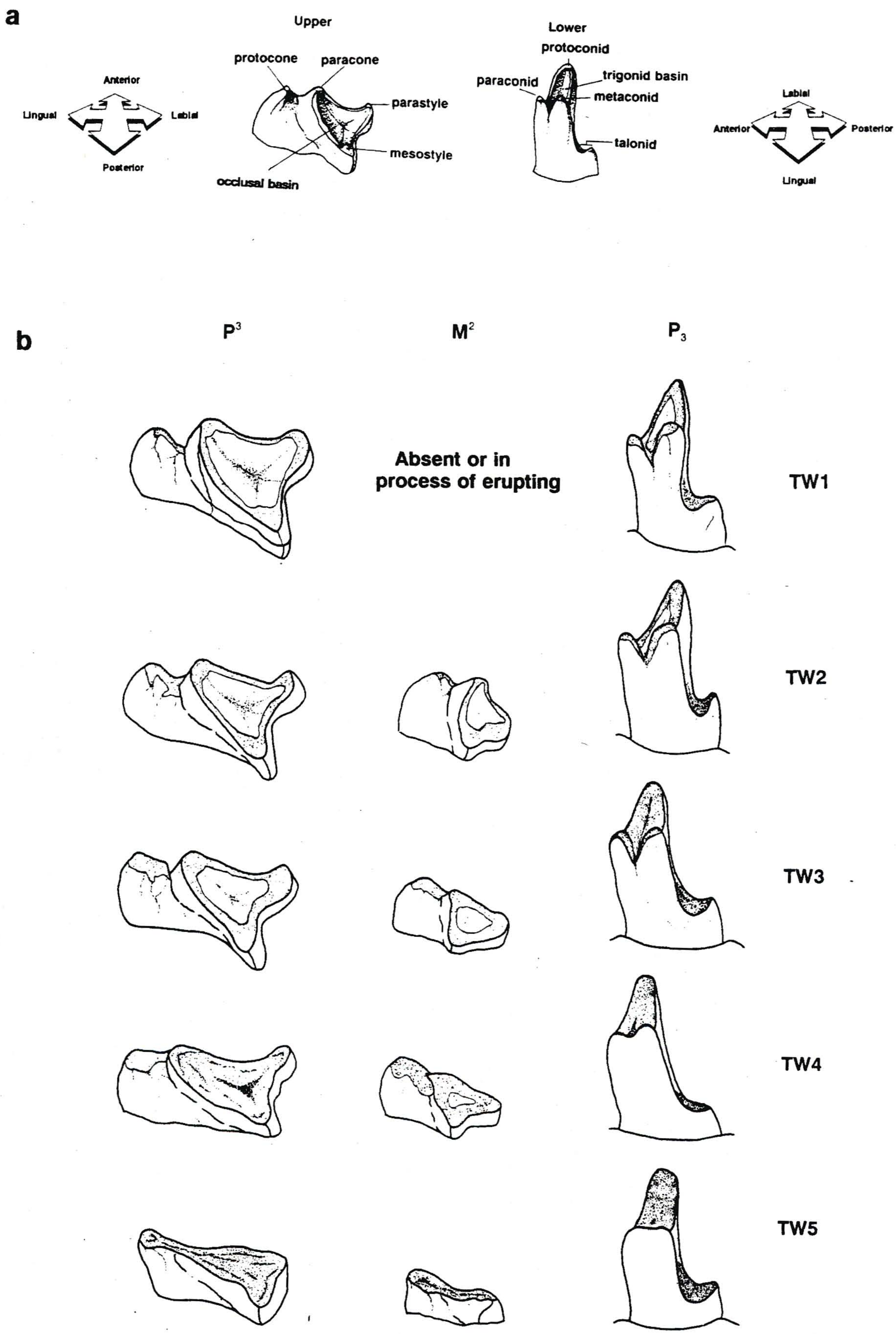
According to Osborn's (1907) terminology for tribosphenic teeth, the upper molar comprises a lingual protocone, with a distal metacone, mesial paracone and several buccal cusps situated labially. Similarly, the lower molar comprises a buccal protoconid, and lingually a distal metaconid and mesial paraconid, with a low distal heel called the talonid. This terminology is still widely used (Hillson 1986).

Osborn's (1907) terminology is used here for cusps on the lower molars of chrysochlorids (Fig. 2.1a). Cusp names for the upper molars are those of Broom (1916a), who demonstrated that the metacone triangle in chrysochlorids has been lost, so that the tooth comprises a low lingual protocone and three elevated cusps (paracone, parastyle and mesotyle) which are connected by well-developed crests to form a high crushing basin.

2.2.2 Toothwear classes

Based on the little information available on post-natal development in chrysochlorids, the young appear to have reached adult proportions by the time they leave the nest and become trapable (Broom 1907a; Kuyper 1985). Non-adult specimens do, however, find their way into museum collections. In the present study, 35 of the specimens examined were juveniles or subadults. Assessment of age-related variation, and the extent to which this may interfere with the interpretation of patterns of geographic variability, is thus imperative to a proper understanding of craniometric variation in chrysochlorids. Unfortunately, locality series for all but one species were too short to allow independent analyses of species-specific ageing criteria. The criteria below were formulated for *Amblysomus hottentotus* (the most widespread species, and best represented in museum collections), and then applied to all taxa examined,

Fig. 2.1. Selected teeth of *Amblysomus hottentotus hottentotus*, showing: a) cusp terminology for the cheekteeth, from Osborn (1907) and Broom (1916b); and b) toothwear classes (TW) used to assess the relative age(s) of specimen(s).


a
Upper
protocone
paracone
parastyle
mesostyle
occlusal basin
Anterior
Lingual
Labial
Posterior
Lower
protoconid
paraconid
trigonid basin
metaconid
talonid
Labial
Anterior
Posterior
Lingual
b
P3
M2
P3
Absent or in process of erupting
TW1
TW2
TW3
TW4
TW5

notwithstanding the possibility that these parameters may vary between species in relation to different diets.

Distinguishing age categories in young cohorts, which is usually achieved by using tooth eruption criteria, is imprecise in chrysochlorids due to their unusual sequence of tooth replacement whereby the deciduous teeth are replaced only late in life, sometimes only after the molars have been lost (Broom 1907a, 1916b). It was thus not possible to examine changes in cranial morphology associated with post-natal growth and maturation during the present study. Instead, juveniles and subadults were identified by the absence of molars (see below), and then excluded from further analyses. Consideration of age-related variation was thus confined to the adult cohorts.

To exclude the possible influence of sexual and geographic morphometric variation, 50 male *A. hottentotus* originating from a single locality (King Williams Town) were examined. This allowed the recognition of five, in theory non-overlapping, toothwear classes based primarily on the extent of erosion of the cheekteeth. Specimens were allocated to these classes according to the following criteria (Fig. 2.1b):

TOOTHWEAR CLASS 1 (TW1): M2-3 either absent or in the process of erupting; little toothwear, with cusps and crests of cheekteeth high and sharp.

TOOTHWEAR CLASS 2 (TW2): molars fully erupted in all quadrants; cusps of incisors and cheekteeth high and sharp; crests of cheekteeth with only narrow erosion surfaces; occlusal crushing basins deep; paracone higher than protocone on M^2; talonids (if present) on lower molars pointed and elevated.

TOOTHWEAR CLASS 3 (TW3): molars fully erupted in all quadrants; moderate toothwear, with cusps of cheekteeth high but rounded; crests of cheekteeth with wide erosion surfaces nearly replacing the (shallow) occlusal basins; paracone and protocone of M^2 about the same height; talonids (if present) still high, but rounded; paraconids and metaconids of lower molars separate and distinct.

TOOTHWEAR CLASS 4 (TW4): molars fully erupted in all quadrants; heavy toothwear, so that occlusal basins are completely replaced by flat surfaces; paracone on M^2 (and often other cheekteeth) severely eroded so that protocone is the highest cusp;

talonids (if present) low and shelf-like; paraconids and metaconids of lower molars not distinct, and often fused by a flat toothwear surface.

TOOTHWEAR CLASS 5 (TW5): molars fully erupted in all quadrants; extremely heavy toothwear, so that occlusal basins are replaced by flat erosion surfaces sloping lingually; paracones and protocones of upper cheekteeth completely eroded; incisors and canines are low and peg-like, whereas cheekteeth are narrow and often broken or reduced to stumps; talonids (if present) low or indistinct.

As no known-age specimens were available for calibration purposes, these toothwear classes are arbitrary, and have no clearcut biological significance. They serve only to reflect the relative ages of the specimens.

2.2.3 Qualitative dental characters

Qualitative dental characters have featured prominently in most previous taxonomic works on chrysochlorids (Meester 1974; Roberts 1951; Simonetta 1968). In particular, the number of teeth in each quadrant, and the morphology of P1, have been used for diagnostic purposes. However, Ellerman *et al* (1953) found that the number of teeth in each quadrant varies within species (and even within specimens), implying that the dental formula is not a valid taxonomic character. The suitability of most other commonly used dental characters has never been unequivocally established. To test the usefulness of these characters, and to determine consistent character states for interspecific analyses, the characters below (Fig. 2.2) were scored for each specimen examined.

INCISOR MORPHOLOGY - recorded as unicuspid (= sectorial) or bicuspid (with well-developed postero-labial cusp).

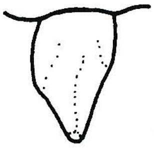
CANINE MORPHOLOGY - recorded as unicuspid (only one, high cusp) or biscuspid (one high main cusp connected with smaller postero-labial cusp via a low crest).

UPPER PREMOLAR 1 (P^1) - presence/absence of a protocone.

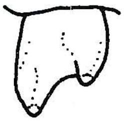
UPPER PREMOLAR 1 (P^1) MORPHOLOGY - recorded as sectorial (parastyle and mesostyle absent or poorly developed); pseudo-molariform (parastyle and mesostyle

Fig. 2.2 Diagrams showing variation in the morphology of the canines, first premolars, talonids and M3 among chrysochlorids. Labels indicate character-states referred to in the text.

Canine

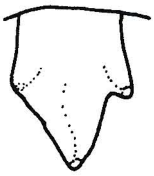


Unicuspid

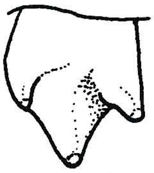


Bicuspid

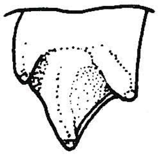
P^1



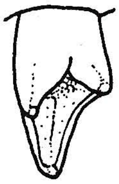
Sectorial



Pseudo-molariform

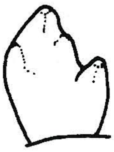


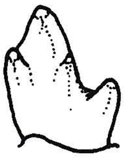
Semi-molariform

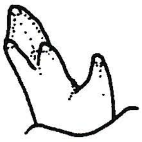


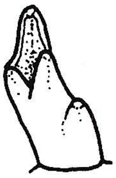
Molariform

P_1

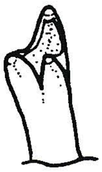




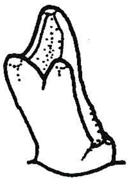




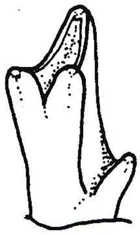
Lower molars



Talonid absent



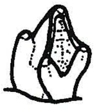
Talonid weak



Talonid well developed

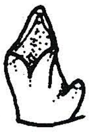
M3

M^3 molariform

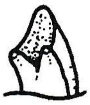


M^3 peg-like

Labial
Anterior ◄ ▲▼ ► Posterior
Lingual



M_3 molariform
(+ talonid)



M_3 molariform
(- talonid)

well-developed but low so that the tooth is approximately the same height as the canine); semi-molariform (parastyle and mesostyle well-developed and elevated, with a well-developed posterior basin, but tooth is not as high as other premolars); and molariform (parastyle and mesostyle high and are connected to paracone by well-developed crests so that a large occlusal basin is formed).

LOWER PREMOLAR (P_1) MORPHOLOGY - recorded as sectorial (paraconid and metaconid absent or poorly developed); pseudo-molariform (paraconid and metaconid present but low, tooth about the same height as the canine); semi-molariform (paraconid and metaconid well-developed and somewhat elevated, but tooth is lower than other premolars); and molariform (paraconid and metaconid high and well-developed, and connect with protoconid via crests to form a trigonid basin).

PRESENCE/ABSENCE OF TALONIDS ON P_2 - M_{2-3} - and if present, whether the talonids are feeble or well-developed.

PRESENCE/ABSENCE OF M3 - and if present, whether morphology is similar to that of other molars, or merely reduced and peg-like.

2.3 CRANIOMETRIC CHARACTERS

3.2.1 Selection of craniometric characters

The selection and screening of variables are critical, but often neglected, steps in morphometric studies (Mayr and Ashlock 1991). Variables are usually chosen on the basis of either previous use or experience, without the criteria for their selection being specified, or any objective evaluation of their reliability being performed. Although variables chosen arbitrarily or on the basis of convention may perform well in biometric studies, they often have inherent biases (Strauss and Bookstein 1982). Characters with high inter-correlations may reflect the same epigenetic information, and indiscriminate use thereof increases the risk of redundancy and colinearity in data suites, which may in turn lead to computational problems during multivariate analyses. One should, therefore, replace or supplement traditional measurements with the best possible balance of multidimensional measures (chosen with reference to morphological landmarks) outlining the material to be studied. The reliability of these variables should then be assessed in a preliminary study designed to identify the best subset of characters which is free from redundancy yet still summarizes the phenotype adequately. An added advantage of this procedure is improved experimental economy (Chimimba and Dippenaar 1995; Pimentel and Smith 1986; Thorpe 1985).

In designing a craniometric data suite for this study, 68 cranial and dental measurements (including diagnostic characters and variables used by previous workers) were initially identified (Table 2.1). To exclude the possible influence of sexual, age- or geographical variation in cranium size and shape, these measurements were then taken for each of 20 TW2 male *A. hottentotus* originating from the same locality (King Williams Town). The resulting data matrix was then submitted to outlier analyses and tests (for homoscedasticity, skewness, kurtosis, normality and randomness of samples) to ensure that statistical assumptions were satisfied. The data were then entered into a R-mode principal components analysis, which terminated due to matrix singularity and ill-conditioning (dispersion determinant = 0), indicating the presence of serious redundancy and linear dependency in the data suite.

Re-examination of the 68 variable suite revealed the presence of five ipsative and/or semi-ipsative variables, and of 23 variables (including all tooth measurements) with unacceptably high ($>10\%$) measuring error (as determined using the method of Taylor, Meester and Rautenbach 1990), which were rejected for further use (Table 2.1). The revised data suite containing 40 variables was then subjected to "phenotypic set analysis" (Cheverud 1982). The data matrix was submitted to a Q-mode principal components analysis, with all of the components being retained. Each variable's loading on these 20 vectors was then used to project the variables into multi-dimensional component space. Euclidean distances between the variables in component space were then computed, and entered into Ward's (1963) minimum-variance hierarchical clustering algorithm, which produces relatively homogenous clusters with high intra- and low inter-correlations. Theoretically, the major clusters represent "phenotypic sets" (P-sets) of variables which approximate "functional sets" (F-sets) of characters that are developmentally and genetically interdependent (Cheverud 1982; Olson and Miller 1958).

This procedure gave equivocal results. Despite the division of variables into two major sub-clusters (designated α and ß in Fig. 2.3) at a high Euclidean distance of ±18, these subclusters did not distinguish between the Orofacial and Neurocranial sets as would be expected on the basis of Olson and Miller's (1958) distinction between

Table 2.1

List of 68 cranial and dental measurements initially identified for possible use in this study. These measurements include putative diagnostic variables, and characters used in the most recent studies on chrysochlorid taxonomy by Meester (1974), Petter (1981) and Simonetta (1968). Asterisks indicate variables rejected on the grounds of ipsativity and/or high measuring error.

LENGTH MEASUREMENTS

BSL - basal length
BsL - basilar length
CbL - condylobasilar length
CBL - condylobasal length
CCL - condylocanine length
FML - foramen magnum length
GSL - greatest skull length
IFL - infra-orbital foramen length
IMR - inciso-molar length
IOL - inciso-orbital length
MDL - mandible length
MDT - mandibular toothrow length
MTL - maxillary toothrow length
NSL - length of nasals
OBL - orbital length
PaL - palatilar length
PAL - palatal length
PPL - post-palatal length
TBL - tympannic bulla length
USL - upper skull length
VOL - ventral orbit length*

HEIGHT MEASUREMENTS

CAG - coronoid-angular gap*
GSH - greatest skull height
MRH - mid-rostrum height*
PAH - parietal height*
PSH - posterior skull height*
SOH - supraoccipital height*
ZPH - height of zygomatic plate*

WIDTH MEASUREMENTS

AIO - anterior intra-orbital width
ANW - anterior nasals width
APM - angular process minimum width*
APW - ascending process of mandible width
APX - angular process maximum width*
ARB - anterior rostral breadth
BBW - bi-bullar width
BCB - braincase breadth
CCW - width across canines
CFW - width between condylar foramina*
CPW - coronoid process width
EXW - width across exoccipitals
FMW - foramen magnum width*
IBW - inter-bullar width*
IOW - width between infra-orbital foramina
IPG - inter-pterygoid width
PBM - width between M^2
MIO - mid intra-orbital width
ZMB - mastoidal breadth
OCW - width across occipital condyles
P@P - width across P^2
PIO - posterior intra-orbital width*
PSW - width between post-squamosal foramina*
RBM - rostral breadth at M^1
SOW - supra-occipital width*
TBW - tympannic bulla width
EAM - diameter of external auditory meatus

DENTAL MEASUREMENTS

M_1H - height of M1*
M^1H - height of M^1*
P_1H - height of P_1*
P^1W - width of P^1*
P_1W - width of P_1*
P_2H - height of P_2*
P^2H - height of P^2*
P_2W - width of P_2*
P^2W - width of P^2*
P_3H - height of P_3*
P^3H - height of P^3*
P_3W - width of P_3*
P^3W - width of P^3*

these fundamental cranial units (see Table 2.2). Instead, the major subclusters distinguished small measurements pertaining to foramen diameters (FML, EAM, IFL - subclusters VIII - IX) and variables representing the orofacial (oral/frontal/ masticatory) submatrices (subclusters V - VII), from characters portraying neurocranial and "mixed" neurocranial-orofacial F-sets (subclusters I - IV). Within the largest major cluster (designated ß in Fig. 2.3), distinction between "mixed-unit" logical subsets was first evident at the 12-cluster stage, with the subclusters A and B representing overall size measurements spanning several F-sets of both functional units, including most of the traditional cranial measurements for mammals. This supports Strauss and Bookstein's (1982) claim that traditional variables tend to conform to only a single axis reflecting overall size. Subclusters C and D included mixed orofacial-neurocranial measurements crossing two or more subunits, while subclusters E and F represented "mixed" neurocranial subunits (parietal/occipital), and subclusters G represented "mixed" orofacial subunits (nasal/orbital+masticatory). Six variables were interpreted as not belonging to their designated subsets (Table 2.2), possibly as a result of distortions produced by the clustering algorithm.

A total of 18 "phenotypic sets" of variables was thus identified (Fig. 2.3). One variable from each of the 18 phenotypic sets was then selected (on the basis of measuring error and size, bearing in mind that smaller measurements summarize local rather than average variation - Pimentel and Smith 1986) for use in further analyses. To confirm the reliability of the revised data suite, another R-mode principal components analysis was performed. This analysis did not terminate owing to matrix singularity, and no zero eigenvalues were computed, indicating that the data were free of linear dependency. The dispersion determinant for this analysis was $1X10^{-10}$, which is well above the value of $1X10^{-30}$ that in general typifies ill-conditioned matrices (Pimentel and Smith 1986).

2.3.2 Character suite and measuring error

This variable suite (which included eight length, eight width and two height measurements; Fig. 2.4), along with four external measurements, was assumed to be one of many possible optimal subsets of characters. Thorpe (1985) has shown that 18

Fig. 2.3 Phenogram based on Ward's (1963) hierarchical clustering of euclidean distances between 40 craniometric variables (see Table 2.1) in 20-dimensional principal components space, computed from single-standardized data for 20 TW2 male *A. h. hottentotus* from King Williams Town. Roman numerals and letters indicate subsets of correlated measurements formed at the 9 and 12 cluster stage; vertical lines and numbers indicate "F-sets" of measurements assumed to be developmentally and genetically interdependent - see Table 2.2. Arrows denote characters selected for use in subsequent morphometric analyses.

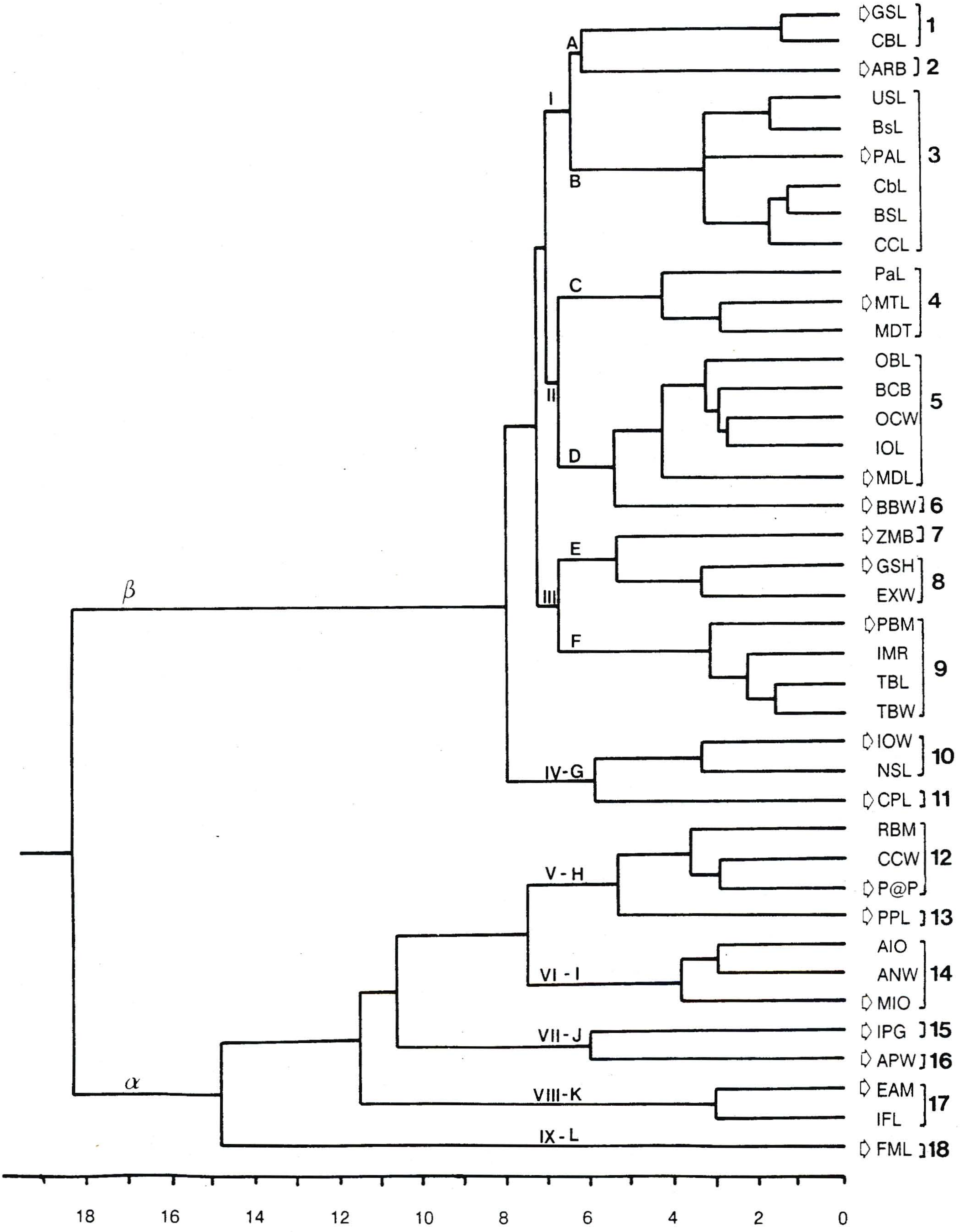

β
α
A
I
B
C
II
D
E
III
F
IV-G
V - H
VI - I
VII - J
VIII-K
IX - L
▷GSL
CBL
1
▷ARB
2
USL
BsL
▷PAL
CbL
BSL
CCL
3
PaL
▷MTL
MDT
4
OBL
BCB
OCW
IOL
▷MDL
5
▷BBW
6
▷ZMB
7
▷GSH
EXW
8
▷PBM
IMR
TBL
TBW
9
▷IOW
NSL
10
▷CPL
11
RBM
CCW
▷P@P
12
▷PPL
13
AIO
ANW
▷MIO
14
▷IPG
15
▷APW
16
▷EAM
IFL
17
▷FML
18
18
16
14
12
10
8
6
4
2
0

Table 2.2

Summary of correlated subsets of cranial measurements in male TW2 *A. h. hottentotus* from King Williams Town (n=20), derived from a phenogram based on Ward's (1963) hierarchical clustering of euclidean distances between variables in 20-dimensional principal components space (Fig. 2.3). Roman numerals, letters and numbers indicate sets formed at the nine, 12 and 18 cluster stages of analysis. Characters designated by question marks [?] were interpreted as not belonging to their designated F-sets. Asterisks denote characters selected for use in subsequent morphometric analyses.

Clusters and subclusters	Measurements
I. MIXED OROFACIAL AND NEUROCRANIAL F-SET (3 OR MORE F-SETS SPANNED)	
A. Overall size distances	
1. Greatest skull lengths	GSL*, CBL
2. Orofacial (nasal) width	ARB*[?]
B. Orofacial (oral/nasal) and neurocranial (occipital)	
3. Ventral skull lengths	USL[?],BsL,PAL*,CbL,BSL,CCL
II. MIXED OROFACIAL AND NEUROCRANIAL F-SET (<3 F-SETS SPANNED)	
C. Orofacial component	
4. Orofacial (oral/masticatory) lengths	PaL, MTL*,MDT
D. Neurocranial component	
5. Mixed neurocranial (frontal/parietal/occipital) subunits	OBL,BCB,OCW,IOL,MDL*
6. Neurocranial (occipital only) subunit	BBW*
III. MIXED NEUROCRANIAL (PARIETAL/OCCIPITAL) F-SET	
E. Neurocranial (parietal/occipital) subunit	
7. Parietal subunit only (width)	ZMB*
8. Parietal + occipital subunits	EXW,GSH*
F. Neurocranial (occipital) subunit	
9. Bullae dimensions	TBL,TBW,PBM*[?],IMR[?]
IV. MIXED OROFACIAL (NASAL/ORBITAL/MASTICATORY) F-SET	
G. 10. Orofacial (nasal) subunit	IOW*,NSL
11. Orofacial (orbital/masticatory) subunit	CPL*
V. OROFACIAL (ORAL) F-SET	
H. 12. Orofacial (oral) widths	RBM,CCW,P@P*
13. Orofacial (oral) [+ neurocranial occipital??] length measurement	PPL*
VI. OROFACIAL (FRONTAL) F-SET	
I. 14. Orofacial (frontal) width measurements	AIO,ANW[?],MIO*
VII. MIXED OROFACIAL (ORAL/MASTICATORY) F-SETS	
J. 15. Orofacial (oral/masticatory) "oblique" width	APW*
16. Orofacial (oral) width	IPG*[?]
VIII. MIXED FORAMEN DIAMETERS	
K. 17. Auditory meatus/infra-orbital foramen	EAM*,IFL
IX. FORAMEN MAGNUM DIAMETER	
L. 18. Foramen magnum diameter	FML*

variables are sufficient to reveal patterns of geographic variation with 97% confidence, and that beyond this point it may not be cost-effective to examine more characters.

Specimens representing the other species included in this study were then examined to confirm measurement homologies across all taxa, and replicate measurements of five specimens per species were taken to assess measurement error. Mean measurement error ranged from 1,25 - 9,06% (Table 2.3). Errors of this magnitude are typical in morphometric studies , and should not obscure major trends in geographic variation. The 18-measurement craniometric data suite (Table 2.4, Fig. 2.4), along with chromosomal (Chapter 3) and hyoid (Chapter 4) characters, was thus used for all taxa examined during this study.

This design procedure represents an attempt to objectively screen variables and maximize experimental economy. However, this procedure has several theoretical and practical shortcomings. The samples used for assumption testing and character selection were small, with the result that the variable elimination process might justifiably be labelled as cavalier. Furthermore, variable relationships within only one toothwear class of one sex from a single locality were considered, and the underlying assumption that these relationships hold true for both sexes at all localities, as well as for other species, was not tested owing to prohibitively small samples for most localities and taxa. The failure of this technique to differentiate between the main cranial functional units whilst distinguishing between smaller subunits, especially those belonging to the neurocranial component, at relatively low Euclidean distances (Fig. 2.3) may be attributed to two factors. First, the chrysochlorid skull has been greatly modified in adaptation to burrowing habits (Butler 1956), implying that the gross functional topography of the cranium may be fundamentally different, or masked, relative to that of other mammals, but that at the micro-topographical level the various subunits still function as semi-independent subsystems, and thus can be recognized. Second, reconciling P-sets of variables with F-sets is a somewhat arbitrary procedure since the boundaries of the various functional units of the cranium have been only vaguely defined in the literature. Assignment of characters to F-sets is thus partly subjective, and prone to erroneous interpretation. Furthermore, and perhaps most importantly, there is no guarantee that the data suite designed will function well in multivariate analyses involving greater numbers of specimens and/or reduced subsets of

Fig. 2.4. Skull of *A. hottentotus* illustrating reference points of 18 cranial measurements used in morphometric analyses. Terminology follows Broom (1915), deBlase and Martin (1981), and Thomas (1905) - see Table 2.3 for full names and descriptions of measurements.

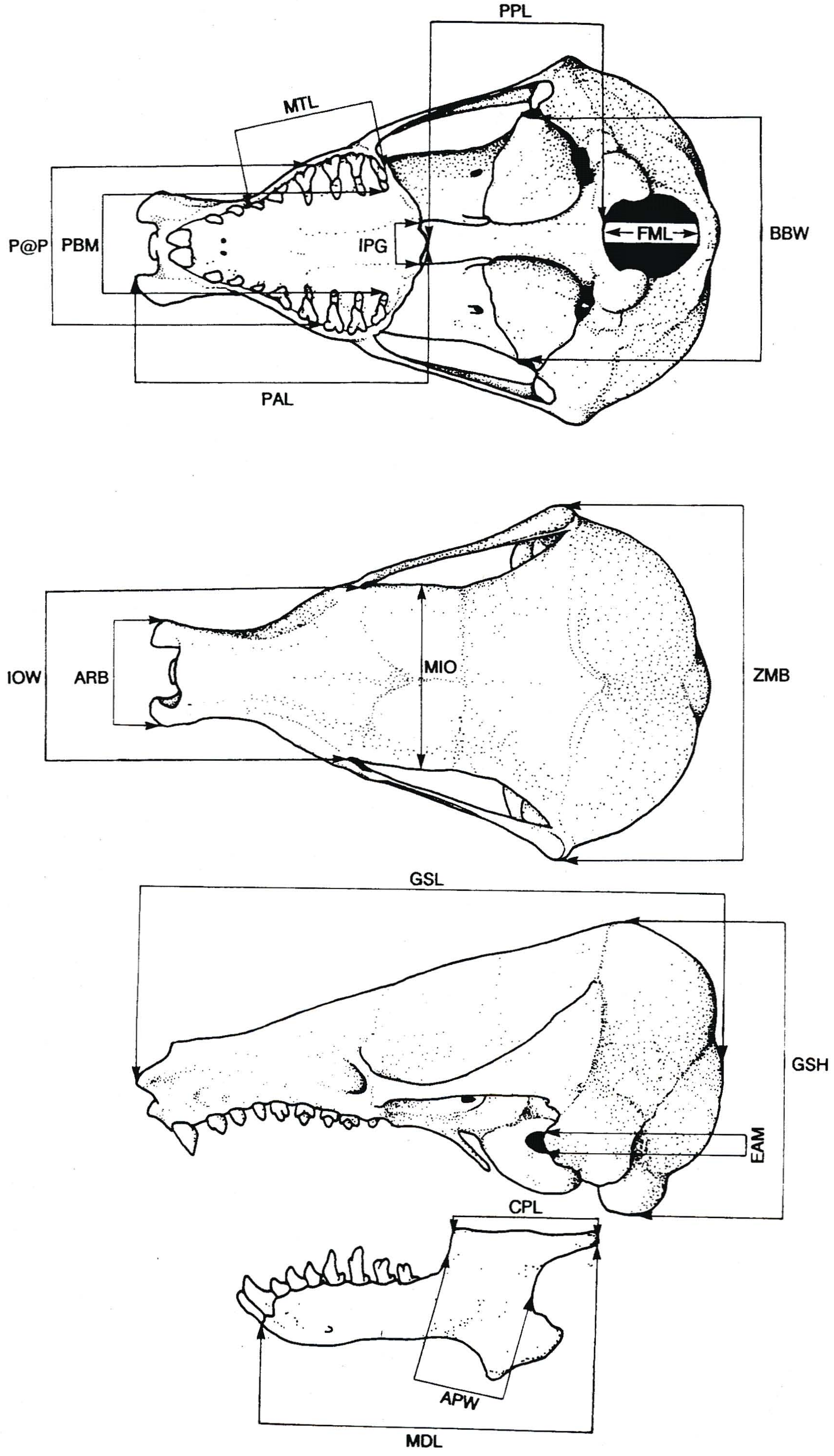

PPL
MTL
P@P
PBM
IPG
FML
BBW
PAL
IOW
ARB
MIO
ZMB
GSL
GSH
EAM
CPL
APW
MDL

Table 2.3

Final measurement suite for the Chrysochloridae. Mean measuring error (ME) ± one standard deviation, calculated from data for 5 replicates per species using the formula of Taylor *et al.* (1990), is expressed as a percentage of the range of each variable.

CRANIAL MEASUREMENTS

1) *Anterior rostral breadth (ARB)* - greatest breadth of the rostrum anteriorly, in anterior view. (ME=2,0±0,55)

2) *Mid inter-orbital width (MIO)* - greatest width of the frontals in the mid inter-orbital region, in dorsal view. (ME=3,52±1,65)

3) *Zygomatic breadth (ZMB)* - greatest width of skull, taken between zygomatic processes of squamosals, in dorsal view (ME=1,25±0,77)

4) *Greatest skull length (GSL)* - measured from most anterior tip of premaxillae to most posterior point of supraoccipital, in dorsal view (ME=2,16±1,34)

5) *Greatest skull height (GSH)* - between highest point on skull at midline, and the base of the occipital condyles, in posterior view. (ME=3,17±1,61)

6) *Palate width across P^2 (P@P)* - measured between labial edges of P^2, in ventral view. (ME=4,05±2,20)

7) *Palate width between M^2 (PBM)* - between most medial points of M^2 at palate level, in ventral view. (ME=7,12±4,72)

8) *Palatal length (PAL)* - from most anterior point of premaxilla to posterior of palate, in ventral view. (ME=3,68±3,81)

9) *Maxillary toothrow length (MTL)* - measured labially from anterior of canine to the posterior of the last molar, in lateral profile. (ME=7,05±4,43)

10) *Interpterygoid width (IPG)* - greatest width between ptergoids measured at posterior of palate, in ventral view. (ME=9,06±4,89)

11) *Post-palatal length (PPL)* - from anteriormost point on posterior edge of palate to anteriormost point on the lower edge of the foramen magnum, in ventral view. (ME=6,32±3,45)

12) *Bi-bullar width (BBW)* - greatest breadth across bullae, between most lateral points of external auditory meati, in ventral view. (ME=5,25±2,85)

13) *Foramen magnum diameter (FML)* - greatest diameter (length) of the foramen magnum, in caudoventral view. (ME=6,42±4,53)

14) *Coronoid process length (CPL)* - from most anterior to most posterior point of mandibular condyle, in dorsal view. (ME=6,67±3,94)

15) *Ascending process width (APW)* - between anteriormost point at base of coronoid process, to most anterior point on posterior edge of coronoid process, in lateral profile. (ME=7,34±4,65)

16) *Mandible length (MDL)* - from most anterior point of dentary below I_1, to most posterior point of mandibular condyle, in lateral profile. (ME=4,37±2,69)

17) *Infra-orbital width (IOW)* - width of rostrum between most distal points on interior(s) of infra-orbital foramina, in anterior view. (ME=4,74±2,62)

18) *External auditory meatus diameter (EAM)* - greatest diameter of the external auditory meatus, in lateral view. (ME=8,34±1,25)

EXTERNAL MEASUREMENTS

19) *Basal claw width (BCW)* - greatest width of the third foreclaw measured proximally at point of emergence from skin. (ME=6,50±2,60)

characters to compensate for missing measurements. Despite extensive screening of variables using this and other analytical techniques on samples of *Myosorex*, Kearney (1992) still experienced computational problems resulting from singular and ill-conditioned matrices in principal components and canonical variate analyses, implying that sources of serious colinearity were still inherent in the data.

More detailed techniques utilizing correspondence analysis and canonical variate loadings of characters have recently been developed (Chimimba and Dippenaar 1995). These appear to be more objective, but they suffer some of the same shortcomings discussed above, and furthermore require intensive analyses to the extent that the preliminary screening of variables tends to become a major study in itself.

2.4 STATISTICAL ANALYSES

Univariate and multivariate phenetic analyses were conducted using the BIOΣTAT1 and BIOΣTAT2 statistical packages (Pimentel and Smith 1986, 1990), and the NT-SYS package (Rohlf 1986) on a DTK 286AT microcomputer. Cladistic analyses were performed using PAUP Version 2.4 and 3.2 (Swofford 1985, 1991).

The analytical methods used largely follow those documented by Dippenaar and Rautenbach (1986), and are discussed in detail by Blackith and Reyment (1971), Jardine and Sibson (1971), Neff and Marcus (1980), Pimentel (1979), Pimentel and Smith (1986, 1990), Sneath and Sokal (1973), Thorpe (1976) and Zar (1974). The external body measurements (TL, HF and mass) were excluded from most analyses because of their alleged unreliability as taxonomic characters.

Univariate analyses included the computation of summary statistics (arithmetic mean, standard deviation, standard error of the mean, coefficient of variation), skewness (*g1*) and kurtosis (*g2*) statistics, single classification analyses of variance followed by Student-Newman-Keuls (SNK) multiple comparison tests for maximally non-significant subsets, and two-way analyses of variance to consider differences between the sexes and toothwear classes simultaneously. Bartlett's test was used for evaluating homoscedasticity, whereas the Serial Correlation *C*-statistic was used to assess the randomness of samples. Deviations from normality were evaluated using the Kolmogorov-Smirnov *D*-statistic, which is more powerful than the chi-square test when sample sizes are small (Pimentel and Smith 1986). When SNK tests did not detect

Fig. 2.5. Map of southern Africa showing new provincial boundaries in South Africa, biogeographical districts and some of the towns referred to in the text.

significant differences between operational taxonomic units (OTUs) that were indicated by analysis of variance, significance was assumed since the SNK test is more susceptible to Type II errors (Zar 1974). Chi-squared tests (X^2) incorporated Yate's correction for continuity.

Multivariate analyses included: 1) cluster analyses (UPGMA) based on among-OTU average taxonomic distances (ATD) and product-moment correlation (CORR) coefficients computed from single standardized data; 2) single-group and multi-group principal components analyses based on among-character correlation coefficients (PCA); 3) two-group and multi-group discriminant functions analyses (MDA); 4) multivariate analyses of variance (MANOVA); 5) minimum spanning trees (MST = minimally connected network analysis) computed from among-OTU average taxonomic distances to assess nearest neighbour relationships, and when superimposed on PCA scattergrams, to evaluate the amount of distortion in graphs of low dimensionality; 6) co-phenetic correlation coefficients for phenograms and PCA-scattergrams.

Cladistic analyses were performed on various subsets of characters with the MULPARS (searches for multiple equally parsimonious trees), SWAP=GLOBAL (performs global branch-swapping to find shortest trees) and branch-and-bound (to select all most parsimonious trees) options of PAUP engaged.

My use of place names is consistent with recent changes in the names and boundaries of geopolitical regions in South Africa. A pull-out map showing the new provincial boundaries, along with the names of biogeographical districts and some towns, is given in Fig. 2.5 (see inside of back cover).

PART II

ASSESSMENT OF ALTERNATIVE DATA SUITES

CHAPTER 3

COMPARATIVE HYOID MORPHOLOGY [1]

3.1 INTRODUCTION

The mammalian hyoid apparatus exhibits considerable morphological plasticity in relation to function and environmental influence (Gasc 1967), which has led to claims that hyoid characters have little phylogenetic value (Grasse 1955). Nevertheless, hyoid morphology has been found to be taxonomically useful in several taxa, including the Rodentia (Sprague 1941), Felidae (Pocock 1916), Chiroptera (Sprague 1943) and certain Insectivora (Sprague 1944).

Although chrysochlorid anatomy has been extensively studied (Broom 1915, 1916a; Bugge 1974; Campbell 1938; Forster Cooper 1928; Parsons 1901; Puttick and Jarvis 1977; Roux 1947; see also Hickman, 1990, and references therein), only Dobson (1882) and Sprague (1944) briefly described the hyoid morphology of some species. These authors noted that the hyoid apparatus of chrysochlorids is unusual, but they did not consider variation in hyoid morphology within and between species. Neither did they recognize that the hyoid bones of golden moles articulate directly with the dentary bones - a feature unique among mammals (Bronner *et al.* 1990).

Potential variation in, and the systematic use of, characters of the specialized hyoid apparatus of chrysochlorids have thus not been adequately considered from a taxonomic perspective. This chapter compares the hyoid morphology of nine golden mole species, and evaluates the potential systematic utility and implications of hyoid characters with reference to seven species traditionally referred to the genera *Amblysomus*, *Calcochloris* and *Chlorotalpa* (see Meester *et al.* 1986). Data are also given for *Chrysochloris asiatica* and *Chrysospalax trevelyani*, taxa that were used as outgroups for cladistic analyses.

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[1] This chapter, together with abstract and relevant references, is essentially the paper by G. N. Bronner that was published in 1991 under the title "Comparative hyoid morphology of nine chrysochlorid species (Mammalia: Chrysochloridae)" in the *Annals of the Transvaal Museum*, **35**: 295-311.

3.2 MATERIALS AND METHODS

3.2.1 General

The hyoid apparatus of 135 specimens representing five genera and nine species (Appendix 3.1) housed in the Transvaal Museum mammal collection, were examined and measured. Measurements (defined below) were taken to the nearest 0,1 mm using an optical micrometer on a Wild-Heerbrugg M5 stereo microscope.

Ten quantitative and five qualitative hyoid characters considered to be homologous across all species were initially identified for possible use (Table 3.1). Three of the qualitative characters - basihyal shape (rod-like with or without latero-rostral flange adjoining ceratohyal), thyrohyal shape (distally bulbous or tapered) and epihyal shape (triangular or rod-shaped) - were subsequently rejected for further use because they were difficult to score (owing mainly to preparation damage), and had low repeatability. Similarly, three measurements (ceratohyal greatest width; styloid process length; styloid process - articular surface distance) were eliminated from the data suite owing to unacceptably high (> 5 %) measuring error (Table 3.1). Another two variables - stylohyal greatest width and epihyal greatest width - were rejected because of strong colinearity with other variables: stylohyal length and width were linearly correlated ($y = 0{,}716x - 0{,}719$; $t = 2{,}44$; $p = 0{,}047$; $r = 0{,}678$); similarly, epihyal length and width were linearly related ($y = 2{,}05x + 0{,}614$; $t = 2{,}53$; $p = 0{,}003$; $r = 0{,}691$). The remaining suite of five measurements (Fig. 3.1) and several qualitative characters (ceratohyal shape, stylohyal shape, styloid angle, styloid process morphology) were then measured in all available material, and entered into statistical analyses.

3.2.2 Procedure

Intra-specific variation in hyoid mensural data was assessed in only *A. hottentotus*, as sample sizes of other species were too small for meaningful statistical treatment. For the evaluation of sexual and age-related variation, data for 23 (10 males; 13 females) *A. hottentotus* originating from Durban, KwaZulu-Natal, and belonging to two adult toothwear classes (TW2 and TW3) were compared. Geographic variation within the species was assessed by comparing data suites for six locality and/or pooled samples (Fig. 3.2), for each measurement individually, and for all

Table 3.1

Statistics used to evaluate suitability of 10 hyoid measurements initially identified for use. *CV*: coefficient of variation; *R*: resolution, and *ME*: measuring error expressed as a percentage of observed range, calculated using replicated measurements according to the formulae of Taylor *et al.* (1990).

Measurement	***CV***	***R***	***ME*(%)**
Basihyal greatest length	13,6	15,1	4,1
Thyrohyal greatest length	10,9	22,0	2,9
Ceratohyal greatest length	10,7	9,5	4,9
Ceratohyal greatest width	11,0	3,5	7,3
Epihyal greatest length	8,6	10,0	4,5
Epihyal greatest width	12,9	5,1	4,6
Stylohyal greatest length	6,0	12,0	3,9
Stylohyal greatest width	11,0	11,1	5,0
Styloid process length	5,1	8,0	12,7
Styloid process-articular surface distance	9,1	8,0	8,1

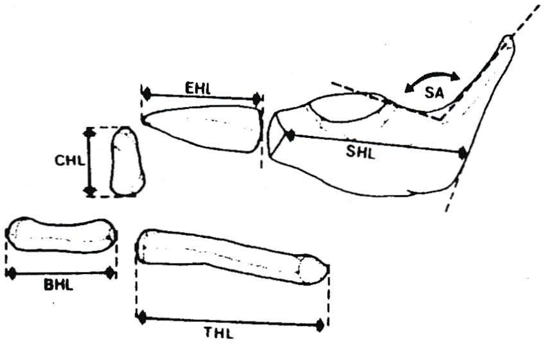


Fig. 3.1 A generalized representation of the hyoid apparatus in chrysochlorids, indicating measurements taken for statistical analysis. BHL = basihyal length; THL = thyrohyal length (measured along longitudinal axis); CHL = ceratohyal length; EHL = epihyal length; SHL = stylohyal length (assessed visually).

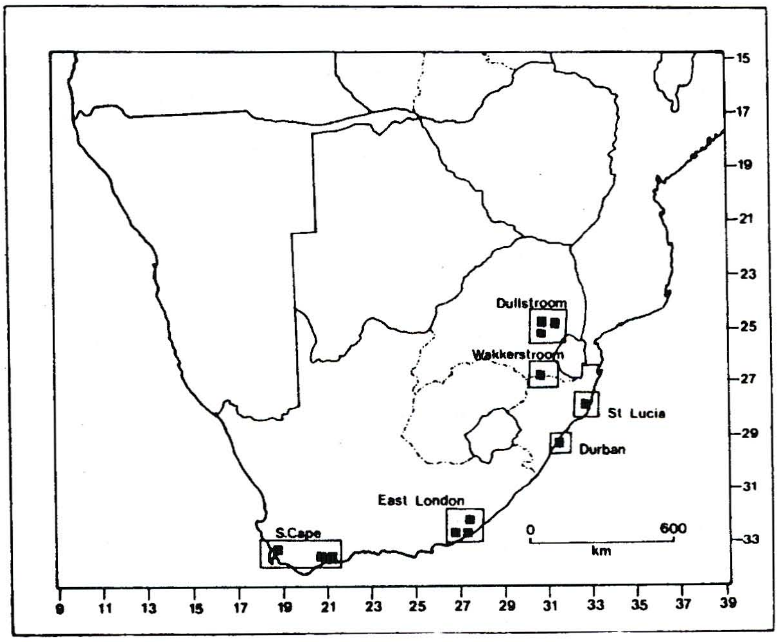


Fig. 3.2. Geographical samples of *Amblysomus hottentotus* analysed, plotted by quarter-degree square, and pooled as population samples.

measurements simultaneously. Inter-specific phenetic analyses were undertaken using mean measurements of each species, and pooled sample means of species that displayed significant geographic variation.

Cladistic analyses were performed using eight binary and multistate characters (Appendix 3.2), engaging the MULPARS (multiple equally parsimonious trees), SWAP=GLOBAL (global branch swapping to find shorter trees) and BANDB (branch and bound method to select all most parsimonious trees) options of PAUP.

3.3 RESULTS

3.3.1 Description of hyoid morphology

The general morphology and topography of the chrysochlorid hyoid apparatus were described by Bronner *et al.* (1990), whose terminology is followed here. The hyoid apparatus is bicornuate, and comprises five ossified segments linking the larynx with the cranium and dentaries (Fig. 3.3). The basihyal is a short, transverse bar of paired origin ankylosed distally with long, cylindrical thyrohyals which run caudolaterally to join the thyroid cartilage via the chondrohyoid cartilages, and the anterior hyoid cornua. Each anterior cornu consists of (in proximal-distal and increasing size order): a small ceratohyal running rostromedially; a wedge-shaped epihyal, projecting laterally; and an enlarged, specialized stylohyal bone with a rostral articular surface (that meets synovially with the angular processes of the dentaries) and a tapering distal extremity (the styloid process) that projects rostrodorsally to join with the tympanic bulla via a slender tympanohyoid cartilage. The tympanohyoid cartilage attaches to the auditory bulla via a groove (*vagina processus hyoidei*) situated slightly anterior to the stylomastoid foramen - a condition Howes (1896) termed 'protrematic'.

3.3.2 Intra-populational variation

The hyoid apparatus of Durban *A. hottentotus* comprises: simple, unspecialized basihyals, thyrohyals and epihyals; rectangular or wedge-shaped ceratohyals with a length:breadth index ranging from 1,88 to 2,46 ($\bar{x}$ = 2,13 ± 0,164), and robust, bulbous stylohyal bones with acute styloid angles. Variation in the shape of the hyoid bones is slight.

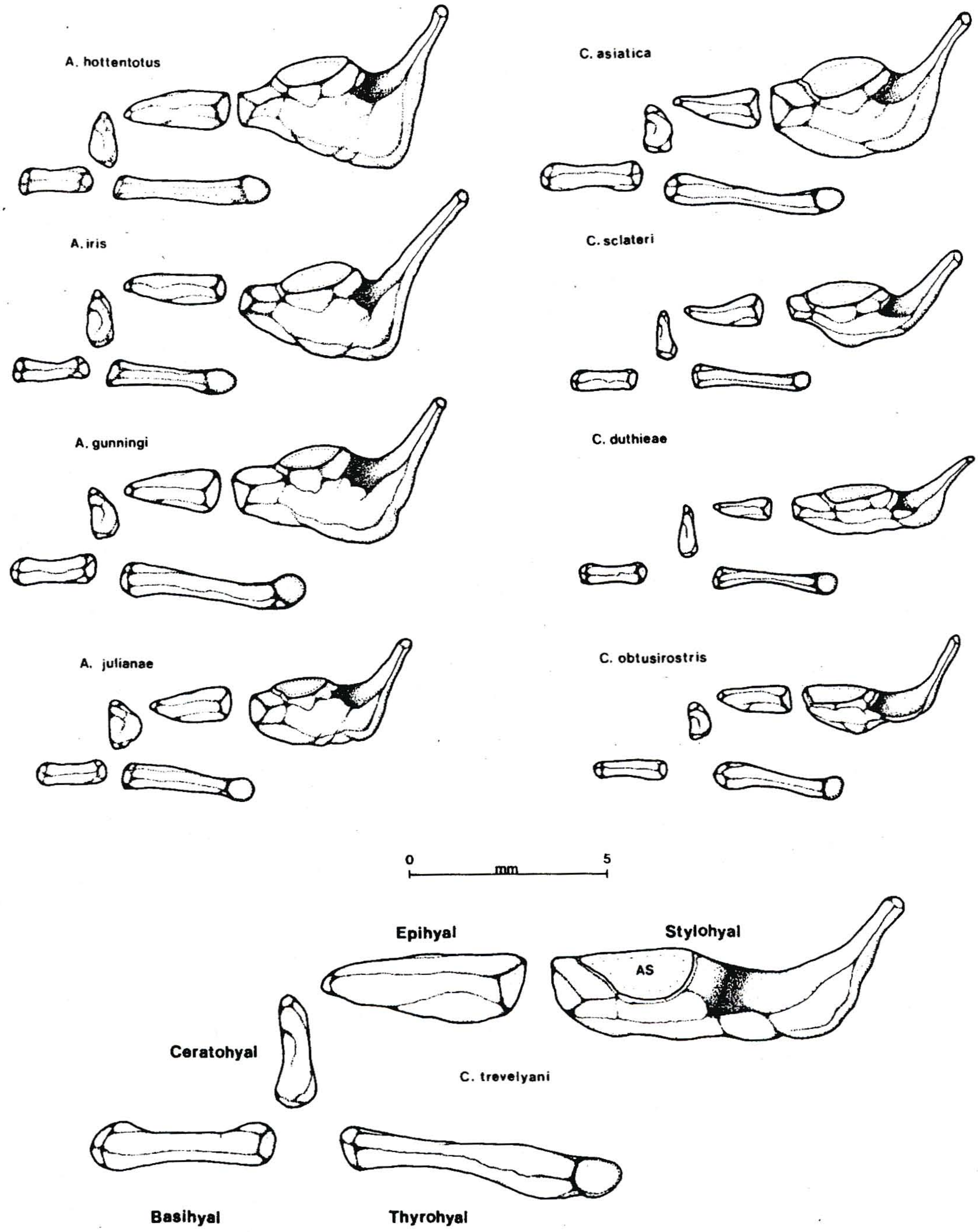


Fig. 3.3. The hyoid apparatus of nine golden mole species. AS = articular surface.

Hyoid mensural data for Durban male and female *A. hottentotus* belonging to TW2 and TW3 satisfied the criteria of randomness, normality and homoscedasticity. The sex-toothwear classes did not differ significantly in either individual measurements (Table 3.2), or combinations of measurements (MANOVA: $F = 0{,}760$; $p = 0{,}709$). A four-group discriminant functions analysis resulted in a 65 % overall *a posteriori* classification of specimens (males: TW2 60%, TW3 50%; females: TW2 75%, TW3 75%). In scattergrams of principal components I and II (which together accounted for 71 % of the sample variance), the sex-toothwear classes overlapped broadly (Fig. 3.4a). Sex and toothwear had no detectable effect on clustering based on average taxonomic differences (Fig. 3.4b); similarly, correlation phenograms (not illustrated here) failed to differentiate between the sexes and toothwear groups.

3.3.3 Geographic variation

Inter-population variation in the shape of the hyoid bones in *A. hottentotus* is slight. All specimens examined displayed rectangular or wedge-shaped ceratohyals with a length:breadth index ranging from 1,88 to 2,48 ($\bar{x} = 2{,}21 \pm 0{,}254$), and robust, bulbous stylohyals. Statistical evaluation of mensural data for six locality and pooled samples (Fig. 3.2) indicated, however, that significant size variation exists (MANOVA: $F = 3{,}05$; $p < 0{,}001$). All measurements except epihyal length showed a slight but regular pattern of geographic variation, resulting in significant differences between populations, and discrete or minimally overlapping maximally non-significant subsets (Table 3.3). Comparison of arithmetic means revealed that the basihyal and ceratohyal bones are significantly smaller in *A. hottentotus* from the St Lucia district, and that the thyrohyal is significantly larger in the Dullstroom population. Differences between the other populations (Western Cape, East London, Durban and Wakkerstroom) are not statistically significant.

The distinctness of St Lucia and Dullstroom *A. hottentotus* from the other populations studied is illustrated in Fig. 3.4c, where the first two axes from a principal components analysis are compared. The St Lucia and Dullstroom samples separated well from the other populations along the first component, which reflected mainly inter-population variation in overall hyoid size, as indicated by the high, positive

Table 3.2

Results of two--way analyses of variance to test for sexual dimorphism and age variation (toothwear classes 2 & 3) in *Amblysomus hottentotus* from Durban, KwaZulu-Natal. $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size. Asterisks denote significant *F*-values at $p \leq 0,05$.

Sex	**TW**		**Measurements**				
			BHL	**THL**	**CHL**	**EHL**	**SHL**
MALES	2	$\bar{x}$	2,13	3,68	1,43	2,50	4,20
		sd	0,087	0,366	0,183	0,372	0,307
		n	6	5	6	6	6
		Range	2,0-2,3	3,3-4,0	1,1-1,6	2,2-3,0	3,7-4,5
	3	$\bar{x}$	2,16	3,88	1,49	2,47	4,27
		sd	0,061	0,244	0,123	0,234	0,190
		n	6	6	6	7	7
		Range	2,1-2,2	3,5-4,2	1,3-1,6	2,0-2,7	4,1-4,5
FEMALES	2	$\bar{x}$	2,22	3,76	1,53	2,45	4,07
		sd	0,122	0,325	0,141	0,091	0,182
		n	4	4	5	5	4
		Range	2,1-2,4	3,5-4,2	1,3-1,7	2,4-2,6	3,9-4,2
	3	$\bar{x}$	2,07	3,22	1,33	2,28	4,08
		sd	0,192	0,440	0,136	0,195	0,083
		n	4	4	5	5	5
		Range	1,9-2,3	2,7-3,7	1,2-1,6	2,0-2,5	4,0-4,1
F-VALUES:							
SEX			0,003	3,562	0,211	1,283	3,000
TOOTHWEAR			0,572	0,399	0,820	0,660	0,246
INTERACTION			2,950	5,449*	4,734*	0,494	0,119

Fig. 3.4. Phenetic relationships within and among populations of *A. hottentotus*, as indicated by: a) pairwise comparison of the first two principal components, computed from single-standardized data for male and female *A. hottentotus* (TW2-3) from Durban (cophenetic correlation = 0,925); b) a distance phenogram based on standardized data for Durban specimens (cophenetic correlation = 0,722); c) pairwise comparison of the first two principal components with a superimposed minimum spanning tree, computed from single-standardized data for six populations (cophenetic correlation = 0,998); and d) a distance phenogram based on cluster analysis (UPGMA) of standardized data for six populations (cophenetic correlation = 0,740).

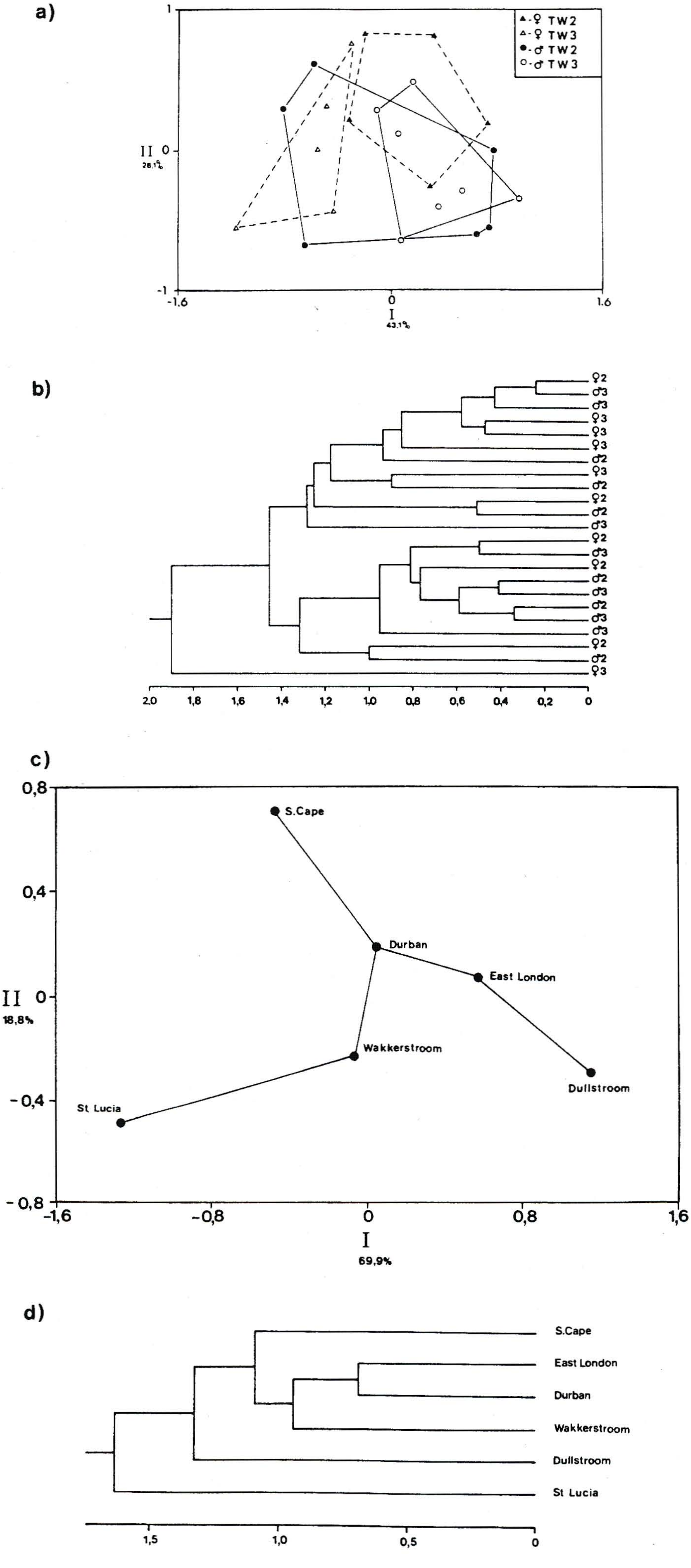

a)
▲-♀ TW2
△-♀ TW3
●-♂ TW2
○-♂ TW3
1
II 0
28,1%
-1
-1,6
0
1,6
I
43,1%
b)
♀2
♂3
♂3
♀3
♀3
♀3
♂2
♀3
♂2
♀2
♂2
♂3
♀2
♂3
♀2
♂2
♂3
♂2
♂3
♂3
♀2
♂2
♀3
2,0
1,8
1,6
1,4
1,2
1,0
0,8
0,6
0,4
0,2
0
c)
S.Cape
Durban
East London
Wakkerstroom
Dullstroom
St Lucia
0,8
0,4
II 0
18,8%
-0,4
-0,8
-1,6
-0,8
0
0,8
1,6
I
69,9%
d)
S.Cape
East London
Durban
Wakkerstroom
Dullstroom
St Lucia
1,5
1,0
0,5
0

Table 3.3

Summary statistics and results of single-classification analyses of variance to test for significant geographic variation between selected populations of *A. hottentotus*. Vertical lines denote maximally non-significant subsets. $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size; THL = total mean hyoid length; * = $p < 0{,}01$; ** = $p < 0{,}001$

Population		**Greatest length (mm)**					
		Basihyal	Cerato-hyal	Thyrohyal	Epihyal	Stylohyal	THL
A. h. hottentotus	$\bar{x}$ *(n)*	1,91(8)	1,24(9)	3,69(7)	2,32(9)	3,83(9)	12,99
(St. Lucia)	*sd*	0,212	0,123	0,175	0,292	0,326	
	Range	1,5-2,2	1,0-1,4	3,4-3,9	1,8-2,7	3,4-4,2	
A. h. devilliersi	$\bar{x}$ *(n)*	2,07(5)	1,58(5)	3,60(5)	2,37(7)	3,87(7)	13,49
(Southern Cape)	*sd*	0,123	0,123	0,240	0,277	0,254	
	Range	1,9-2,2	1,5-1,8	3,2-3,9	1,9-2,7	3,4-4,1	
A. h. hottentotus	$\bar{x}$ *(n)*	2,17(7)	1,40(7)	4,03(6)	2,44(7)	3,85(7)	13,89
(Wakkerstroom)	*sd*	0,107	0,168	0,064	0,204	0,388	
	Range	2,0-2,4	1,2-1,6	3,9-4,1	2,1-2,7	3,1-4,2	
A. h. hottentotus	$\bar{x}$ *(n)*	2,15(5)	1,50(5)	3,91(5)	2,59(6)	4,20(5)	14,35
(East London)	*sd*	0,119	0,261	0,524	0,522	0,510	
	Range	2,0-2,3	1,3-1,9	3,5-4,8	2,2-3,6	3,7-5,0	
A. h. hottentotus	$\bar{x}$ *(n)*	2,16(22)	1,45(25)	3,69(21)	2,46(26)	4,15(26)	13,91
(Durban)	*sd*	0,129	0,148	0,386	0,248	0,223	
	Range	1,9-2,4	1,1-1,7	2,7-4,2	2,0-3,0	3,6-4,5	
A. h. hottentotus	$\bar{x}$ *(n)*	2,24(10)	1,49(11)	4,27(10)	2,59(12)	4,38(13)	14,89
(Dullstroom)	*sd*	0,078	0,134	0,294	0,264	0,209	
	Range	2,2-2,4	1,2-1,6	4,0-4,9	2,2-2,9	4,0-4,7	
F VALUES:		$6{,}318^{**}$	$4{,}270^{*}$	$5{,}524^{**}$	1,349	$6{,}295^{**}$	

loadings for most characters (Table 3.4a). The St Lucia sample plotted below the others along the second component with ceratohyal and epihyal length loading most heavily. The Western Cape sample plotted above the others along the second component. This can be ascribed to the relatively (but not significantly; see Table 3.3) larger ceratohyal bones in this population, as indicated by the high positive loading for this variable along axis two (Table 3.4b).

A distance phenogram also differentiated the St Lucia and Dullstroom samples from the other populations, at a relatively high average taxonomic distance of 1,34 (Fig. 3.5d).

Multiple discriminant function analysis resulted in an overall *a posteriori* classification of only 67 % (Table 3.5). The St Lucia and Dullstroom samples showed high (>90%) percentages of correct specimen classification, which confirms the distinctness of these populations. The percentages of specimens correctly classified into the other samples were low, indicating poor differentiation between these populations.

Based on these results, the Dullstroom and St Lucia samples were analysed separately from the other populations, data for which were pooled during inter-specific analyses of hyoid measurements.

3.3.4 Inter-specific variation

The morphology and relative sizes of the various hyoid bones show considerable inter-specific variation, as follows (Fig 3.3):

1) The basihyal is simple and generalized in structure across the species, and comprises a rod- or dumbbell-shaped bar of bone slightly flattened in a dorso-ventral plane. In overall size, it is the second smallest hyoid bone in all species (Table 3.6). In *Amblysomus* (excluding *A. julianae*) and *Chlorotalpa*, the basihyal is relatively short, with a length of 14 - 15 % of the total hyoid length (THL). In the other taxa examined, the basihyal is relatively longer, and exceeds 17 % of the THL.

2) The thyrohyals of all species are spatulate or cylindrical bones second in size only to the stylohyals. Relative length is lowest in *C. sclateri* (*c.* 25 % of THL), and largest in *A. gunningi* (*c.* 30% of THL).

3) Ceratohyals: these are the smallest hyoid bones in all species, and display considerable variation in both shape and relative size. In *Chlorotalpa*, the ceratohyals

Table 3.4

Factor matrix from principal components analyses of hyoid measurements for: a) various *A. hottentotus* population samples; and b) various species and pooled population samples of *A. hottentotus*.

Measurements	Factor I	Factor II
a) *A. hottentotus* population samples.		
Basihyal length	0,926	0,116
Ceratohyal length	0,580	0,734
Thyrohyal length	0,772	-0,530
Epihyal length	0,958	-0,856
Stylohyal length	0,886	-0,087
b) Species and pooled *A. hottentotus* samples.		
Basihyal length	0,973	-0,112
Ceratohyal length	0,973	0,230
Thyrohyal length	0,981	-0,142
Epihyal length	0,993	-0,004
Stylohyal length	0,994	0,028

Table 3.5

A posteriori classification summary based on discriminant functions analysis of *A. hottentotus* samples, showing the percentage assignments of specimens to the various populations.

	% Specimens predicted into each population					
Populations(*n*)	1	2	3	4	5	6
1. S. CAPE (5)	60	0	40	0	0	0
2. EAST LONDON (4)	0	25	25	25	0	25
3. DURBAN (18)	17	17	44	6	17	0
4. ST. LUCIA (6)	0	0	0	100	0	0
5. WAKKERSTROOM (9)	0	0	11	0	78	11
6. DULLSTROOM (6)	0	0	0	0	7	93

Table 3.6

Summary statistics for five hyoid measurements in various single and pooled samples of nine species of golden moles. $\bar{x}$ = arithmetic mean based on all available specimens; n = sample size; *sd* = standard deviation; THL = total mean hyoid length.

Taxon		**Greatest length (mm)**					
		Basihyal	Cerato-hyal	Thyrohyal	Epihyal	Stylohyal	THL
A. hottentotus (St Lucia)	$\bar{x}$ *(n)*	1,91(8)	1,24(9)	3,69(7)	2,32(9)	3,83(9)	12,99
	sd	0,212	0,123	0,175	0,292	0,326	
	Range	1,5-2,2	1,0-1,4	3,4-3,9	1,8-2,7	3,4-4,2	
	%THL	14,7	9,5	28,4	17,9	29,5	
A. hottentotus hottentotus	$\bar{x}$ *(n)*	2,13(49)	1,43(48)	3,78(46)	2,42(56)	4,08(53)	13,84
	sd	0,170	0,138	0,271	0,239	0,251	
	Range	1,5-2,4	1,2-1,7	3,1-4,4	1,8-3,0	3,4-4,5	
	%THL	15,4	10,3	27,3	17,5	29,5	
A. hottentotus (Dullstroom)	$\bar{x}$ *(n)*	2,24(10)	1,49(10)	4,25(9)	2,53(10)	4,38(10)	14,89
	sd	0,078	0,141	0,300	0,250	0,240	
	Range	2,2-2,4	1,2-1,6	4,0-4,9	2,2-2,9	4,0-4,7	
	%THL	15,0	10,0	28,5	17,0	29,7	
A. iris	$\bar{x}$ *(n)*	1,82(16)	1,41(18)	3,52(13)	2,24(18)	3,82(18)	12,81
	sd	0,186	0,154	0,226	0,149	0,216	
	Range	1,6-2,2	1,0-1,7	3,0-3,8	2,0-2,6	3,5-4,2	
	%THL	14,2	11,0	27,5	17,5	29,8	
A. julianae	$\bar{x}$ *(n)*	2,10(7)	1,22(8)	3,34(8)	2,18(8)	3,38(8)	12,22
	sd	0,083	0,084	0,089	0,103	0,116	
	Range	2,0-2,2	1,1-1,3	3,2-3,5	2,0-2,4	3,2-3,5	
	%THL	17,2	9,9	27,3	17,8	27,7	
A. gunningi	$\bar{x}$ *(n)*	2,02(5)	1,19(5)	4,18(5)	2,43(5)	4,07(5)	13,89
	sd	0,146	0,090	0,113	0,163	0,090	
	Range	1,8-2,2	1,1-1,3	4,1-4,4	2,3-2,6	4,0-4,2	
	%THL	14,5	8,6	30,1	17,5	29,3	
C. sclateri	$\bar{x}$ *(n)*	1,63(6)	1,30(7)	2,82(6)	1,96(7)	3,44(7)	11,15
	sd	0,080	0,204	0,443	0,454	0,368	
	Range	1,6-1,8	1,1-1,4	2,4-3,7	1,6-2,8	3,0-4,2	
	%THL	14,6	11,7	25,3	17,6	30,9	
C. duthieae	$\bar{x}$ *(n)*	1,62(3)	1,23(2)	3,16(3)	1,78(2)	3,63(2)	11,42
	sd	0,130	0,049	0,090	0,099	0,106	
	Range	1,5-1,7	1,2-1,3	3,1-3,3	1,7-1,9	3,5-3,7	
	%THL	14,2	10,6	27,7	16,6	31,8	
C. obtusirostris	$\bar{x}$ *(n)*	1,97(10)	1,05(13)	3,10(13)	1,88(13)	3,27(13)	11,27
	sd	0,116	0,075	0,172	0,113	0,076	
	Range	1,9-2,3	1,0-1,1	2,8-3,3	1,8-2,0	3,2-3,4	
	%THL	17,5	9,3	27,5	16,7	29,0	
C. asiatica	$\bar{x}$ *(n)*	2,20(5)	1,14(5)	3,41(5)	1,90(5)	3,64(5)	12,29
	sd	0,138	0,114	0,315	0,179	0,211	
	Range	2,1-2,4	1,0-1,2	3,1-3,8	1,7-2,2	3,5-4,0	
	%THL	17,9	9,3	27,7	15,5	29,6	
C. trevelyani	$\bar{x}$ *(n)*	4,52(3)	2,59(3)	6,61(4)	4,56(4)	7,17(4)	25,45
	sd	0,127	0,127	0,336	0,438	0,270	
	Range	4,4-4,6	2,5-2,7	6,2-6,7	4,1-5,0	7,0-7,1	
	%THL	17,8	10,2	26,0	17,9	28,2	

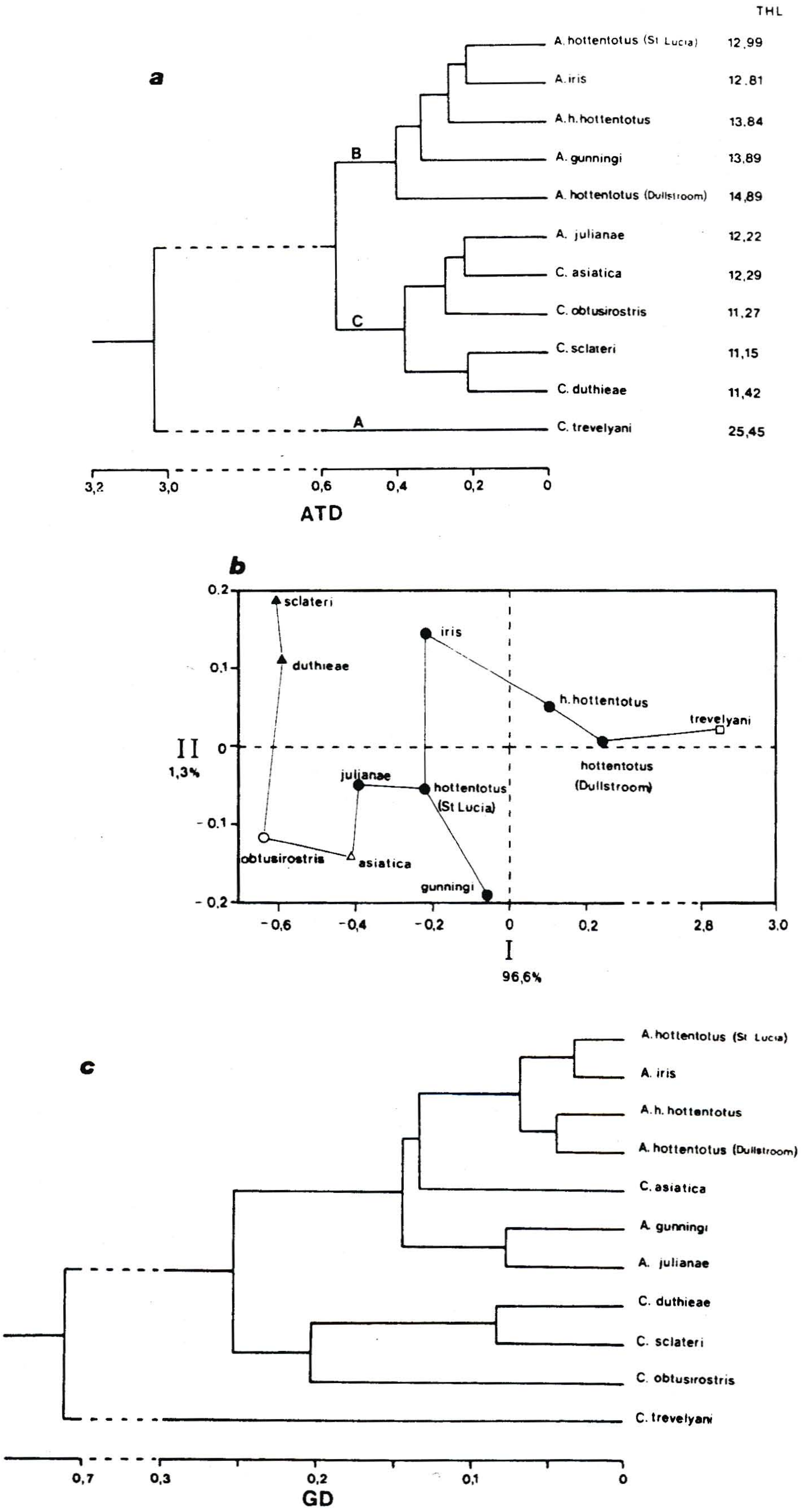
are relatively the largest (*c.* 11% of THL), and have a fusiform or wedge-shape with a length:breadth index exceeding 2,5. *A. gunningi* and *A. julianae* display the opposite extreme, with relatively shorter ceratohyals (8,6 - 9,9 % of THL) that are broadened basally, resulting in a squat, triangular shape with a length:breadth index below 1,75. The ceratohyals of the other species vary slightly in relative size (9,3 - 10,3 % of THL), but are rectangular or wedge-shaped with a distinctive length:breadth index ranging from 1,75 - 2,50.

4) The epihyals are short, triangular or wedge-shaped bones in all species. In *C. asiatica*, the epihyals are relatively shorter (15,5 % of THL) than in the other taxa (> 16,5 % of THL).

5) Stylohyals: of all the hyoid bones, the stylohyals display the most inter-specific variation in size and shape. In *Amblysomus*, the stylohyals are robust and bulbous owing to dorso-ventral expansion, with a well-developed styloid process, a large, elevated articular surface, a sharp styloid angle, and a deep styloid basin. The stylohyals of *C. asiatica* are also bulbous, although not to the same extent, but the styloid angle is less sharp. In *Chlorotalpa*, the stylohyals are relatively the longest (> 30 % of THL), but the styloid angle is gentle and curved. The articular surfaces are neither as robust as in *Amblysomus*, nor are the styloid basins as deep. *Chlorotalpa sclateri* differs from *C. duthieae* in that the stylohyal is still bulbous in the medial region in the former, whereas in the latter no evidence of dorso-ventral expansion is present. The stylohyal of *C. trevelyani* resembles that of *C. duthieae* in shape, but is relatively shorter, and distinctive in that the articular surface is not elevated and slopes ventrally. The stylohyal of *C. obtusirostris* has perhaps the most unusual shape of all - the articular surface is situated more proximally than in other species, the styloid process is gracile with an antero-medial flange, and the styloid basin is almost completely replaced by a smooth, curved surface.

Differences in the hyoid measurements of the various species (Table 3.6) were highly significant (MANOVA: $F = 8{,}08$; $p < 0{,}001$). Cluster analysis based on means of mensural data separated the samples into three major clusters on the basis of overall hyoid size (Fig. 3.5a): Cluster A, containing only *C. trevelyani*, with THL exceeding 25 mm; Cluster B, containing *Amblysomus* (excluding *A. julianae*), with THL exceeding 12,8 mm; and Cluster C, containing *A. julianae*, *Chlorotalpa* and

Fig. 3.5. Phenetic relationships among various species and population samples of golden moles. a) Distance phenogram based on cluster analysis (UPGMA) of five hyoid measurements (cophenetic correlation = 0,987); b) pairwise comparison of the first two principal components (cophenetic correlation = 0,998), with a minimum spanning tree superimposed; and c) a Gower's-distance (GD) phenogram based on cluster analysis (UPGMA) of five mensural and two qualitative shape characters (cophenetic correlation = 0,850).


THL
a
A. hottentotus (St Lucia) 12,99
A. iris 12.81
A. h. hottentotus 13.84
A. gunningi 13,89
A. hottentotus (Dullstroom) 14,89
A. julianae 12,22
C. asiatica 12,29
C. obtusirostris 11,27
C. sclateri 11,15
C. duthieae 11,42
C. trevelyani 25,45
B
C
A
3,2
3,0
0,6
0,4
0,2
0
ATD
b
0.2
0.1
0
- 0.1
- 0.2
II
1,3%
sclateri
duthieae
iris
h. hottentotus
trevelyani
hottentotus (Dullstroom)
julianae
hottentotus (St Lucia)
obtusirostris
asiatica
gunningi
- 0,6
- 0,4
- 0,2
0
0,2
2,8
3,0
I
96,6%
c
A. hottentotus (St Lucia)
A. iris
A. h. hottentotus
A. hottentotus (Dullstroom)
C. asiatica
A. gunningi
A. julianae
C. duthieae
C. sclateri
C. obtusirostris
C. trevelyani
0,7
0,3
0,2
0,1
0
GD

Calcochloris, with THL below 12,3 mm. Similarly, separation of the samples along the first principal component reflected mainly inter-specific differences in overall size (Fig. 3.5b), with *Chlorotalpa*, *Chrysochloris* and *A. julianae* plotting to the left, *C. trevelyani* to the extreme right, and *Amblysomus* between. *Chlorotalpa* and *A. iris corriae* (= *A. corriae*, see below) plotted above the other samples along the second component, with basihyal and ceratohyal length loading most heavily.

Cluster analysis based on both mensural data and two qualitative variables (ceratohyal and stylohyal shape, see above) separated the samples mainly on the basis of overall size (Fig. 3.5c; *C. trevelyani* vs. other genera; *Calcochloris* and *Chlorotalpa* vs. *Amblysomus* and *C. asiatica*), with sub-clustering influenced largely by ceratohyal morphology (*Calcochloris* vs. *Chlorotalpa*; *A.julianae* and *A. gunningi* vs. *A. hottentotus*, *A. iris* and *C. asiatica*) and stylohyal size and shape (*C. asiatica* vs. *A. hottentotus* and *A. iris*). Greatest overall similarity in hyoid morphology was indicated for the *A. iris* and *A. hottentotus* samples, which clustered together at a distance of only 0,069.

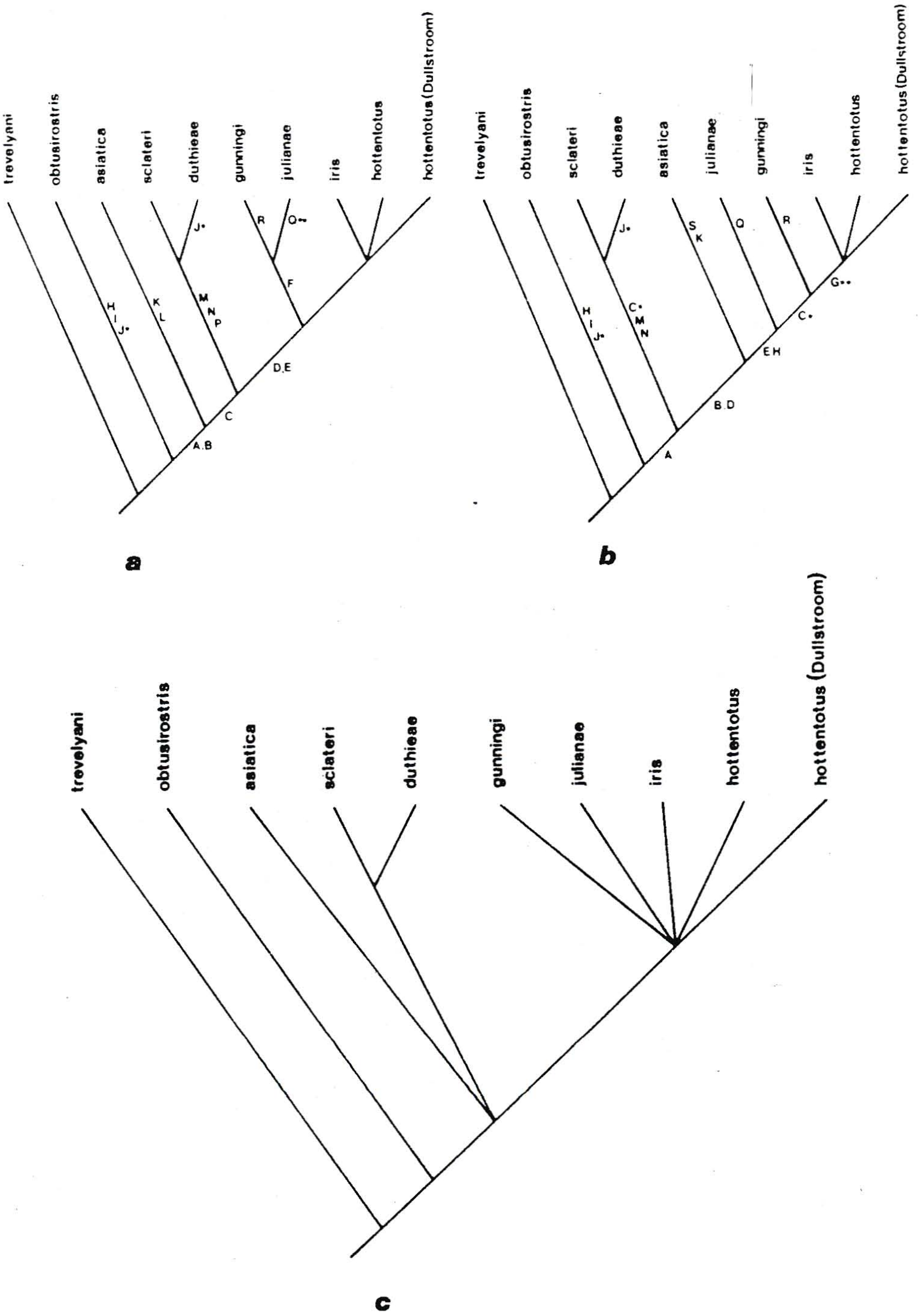
Cladistic analysis (using *C. trevelyani* as the outgroup) yielded 45 equally parsimonious trees, each of 19 steps with consistency indices of 0,789. These trees differed mainly in: 1) the placement of *Chrysochloris* relative to either *Calcochloris* (Fig. 3.6a) or *Amblysomus* (Fig. 3.6b); and 2) in the branching pattern for *Amblysomus* species. The branches leading to *A. hottentotus* samples and *A. iris* were not resolved by any synapomorphies. Most trees displayed two parallelisms (epihyal and basihyal size; J and C in Fig. 3.6), and a single reversal (either stylohyal size or ceratohyal shape; Q and G in Fig. 3.6).

A strict consensus tree derived from these 45 most parsimonious trees was not fully resolved (Fig. 3.6c), and showed one trifurcation (divergence of *Chrysochloris*, *Chlorotalpa* and *Amblysosmus* species), and a multifurcation (divergence of *Amblysomus* species). The consensus information index (*sensu* Mickevich, 1978) for this consensus tree is only 0,400, indicating substantial homoplasy in the cladogram.

3.4 DISCUSSION

The chrysochlorid hyoid apparatus is perhaps the most specialized of those described for insectivores. The anterior cornua are integrocornuate (i.e. fully ossified),

Fig. 3.6. Possible phylogenetic relationships among chrysochlorid taxa, based on two equally parsimonious trees (a and b, arbitrarily selected from 45 maximally parsimonious options), and a strict consensus tree derived from all 45 trees. Annotation represents the following character state changes at the indicated internodes (numerals identify characters = data matrix columns in Appendix 3.2), while superscripts denote hypothesized character state changes). **A** $8^{0\text{-}1}$; **B** $9^{0\text{-}1}$; **C** $1^{0\text{-}1}$; **D** $11^{0\text{-}2}$; **E** $10^{0\text{-}1}$; **F** $5^{0\text{-}1}$; **G** $5^{1\text{-}0}$; **H** $2^{0\text{-}1}$; **I** $7^{0\text{-}1}$; **J** $14^{0\text{-}1}$; **K** $14^{0\text{-}2}$; **L** $11^{0\text{-}1}$; **M** $4^{0\text{-}1}$; **N** $12^{1\text{-}2}$; **P** $9^{1\text{-}0}$; **Q** $12^{1\text{-}0}$; **R** $13^{0\text{-}1}$; **S** $11^{2\text{-}1}$. Asterisks denote parallelisms; double asterisks indicate reversals.


trevelyani
obtusirostris
asiatica
sclateri
duthieae
gunningi
julianae
iris
hottentotus
hottentotus (Dullstroom)
H I J•
K L
M N P
J•
R
Q••
F
D,E
C
A,B
a
trevelyani
obtusirostris
sclateri
duthieae
asiatica
julianae
gunningi
iris
hottentotus
hottentotus (Dullstroom)
J•
H I J•
C• M N
S K
Q
R
G••
C•
E H
B D
A
b
trevelyani
obtusirostris
asiatica
sclateri
duthieae
gunningi
julianae
iris
hottentotus
hottentotus (Dullstroom)
c

a condition found in several insectivores, but not in the tenrecs (Tenrecidae), which several authors regard as the closest extant relatives of the Chrysochloridae (Butler 1956; Van Valen 1967; Eisenberg 1981). The basihyals, thyrohyals, ceratohyals and epihyals are simple and unspecialized, as in certain Erinaceidae, Talpidae, Soricidae and Solenodontidae (see Sprague 1944). The stylohyals are enlarged and highly specialized, however, with a structure not paralleled in the Insectivora. Specialized stylohyal bones are also found in *Solenodon* (Allen 1910), but stylohyal morphology in this taxon is markedly different from that of chrysochlorids, and no hyoid-dentary articulation is present.

Sexual dimorphism and age-related differences in hyoid morphology of *A. hottentotus* from Durban were negligible. Although the hyoid apparatus of male *A. hottentotus* is generally slightly larger than that of females, the sexes did not differ significantly in individual measurements, or in combinations of measurements. Similarly, specimens belonging to TW2 generally had slightly larger hyoid apparatus than those in TW3, but univariate and multivariate differences between the toothwear groups were not significant. This suggests that intra-population variation in the shape and measurements of the hyoid bones of *A. hottentotus* is not sufficiently marked to bias interpretation of patterns of geographic and inter-specific variation. Measurements of the various sex-age groups were therefore pooled in further analyses. Although a practical necessity in the present study owing to small sample sizes, this is a dubious practice as the underlying assumptions - that intra-population sexual and age-related variation in hyoid morphology are practically invariant geographically and inter-specifically - probably cannot be met. Violation of these assumptions would have little effect on the main conclusions below, however, as observed inter-specific differences in hyoid measurements far exceed intra-population differences.

Inter-population variation in the shape of the hyoid bones in *A. hottentotus* is not sufficiently marked to affect the interpretation of inter-specific differences, but size variation is conspicuous, with two distinctive populations (St Lucia and Dullstroom) from the northern part of this species range showing extremes of size. The Dullstroom specimens are characterized by significantly larger hyoids, to the extent that this population separated widely from *A. h. hottentotus*, even in inter-specific analyses.

This morphometric divergence is mirrored by karyotypic differences (Section 4.3.1), and suggests that the Dullstroom OTU represents a cryptic species distinct from *A. hottentotus*.

The St. Lucia specimens, which are significantly smaller than others, may represent not *A. hottentotus* but *A. iris*. Both species occur at this locality, and the only diagnostic criterion for separating them, namely fur colour, shows all stages of intergradation from rufous or chocolate-brown (typical of *A. hottentotus*) to black (typical of *A. iris*), making identification problematic. The apparently smaller size of the hyoid apparatus in St. Lucia specimens may, therefore, be an artefact resulting from contamination of the *A. hottentotus* sample with *A. iris*.

The hyoid apparatus of the nine chrysochlorid species studied differ considerably in both size and shape. Inter-specific differences in absolute size of the hyoid bones mirror variation in general body proportions, as indicated by strong positive correlations between THL and both body mass (r = 0,982; t = 15,46; $p <$ 0,001); and total length (r = 0,991; t = 22,83; $p <$ 0,001). Three discrete size categories (corresponding to the major clusters in Fig. 3.4c) are evident: small - *Chlorotalpa*, *Calcochloris* and *A. julianae*; intermediate - other *Amblysomus* and *C. asiatica*; and large - *C. trevelyani*. Size variation within each of these categories is slight, but variation between the categories is highly significant. The relative sizes of the various hyoid bones are less variable across species than absolute sizes, but conspicuous inter-specific differences exist. The basihyal, thyrohyal and epihyal bones of the species studied, while differing in absolute and relative size, do not differ conspicuously in shape. The stylohyal bones, however, display striking inter-specific shape differences. Three main morphological categories can be recognized: slender, relatively unspecialized stylohyals with obtuse styloid angles and gracile (*Calcochloris*) or semi-bulbous styloid processes (*C. trevelyani*; *Chlorotalpa*); well-developed, slightly bulbous stylohyals with gradual styloid angles (*C. asiatica*); and robust, highly-specialized stylohyals with acute styloid angles and prominent, elevated articular surfaces (*Amblysomus*). As the stylohyal bones of most Insectivora are small and unspecialized, the enlarged but morphologically simple stylohyals present in *Chlorotalpa*, *Calcochloris* and *Chrysospalax* can be considered symplesiomorphic. As a corollary, the robust, specialized stylohyals of *Amblysomus* can be regarded as apomorphic (see Appendix 3.2 for further discussion of hypothesized evolutionary transformation series).

The size of the hyoid apparatus in chrysochlorids is strongly correlated with stylohyal length (r = 0,994; t = 28,16; p < 0,001). A relationship between these variables and increasing morphological specialization of the stylohyal is evident if *C. trevelyani* is excluded from consideration. This correlation does not, however, necessarily reflect co-evolution of hyoid bone size and shape, as cladistic analyses indicate that some size characters are homoplastic. The existence of large but relatively unspecialized stylohyals in *C. trevelyani* can thus be explained in terms of independent evolution of hyoid bone size and shape in chrysochlorids.

Phenetic and cladistic relationships indicated by hyoid data are largely congruent, and support Meester's (1974) classification of the Chrysochloridae. In particular, hyoid characters confirm the distinctness of *Chlorotalpa* and *Calcochloris* (genera that differ markedly in size, colour, dental, cranial characters, and even distribution) from *Amblysomus*, and repudiate Petter's (1981) and Simonetta's (1968) claims that *Calcochloris* and/or *Chlorotalpa* should be included in *Amblysomus*. Hyoid traits also confirm the specific distinctness of *C. sclateri* and *C. duthieae* - taxa that Ellerman *et al.* (1953) and Simonetta (1968) regarded as conspecific. Furthermore, hyoid data indicate that *A. gunningi* and *A. julianae* are phenetically and cladistically distinct from other *Amblysomus*, thus supporting their allocation to the subgenus *Neamblysomus*.

On the other hand, however, hyoid traits do not differentiate *Chrysochloris* from *Amblysomus* - genera that differ markedly in cranial and malleus morphology (Forster-Cooper 1928; Lundholm 1955; Skinner and Smithers 1990). Similarly, few differences in hyoid morphology are evident among the various populations of *A. hottentotus* examined, or between *A. hottentotus* and *A. corriae*. Hyoid characters also do not provide sufficient synapomorphies to fully resolve phylogenetic relationships among chrysochlorids. This may be at least partly because too few suitable characters are available. While coding methods for mensural data have been published (Baum 1988), initial cladistic analyses using hyoid measurements resulted in less parsimonious trees (of at least 78 steps, with low consistency indices) which largely conflicted with topologies indicated by discrete characters.

Characters of the hyoid bones are useful for resolving generic relationships among chrysochlorids, but have less value at lower taxonomic levels. While inter-specific differences in hyoid morphology are conspicuous and constant in *Chlorotalpa*, observed shape variation in *Amblysomus* is negligible, and size variation too graded, to unequivocally resolve specific and intra-specific relationships.

APPENDIX 3.1

SPECIMENS USED FOR ANALYSIS OF HYOID MORPHOLOGY

Chrysochlorid specimens captured for this study were deposited in the Transvaal Museum (TM) mammal collection. Population samples pooled for the analysis of intra-specific variation in *A. hottentotus* are shown in Fig. 3.2. Pooled locality names referred to in the text are italicized and capitalized in the list below.

Chrysochloris asiatica (Linnaeus, 1758). Western Cape Province: Algeria State Forest - 40628; Cape Town - 40747, 41434, 41536, 41537.

Chlorotalpa duthieae (Broom, 1907). Western Cape Province: Nature's Valley - 39456, 40514, 40532.

Chlorotalpa sclateri (Broom, 1907). Western Cape Province: Karoo National Park - 39439; Free State: Ficksburg - 41571, 41578, 41591, 41594, 41595 - 41597.

Chrysospalax trevelyani (Günther, 1875). Eastern Cape Province: Transkei, Nqadu Forest - 39438; Kalogha Forest - 39927, 40501, 40502.

Calcochloris obtusirostris (Peters, 1851). KwaZulu-Natal: Kosi Lake - 40452, 40458, 40459, 40462, 40463, 40469-40471; Lalanek - 40444, 40446 - 40448, 40450; Northern Province: Kruger National Park, Nyadu Sandveld - 39470.

Amblysomus gunningi (Broom, 1908). Northern Province: Tzaneen, De Hoek State Forest - 41766, 40772, 40778, 40779, 40780.

Amblysomus julianae Meester, 1972. Gauteng: Pretoria, Shere - 39932, 40126, 40173, 40220, 40221, 40271, 40731, 40732, 41422; Mpumalanga: Kruger National Park, Pretoriuskop Camp - 39769.

Amblysomus iris Thomas & Schwann, 1905. Western Cape Province: Humansdorp, Hoffmansbos - 39164 - 39171, 39173, 39174, 39176; Saasveld Forest Institute, George - 39451 - 39453; Nature's Valley - 40534, 40536; KwaZulu-Natal: Verulam, Hazelmere Dam - 39933, 39204; Mtubatuba, Dukuduku Forest - 40379, 40395, 40412, 40423, 40440.

Amblysomus hottentotus (A.Smith, 1829).

INDIVIDUAL SPECIMENS EXAMINED. Eastern Cape Province: Transkei, Port St. Johns - 12386, 12387, 12390; KwaZulu-Natal: Verulam, Hazelmere Dam - 39260; Ngome Forest - 39847; Pietermaritzburg - 40115; Mpumalanga: Graskop - 40781, 40789, 40790.

POOLED LOCALITIES. Western Cape Province: (*S.CAPE*) Stellenbosch, Jonkershoek Research Station - 40549, 40556, 40562, 40563; Heidelberg, Grootvadersbosch Forest - 41688, 41694; Eastern Cape Province: (*EAST LONDON*) Kidds Beach District - 41675 - 41677, 41689, 41698; King Williams Town - 39457; KwaZulu-Natal: (*DURBAN*) Botanic Gardens, Country Club and University Campus 39200 - 39203, 39205, 39206, 39240, 39246, 39248, 39296, 39297, 39422, 39423, 40000, 40020, 40023, 40097, 40098, 41128, 41129, 41130, 41140, 41142, 41143; (*ST LUCIA*) Mtubatuba, Dukuduku Forest - 40392, 40396, 40441, 40413, 40439, 40439; St Lucia Forest Station - 40425, 40427; Charters Creek - 40426; Mpumalanga: (*WAKKERSTROOM*) Tafelkop Farm - 39861, 39871, 39872, 39876, 41600, 41604, 41613; (*DULLSTROOM*) Verloren Vallei Provincial Nature Reserve - 38467, 38468, 39163, 39181, 41659 - 41663, 41666; Belfast - 39966, 40062, 40063, 40903.

APPENDIX 3.2

HYOID CHARACTERS USED AND CODING FOR CLADISTIC ANALYSIS.

Eight binary and multistate hyiod characters were used for cladistic analyses. Multistate characters that did not display a linear sequence of transformation were input using additive binary coding (Brooks, Caira, Platt and Pritchard 1984). Characters used were as follows:

1) **Basihyal relative length (BHRL)**. State 0: < 16 % of THL. State 1: > 16 % of THL. Polarity 0 → 1.

2) **Styloid process morphology (SP)**. State 0: gracile with antero-medial flange. State 1: bulbous without antero-medial flange. Polarity 0 → 1.

3) **Ceratohyal shape (CHSP)**. State 0 (coded as 100): rectangular or wedge-shaped with length:breadth index of 1,75--2,5. State 1 (coded as 110): fusiform with length:breadth index exceeding 2,5. State 2 (coded as 101): squat and triangular with a length:breadth index less than 1,75.

Polarity

$$\begin{tikzcd} 2 & \\ 0 \arrow[u] \arrow[r] & 1 \end{tikzcd}$$

4) **Stylohyal morphology (SHSP)**. State 0 (coded as 10000): slender with a poorly developed articular surface that slopes ventrally. State 1 (coded 11000): slender with a well--developed articular surface situated proximally. State 2 (coded 10100): slender or semi-bulbous with a well-developed medial articular surface. State 3 (coded 10110): well-developed and bulbous with an elevated, medial articular surface; State 4 (coded 10111): robust and bulbous with an elevated articular surface situated medially.

Polarity

$$\begin{tikzcd} 1 & & & \\ 0 \arrow[u] \arrow[r] & 2 \arrow[r] & 3 \arrow[r] & 4 \end{tikzcd}$$

5) **Styloid angle (SA)**. State 0: obtuse. State 1: gradual. State 2: sharp. Polarity 0 → 1 → 2.

6) **Stylohyal relative length (SHRL).** State 0: < 29 % of THL. State 1: 29 % - 30 % of THL. State 2: > 30 % of THL. Polarity 0 → 1 → 2.

7) **Thyrohyal relative length (THRL).** State 0: < 30 % of THL. State 1: > 30 % of THL. Polarity 0 → 1.

8) **Epihyal relative length (EHRL).** State 0: > 17 % of THL. State 1: 16 % - 17 % of THL. State 2: < 16 % of THL. Polarity 0 → 1 → 2.

The data matrix used in cladistic analyses is shown below. Trees were rooted using *C. trevelyani* as the outgroup, as the hyoid bones are relatively unspecialized (as in other insectivores), and gross morphological and ecological evidence suggests that *Chrysospalax* is an ancient, but highly specialized and independently evolving chrysochlorid taxon (Broom 1907a).

	Characters							
	BHRL	SP	CHSP	SHSP	SA	SHRL	THRL	EHRL
C. trevelyani	0	0	100	10000	0	0	0	0
A. hottentotus	1	0	100	10111	2	1	0	0
A. hottentotus (Dullstroom)	1	0	100	10111	2	1	0	0
A. iris	1	0	100	10111	2	1	0	0
A. gunningi	1	0	101	10111	2	1	1	0
A. julianae	0	0	101	10111	2	0	0	0
C. sclateri	1	0	110	10100	0	2	0	0
C. duthieae	1	0	110	10100	0	2	0	1
C. obtusirostris	0	1	100	11000	0	1	0	1
C. asiatica	0	1	100	10110	1	1	0	2

CHAPTER 4

CYTOGENETIC PROPERTIES OF NINE GOLDEN MOLE SPECIES[1]

4.1 INTRODUCTION

Currently available data on the karyology of fossorial mammals pertain mostly to subterrestrial rodents (Bathyergidae - Nevo *et al.* 1986; Geomyidae - Patton and Sherwood 1983 ; Spalacidae - Nevo *et al.* 1982; Savic and Nevo 1990) which display karyotypic diversity, the marsupial mole (Calaby *et al.* 1974), and a single family of Insectivora (Talpidae) which is karyotypically conservative (Filipucci *et al.* 1987; Meylan 1966; Nevo 1979). With the exception of a recent report dealing with two taxa (Capanna *et al.* 1989), chromosomal data for the Chrysochloridae - the only other family of fossorial Insectivora - are lacking, primarily due to the difficulty of procuring live study specimens. Such data are potentially valuable, not only for deciphering the problematic taxonomy of the family, but also because they may provide a more balanced perspective of the extent and mechanisms of chromosomal evolution in fossorial mammals.

Nicoll and Rathbun (1990), who included 13 chrysochlorid taxa in IUCN Threatened Species categories, emphasized the need for chromosomal studies to resolve taxonomic problems in the Chrysochloridae. This chapter details the results of karyotypic analyses of nine chrysochlorid species belonging to five genera (and representing 12 currently-recognized taxa) from southern Africa (Meester *et al.* 1986).

4.2. MATERIALS AND METHODS

Eighty-nine golden moles from 31 localities in South Africa were karyotyped (see Appendix 4.1). Somatic metaphase spreads were obtained from bone marrow preparations by a standard in-vitro method (Green *et al.* 1980), following yeast pretreatment (Lee & Elder 1980). G-banding was performed using a trypsin digestion method modified from Wang and Federoff (1972), whereas C-bands were induced using the method of Baker and Qumsiyeh (1988). Nucleolar organizer regions (NORs)

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[1] This chapter, together with abstract and relevant references, is essentially the paper by G. N. Bronner published in August 1995 under the full title "Cytogenetic properties of nine species of golden moles (Insectivora: Chrysochloridae)" in the *Journal of Mammalogy* **76**:957-971.

were detected by the $AgNO_3$ colloidal-developer method of Howell and Black (1980), with counter-staining in 4% Giemsa for one minute to facilitate identification of the NOR-bearing chromosomes.

Interspecific comparisons were made only once the chromosomes of conspecifics were matched and their morphology well known. A minimum of five spreads per individual were analysed. In the absence of satisfactory banding data for all specimens and species, karyograms were prepared by matching homologous chromosomes using relative lengths (expressed as a percentage of the total haploid complement plus X), and centromeric indices (determined from measurements taken to the nearest 0,1 mm on photomicrographs with Tesa Digit-Cal II callipers). Homology within and among taxa was assumed using pairwise comparisons of both the photomicrographed chromosomes, and composite idiograms (not illustrated) prepared from measurements of a minimum of five karyograms per taxon. Determination of homology, both within and between species, was thus somewhat equivocal, and identifications of the chromosomal elements for which banding data were not obtained must thus be regarded as tentative.

The karyotype of *Amblysomus hottentotus hottentotus* was chosen for a standardized numbering system because this taxon displays a diploid number (2n=30) found in most other taxa, and sample sizes (and thus confidence limits) were largest. Chromosomes were arranged and numbered according to relative length, with the two smallest acrocentrics last. In taxa displaying 2n>30, the additional chromosome pairs were arranged in order of decreasing relative size after the two smallest numbered autosomes. This numbering system, although unconventional in that only autosomes are usually enumerated, was used since it expedites interspecific comparisons and the identification of sex chromosomes when no male specimens of a species are available for study.

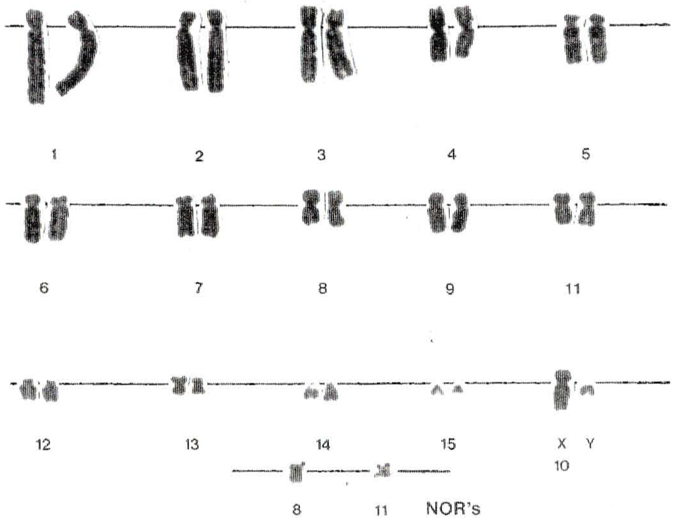
4.3 RESULTS AND DISCUSSION

4.3.1 Karyotypes and Nucleolar Organizer Regions.

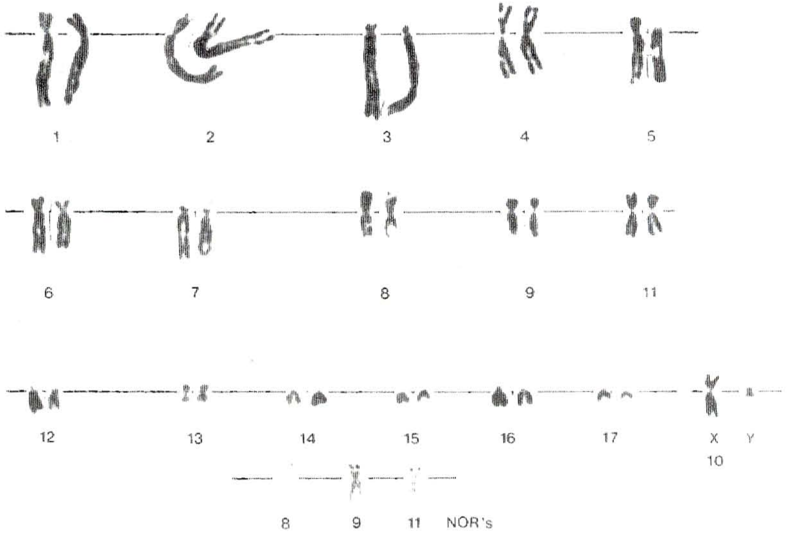
Karyotypes of the species studied are shown in Figures 4.1-4.3, and summarized in Tables 4.1 and 4.2. Six different karyotypes characterized by combinations of four diploid numbers (2n = 28; 30; 34; 36), four fundamental numbers (FN = 56; 60; 62; 68), and four locations of nucleolar organizer regions (NORs), are shown by the nine species examined. Differences in diploid number occur at both the specific level (within *Amblysomus hottentotus* with 2n = 30; 34; 36;

Fig. 4.1. Male karyotypes and nucleolar chromosomes of *A. h. hottentotus*, *A. h. devilliersi*, *A. hottentotus* 2n = 34 cytotype from Wakkerstroom and Ermelo and *A. hottentotus* 2n = 36 cytotype from Dullstroom.

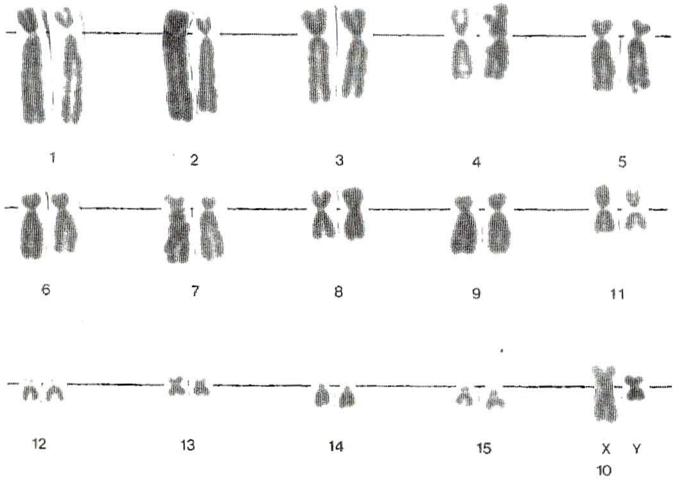
Amblysomus hottentotus (Durban)



Amblysomus hottentotus (Wakkerstroom & Ermelo)



Amblysomus hottentotus devilliersi (Swellendam)



Amblysomus hottentotus (Dullstroom)

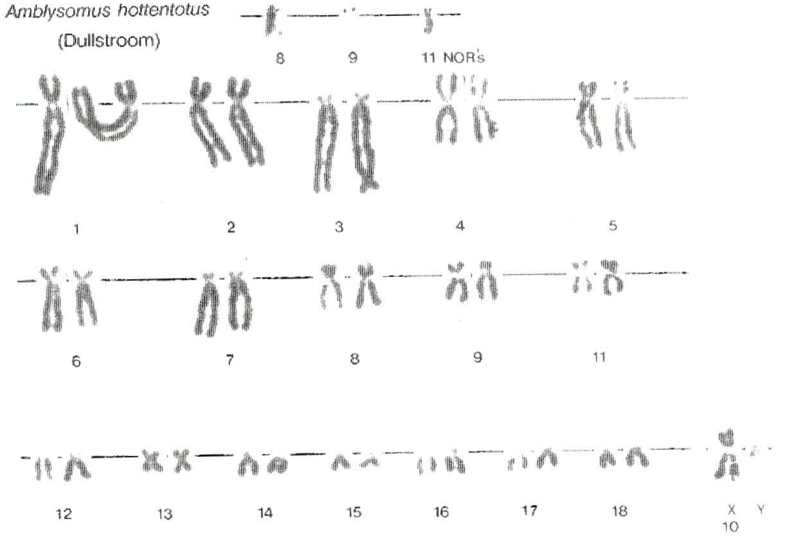
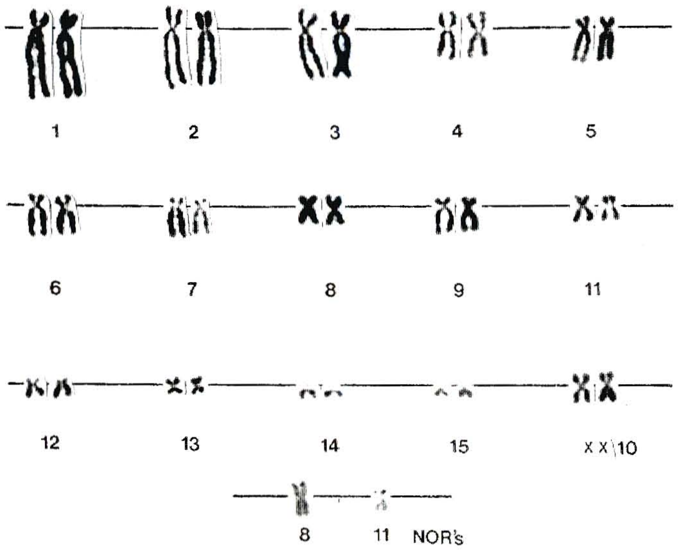
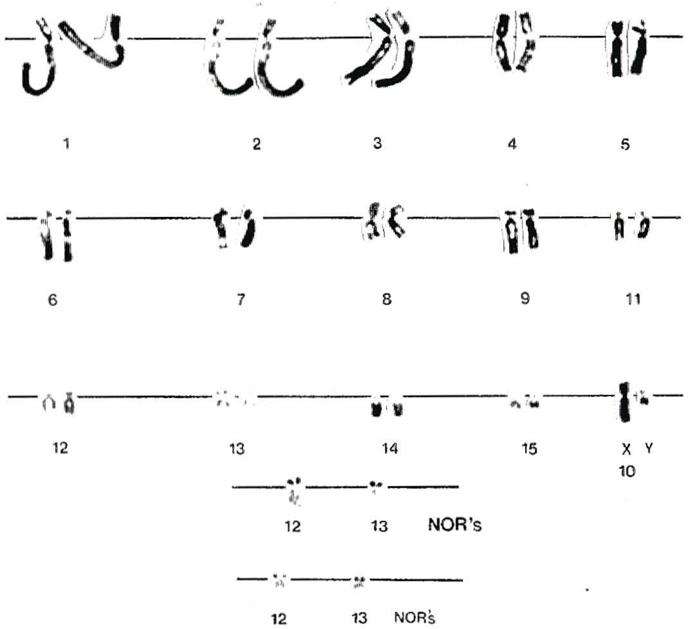


Fig. 4.2. Karyotypes and nucleolar chromosomes of *A. iris*, *A. julianae*, *A. gunningi* and *Calcochloris obtusirostris*. It is speculated that pair 10 corresponds to the X-pair in *A. iris*.

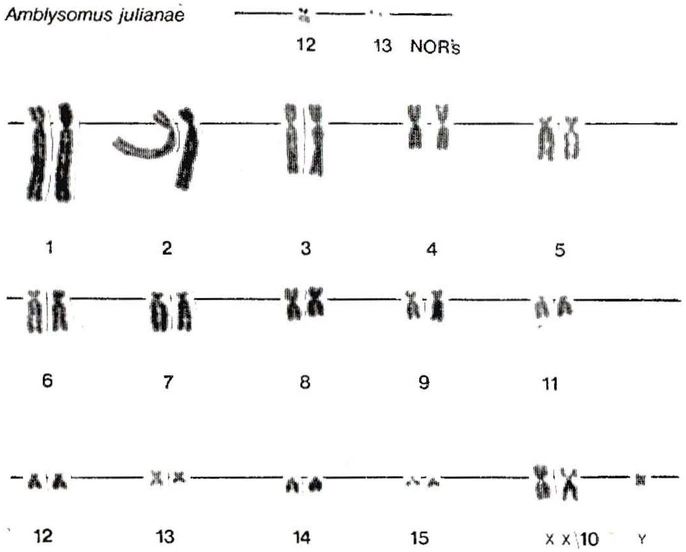
Amblysomus iris iris



Amblysomus gunningi



Amblysomus julianae



Calcochloris obtusirostris chrysillus

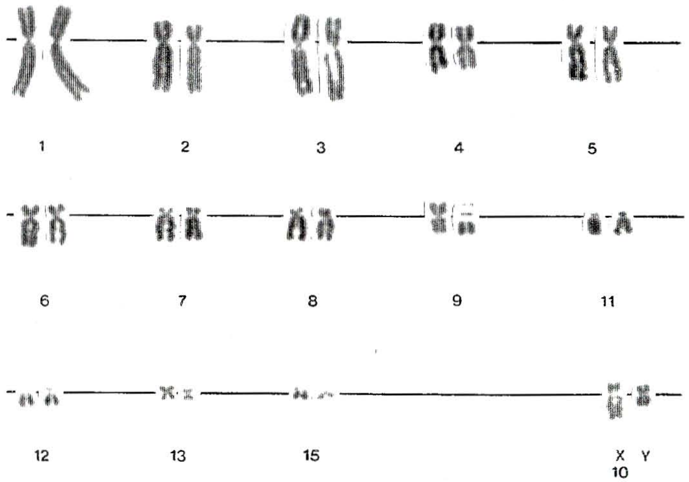
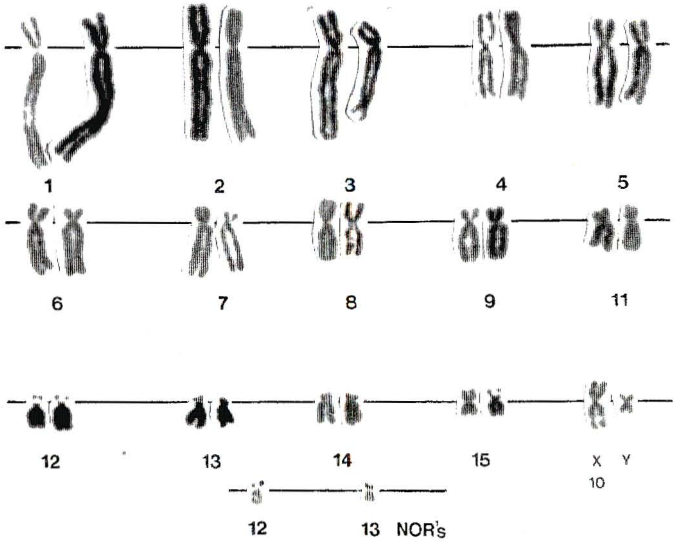
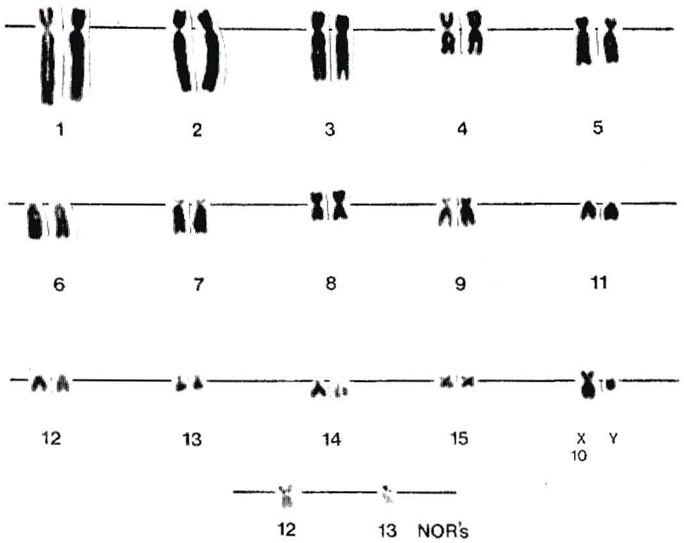


Fig. 4.3. Male karyotypes and nucleolar chromosomes of *Chlorotalpa sclateri*, *Chlorotalpa duthieae*, *Chrysospalax trevelyani* and *Chrysochloris asiatica*.

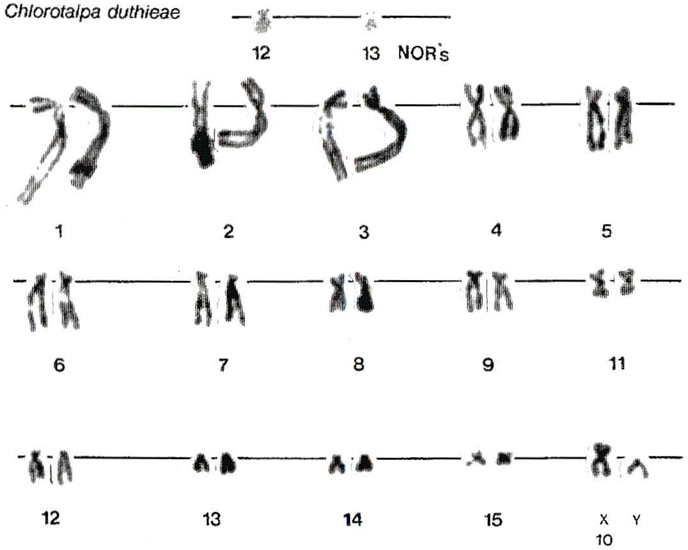
Chlorotalpa sclateri



Chrysospalax trevelyani



Chlorotalpa duthieae



Chrysochloris asiatica

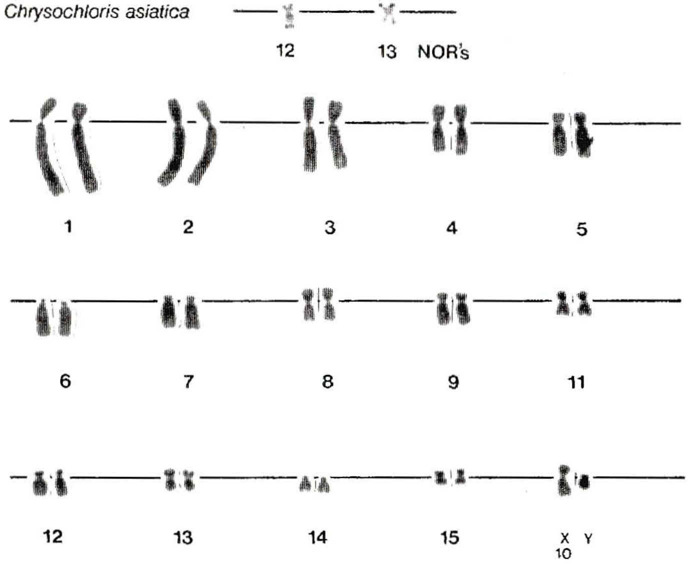


Table 4.1.

Relative chromosome lengths (expressed as a percentage of the haploid karyotype + X chromosome) and centromeric indices for various chrysochlorid taxa, based on measurements taken from a minimum of five karyograms per taxon. RL - mean relative chromosome length ± 1 standard error; ci - mean centromeric index ± 1 standard error.

Chromosome No.	*A.h. hottentotus*		*A. hottentotus (Wakkerstroom & Ermelo)*		*A. hottentotus (Dullstroom)*		*A. julianae*		*A. iris*		*A. gunningi*	
	RL	ci	RL	ci	RL	ci	RL	ci	RL	ci	RL	ci
1	13,2±0,6	23,4±1,4	13,2±1,0	23,0±0,8	12,4±0,1	24,9±0,1	16,1±1,3	22,5±1,7	15,0±0,9	23,8±1,6	16,6±1,2	22,8±0,6
2	11,7±0,4	24,1±3,8	10,3±0,2	27,5±1,3	9,6±0,1	27,0±0,2	12,9±0,6	24,2±1,9	12,0±1,2	26,1±3,7	15,0±1,1	20,6±2,1
3	10,3±0,4	29,3±1,6	9,5±0,8	13,5±3,4	10,4±0,1	13,6±0,6	11,4±0,5	29,2±1,3	12,3±1,9	29,6±3,9	11,9±1,3	27,8±3,3
4	7,8±0,2	42,8±3,8	7,4±0,4	41,2±4,7	7,9±0,1	42,8±0,6	7,8±0,5	45,6±2,2	8,3±1,2	44,1±3,0	8,0±0,3	41,7±3,3
5	7,1±0,3	31,1±5,2	7,9±0,1	26,3±0,8	8,2±0,7	28,8±1,8	7,5±0,5	30,7±1,7	8,0±0,9	29,3±1,8	7,6±0,2	27,7±1,0
6	7,5±0,3	27,7±3,0	6,5±0,3	23,5±2,1	6,7±0,2	22,9±2,6	6,6±0,2	23,4±4,2	7,6±1,1	26,4±1,9	6,8±0,7	17,0±2,4
7	6,8±0,3	26,8±3,4	6,1±0,6	17,3±2,1	6,4±0,1	17,8±0,6	6,9±0,3	21,1±3,8	6,8±0,8	24,3±6,0	5,8±0,2	17,7±1,6
8	6,1±0,7	42,6±3,7	5,4±0,1	42,5±3,0	4,8±0,1	36,3±0,7	5,8±0,4	43,3±1,7	6,3±1,0	45,1±2,8	5,1±0,2	44,6±2,2
9	6,0±0,6	33,5±4,0	5,7±0,2	39,4±2,2	5,0±0,1	32,6±0,6	5,6±0,6	29,5±1,9	6,4±1,2	33,8±2,3	5,3±0,3	26,7±3,8
10(X)	5,7±0,2	42,5±3,2	5,2±0,3	39,2±5,4	5,5±0,1	39,7±0,3	5,6±0,3	42,9±4,2	5,8±0,9	41,3±2,6	4,8±0,9	39,2±5,7
11	5,1±0,2	39,5±2,7	4,9±0,2	33,1±0,9	4,1±0,1	32,1±0,1	3,8±0,4	21,8±1,6	5,8±0,5	40,5±6,0	3,7±0,4	23,0±0,7
12	3,9±0,2	30,8±2,7	4,4±0,4	35,1±2,1	2,7±0,1	29,5±3,2	3,1±0,3	31,7±6,6	4,0±1,1	31,4±4,8	2,8±0,2	28,4±4,4
13	3,6±0,2	45,6±3,4	3,1±0,2	46,7±1,4	2,7±0,2	47,0±1,1	2,8±0,6	45,0±1,0	3,5±0,8	46,5±3,8	2,4±0,3	43,8±2,3
14	2,9±0,2	<12,5	2,5±0,2	<12,5	3,0±0,1	<12,5	2,5±0,3	<12,5	3,0±0,8	<12,5	2,2±0,2	<12,5
15	2,4±0,3	<12,5	2,3±0,1	<12,5	2,9±0,1	<12,5	2,1±0,5	<12,5	2,6±0,7	<12,5	1,8±0,1	<12,5
16			2,9±0,1	<12,5	3,6±0,3	24,2±0,8						
17			2,6±0,1	22,9±0,8	3,1±0,3	24,2±2,1						
18					2,0±0,3	27,1±3,6						

Chromosome No.	*C. duthieae*		*C. sclateri*		*C. obtusirostris*		*C. asiatica*		*C. trevelyani*	
	RL	ci	RL	ci	RL	ci	RL	ci	RL	ci
1	15,7±0,1	21,6±0,4	14,4±1,0	25,0±1,8	15,0±0,7	36,0±3,6	15,0±0,8	24,0±3,2	14,9±0,4	23,5±0,7
2	12,6±0,1	31,8±0,4	12,5±0,3	31,2±2,1	11,1±0,4	28,0±2,1	13,4±0,6	25,4±1,7	12,9±1,1	25,9±0,8
3	12,2±0,2	28,2±5,7	11,4±0,9	28,2±0,9	13,4±0,6	37,8±1,7	11,3±0,9	36,2±1,7	10,7±0,4	29,9±0,6
4	8,1±0,1	38,2±2,2	7,5±0,4	40,1±1,6	8,2±1,0	41,1±3,0	7,4±0,9	47,4±3,4	7,6±0,4	42,4±3,1
5	7,8±0,4	29,9±2,3	7,6±0,2	31,2±1,8	8,4±0,7	32,9±2,2	7,4±0,5	32,0±1,9	8,0±0,4	30,9±2,7
6	6,8±0,2	18,3±3,6	6,9±0,5	29,4±3,2	7,5±0,5	29,0±2,3	5,5±0,4	20,3±1,9	5,9±0,4	25,8±2,9
7	6,7±0,1	17,8±4,4	6,2±0,2	30,1±4,8	5,7±0,2	21,6±0,8	5,6±0,3	< 12,5	5,9±0,3	< 12,5
8	4,9±0,5	33,7±0,9	5,6±0,5	43,0±4,9	6,4±0,4	34,6±1,9	5,5±0,3	43,6±2,2	5,9±0,3	37,1±2,1
9	5,0±0,4	27,0±1,1	5,2±0,1	32,9±3,7	5,6±0,3	28,2±4,9	5,5±0,3	29,7±4,3	5,6±0,2	33,4±2,4
10(X)	5,0±0,9	42,5±2,1	4,9±0,1	40,8±2,5	5,4±0,5	41,6±5,5	4,6±0,7	40,5±2,5	5,3±0,1	47,1±0,5
11	3,0±0,1	24,2±3,9	4,4±0,5	32,6±2,3	3,6±0,2	32,9±1,6	4,2±0,6	34,2±6,3	4,1±0,3	31,3±2,7
12	3,8±0,4	18,7±0,4	3,5±0,2	26,8±2,6	4,0±0,6	22,6±0,3	5,1±0,6	26,6±5,8	3,6±0,4	22,7±5,6
13	3,4±0,2	44,6±5,5	3,5±0,5	30,8±5,1	3,3±0,6	44,9±1,2	3,5±0,4	44,7±1,6	3,4±0,1	38,1±4,7
14	2,8±0,1	30,8±1,8	3,5±0,5	27,3±2,0	/	/	3,0±0,4	<12,5	3,5±0,3	<12,5
15	2,6±0,2	45,2±2,9	2,8±0,3	47,7±2,0	2,3±0,6	45,9±0,5	2,6±0,2	39,9±1,9	3,1±0,3	45,4±0,5

Table 4.2.

Summary of karyotypic properties for 14 chrysochlorid taxa. 2n - diploid number; FN - nombre fundamental, which includes sex elements. Chromosome nomenclature used follows Levan et al. (1964); M - metacentric; SM - submetacentric; ST - subtelocentric; A - acrocentric. NOR designations refer to chromosome number and location on the short (S) and long (L) arms.

			Chromosome No.						
Taxon	**2n**	**FN**	**1**	**3**	**7**	**11**	**14**	**15**	**NORs**
Calcochloris obtusirostris	28	56	SM	M	ST	SM	/	M	12S13S
Chrysochloris asiatica	30	56	ST	SM	A	SM	A	M	12L13S
Chrysospalax trevelyani	30	56	ST	SM	A	SM	A	M	12S13S
Chlorotalpa sclateri	30	60	ST	SM	SM	SM	SM	M	12S13S
Chlorotalpa duthieae	30	60	ST	SM	ST	SM	SM	M	12S13S
Amblysomus julianae	30	56	ST	SM	ST	ST	A	A	12S13S
Amblysomus gunningi	30	56	ST	SM	ST	ST	A	A	12S13S
Amblysomus iris iris	30	56	ST	SM	ST	M	A	A	8S11S
Amblysomus iris corriae	30	56	ST	SM	ST	M	A	A	8S11S
A. h. hottentotus	30	56	ST	SM	ST	M	A	A	8S11S
A. h. marleyi	30	56	ST	SM	ST	M	A	A	8S11S
A. h. devilliersi	30	56	ST	SM	ST	M	A	A	8S11S
A. hottentotus (Ermelo & Wakkerstroom)	34	62	ST	ST	ST	SM	A	A	8S9S11S
A. hottentotus (Dullstroom)	36	68	ST	ST	ST	SM	A	A	8S9S11S

Fig. 4.1) and among genera, whereas differences in fundamental numbers are evident mainly at the inter-generic level. In all taxa, the X chromosome is apparently a medium-sized metacentric, corresponding to pair no. 10 according to the relative size and centromeric index criteria used also by Capanna *et al.* (1990). It constitutes, on average, 5.3±0.4% of the haploid genome. The Y chromosome is a small metacentric or submetacentric in all taxa except *Chlorotalpa duthieae* in which it appears to be a small acrocentric. As no *A. iris* males were analysed, the morphology of the sex chromosomes could not be unambiguously assessed. However, the tenth largest chromosome pair is similar in size (RL = 5,8±0,9) and centromeric index (ci = 41,3±2,6) to that of the X chromosomes in other taxa, and probably represents the XX pair.

The major karyotypic differences observed between and within taxa involve six elements, tentatively identified as chromosomes 1, 3, 7, 11, 14 and 15. In *Calcochloris obtusirostris* (the only taxon with 2n = 28 and FN = 56), the elements corresponding to chromosome pair 14 in other taxa appear to be absent (Fig. 4.2). Pair 1 is submetacentric, and pair 3 metacentric, whereas in other taxa these elements are subtelocentric and subtelocentric/ submetacentric, respectively. *Chrysochloris* and *Chrysospalax* are the only genera in which pair 7 is acrocentric (Fig. 4.3), whereas *Chlorotalpa* is the only genus in which pair 14 is biarmed. The smallest autosomes (pair 15) are acrocentric in *Amblysomus*, but metacentric in the other genera. Chromosome 11 is submetacentric in *Chrysochloris*, *Chrysospalax*, *Calcochloris* and *Chlorotalpa*, but in *Amblysomus* it is either subtelocentric (*A. julianae*, *A. gunningi*) or metacentric (*A. iris*, *A. hottentotus* 2n = 30 cytotype).

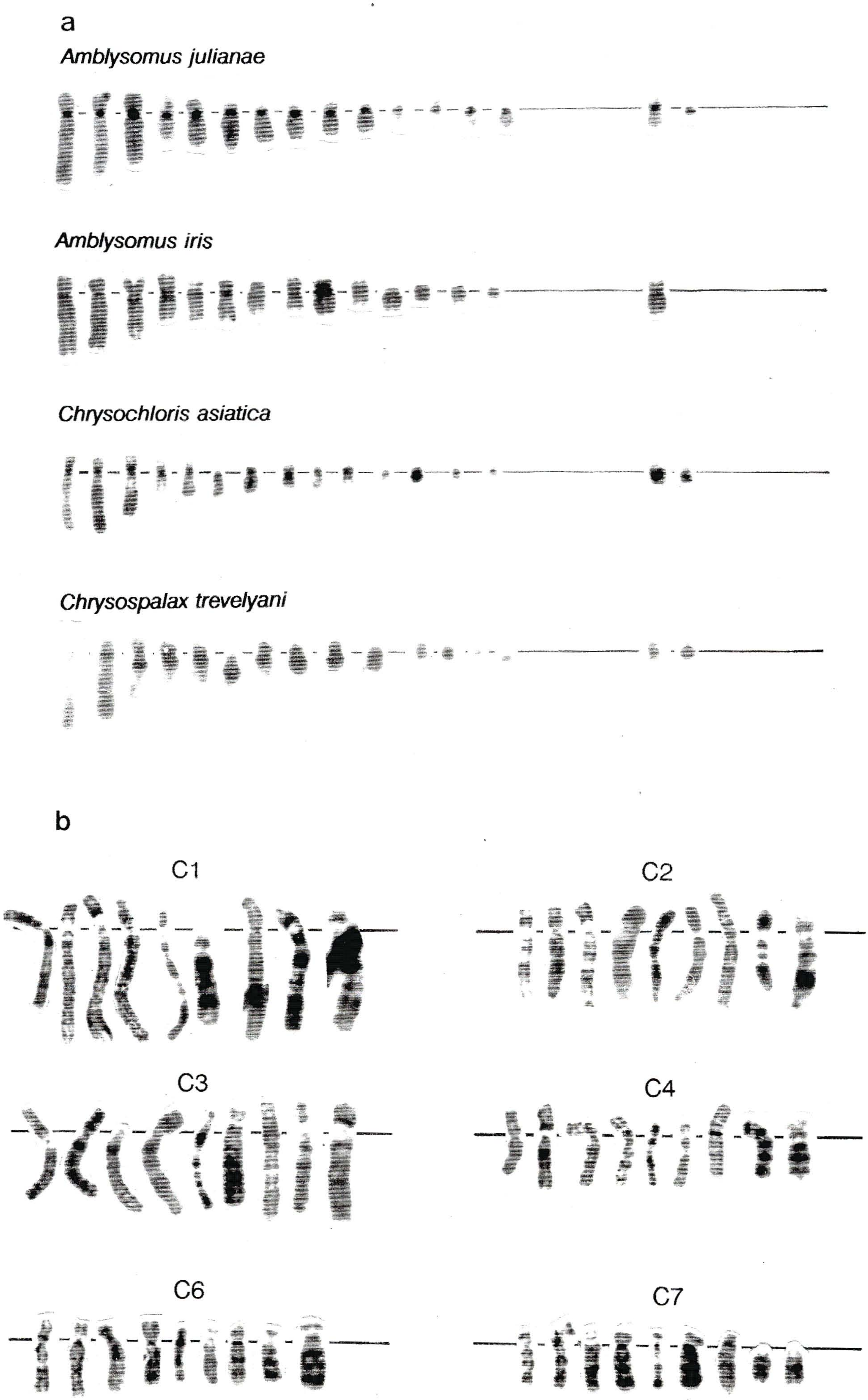
Interpopulational variation in karyotypes is negligible in most species, and was not assessed in *C. duthieae* since specimens from only a single locality were analysed. The only species characterized by appreciable geographic variation is *A. hottentotus*, in which three cytotypes with apparently allopatric distributions occur. Whereas samples from KwaZulu-Natal, Western Cape and the Eastern Cape Province have identical karyotypes with 2n = 30 and FN = 56, two populations from the south-eastern Mpumalanga highveld (Wakkerstroom and Ermelo) show 2n = 34 and FN = 62, and a montane population from the eastern highveld (Dullstroom) is characterized by 2n = 36 and FN = 68 (Fig. 4.1). These differences are due to the presence of an extra acrocentric and subtelocentric pair in the 2n = 34 cytotype, and three extra pairs of submetacentrics/subtelocentrics in the 2n = 36 cytotype. Chromosome pairs 3 and 7 in these populations are characterized by centromeric indices of < 14 and < 18 respectively, markedly lower than those for homologues (ci = 29,3±1.6 and ci = 26,8±3.4, respectively) in nominotypical *A. hottentotus*. The 2n = 34 and 2n = 36 cytotypes are also distinguished by three NORs on pairs 8, 9 and 11, in contrast to the two NORs located on the short arms of chromosomes 8 and 11 (*A. hottentotus* 2n = 30 cytotype and *A. iris*), the short arms of elements 12 and 13 (*A. gunningi*, *A. julianae*, *Calcochloris*, *Chlorotalpa*, *Chrysospalax*), or the long and short arms of pairs 12 and 13 (*Chrysochloris asiatica*).

4.3.2 C- and G-banding

Owing to low mitotic indices, only limited success was achieved with C- and G-banding analyses, so that presumed homologies were, in many cases, not confirmed. Satisfactory C-bands were obtained for *A. julianae*, *A. i. corriae*, *Chrysochloris asiatica* and *Chrysospalax trevelyani* (Fig. 4.4a), which show similar patterns with the constitutive heterochromatin located mainly in the centromeric region of most chromosomes. In *A. i. corriae*, *Chrysochloris asiatica* and *Chrysospalax trevelyani*, heterochromatic blocks also appear to extend along the long arms (pairs 3 and/or 4), the short arms (pair 7), and both arms (pairs 8 and 10) of some chromosomes, and the small metacentric pair 12 is almost entirely heterochromatic. Heterochromatin apparently also occurs along the arms of the large acrocentrics (pair 7) in *Chrysochloris asiatica* and *Chrysospalax trevelyani)*, unlike the pericentromeric bands in the *Amblysomus* species.

G-banding was not successful for *Chlorotalpa duthieae* or the *A. hottentotus* 2n = 36 cytotype. Even in the other taxa G-bands of comparable quality were limited to the larger chromosomes, the sequences on smaller elements being indistinct or ambiguous. Of the six elements for which G-band homologies could be tentatively identified (Fig. 4.4b), major differences among the species and genera apparently involve pairs 1 and 3 in *Calcochloris obtusirostris*, pair 7 in *Chrysochloris asiatica* and *Chrysospalax trevelyani*, and pairs 3 and 7 in the *A. hottentotus* 2n = 34 cytotype. These differences correspond with disparities in relative lengths and centromeric indices (Table 4.1), and appear to be the result of both Robertsonian changes (fusions or fissions) and pericentric inversions.

Fig. 4.4. Differentially-stained chromosomes of selected species: (a) C-banded haploid complements of four chrysochlorid species; and (b) haploid G-banded chromosomes (pairs 1-4 and 6-7) of (from left to right): *Calcochloris obtusirostris*; *A. h. hottentotus* (2n = 30); *A. hottentotus* (2n = 34); *A. i. corriae*; *A. gunningi*; *A. julianae*; *Chlorotalpa sclateri*; *Chrysochloris asiatica*; and *Chrysospalax trevelyani*.

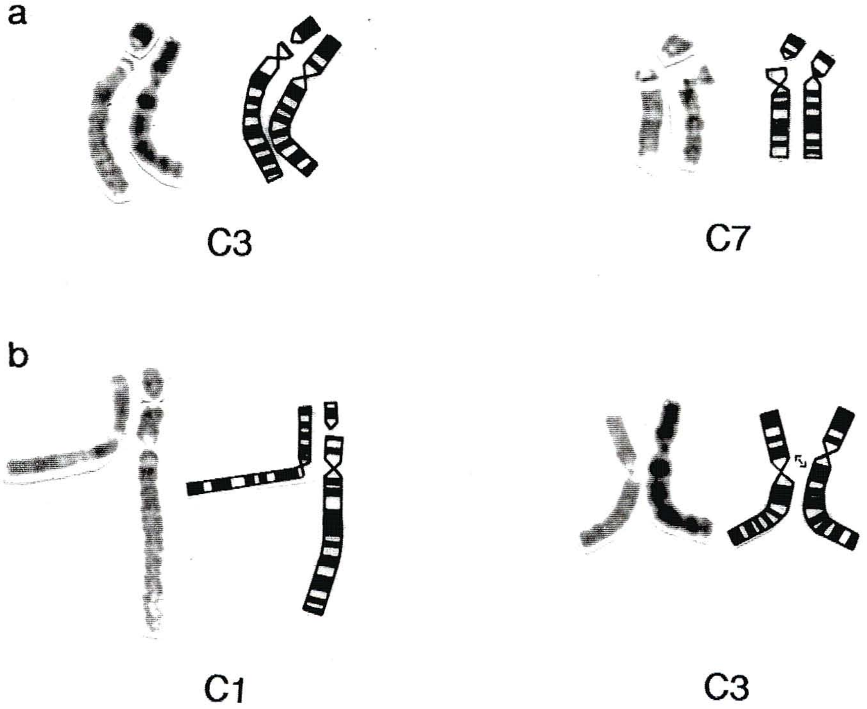

a
Amblysomus julianae
Amblysomus iris
Chrysochloris asiatica
Chrysospalax trevelyani
b
C1
C2
C3
C4
C6
C7

The large acrocentrics (pair 7) in *Chrysochloris asiatica* and *Chrysospalax trevelyani* correspond with the long arms of apparent homologues in other taxa. *Chrysochloris* and *Chrysospalax* can be considered outgroups because these genera show many primitive morphological characters, suggesting that they have evolved independently of *Amblysomus*, *Chlorotalpa* and *Calcochloris*; Broom 1907a). Therefore, the biarmed morphology of pair 7 observed in *Amblysomus*, *Chlorotalpa* and *Calcochloris* must be considered synapomorphic.

Whereas the long arms of chromosomes 3 and 7 in the 2n = 30 and 2n = 34 *A. hottentotus* cytotypes appear directly homologous, the terminal sequences of the short arms in the 2n = 30 cytotype correspond with the extra chromosomes (pairs 16 and 17) of the 2n = 34 cytotype (Fig. 4.5a), indicating that fusions or fissions have occurred. As short arms are still present in chromosomes 3 and 7 of the 2n = 34 cytotype, and the fundamental number (FN = 62) differs from that of the 2n = 30 cytotype (FN = 56), it superficially appears that two tandem fusions may have occurred, leading to a reduction in both diploid and fundamental number. However, the G-banding sequences on the short arm of chromosomes 3 of the 2n = 30 cytotype correspond with those of the outgroups, indicating that the subtelocentric morphology of pair 3 in the 2n = 34 cytotype represents a derived condition. Furthermore, examination of the C-banded karyotypes of *A. hottentotus* published by Capanna *et al.* (1989) reveals that the short arms of chromosomes 3, 7 (their pair no. 6) and 17 in the 2n = 34 cytotype are entirely heterochromatic, whereas in the 2n = 30 cytotype the heterochromatic blocks extend only partially along the short arms of pairs 3 and 7. These data support an alternative hypothesis; namely that the differences between the 2n = 30 and 2n = 34 cytotypes are the result of two fissions (involving pairs 3 and 7), leading to an increase in diploid number; followed by heterochromatic additions to chromosomes 3, 7 and 17, causing a change in fundamental number. Although comparable G-bands for the 2n = 36 *A. hottentotus* cytotype were not obtained, chromosomes 3 and 7 closely resemble those in the 2n = 34 cytotype, suggesting that the subtelocentric morphology of these elements can be considered synapomorphic, and that the 2n = 36 cytotype evolved from the 2n = 34 karyotype.

Capanna *et al.* (1989) speculated that the apparent differences in the absolute lengths of chromosome pair 1 in the 2n = 30 and 2n = 34 cytotypes (mean lengths =

Fig. 4.5. Comparison of homologous elements and idiograms of: a) chromosomes 3 and 7 of the *A. hottentotus* 2n=34 (left) and 2n=30 (right) cytotypes; and b) chromosomes 1 and 3 of *Calcochloris obtusirostris* (left) and *A. hottentotus* 2n=30 cytotype (right).



12.1±2.4μm and 14.2±2.1μm respectively) could be the result of euchromatic additions or deletions, depending on assumed evolutionary polarity. The present data do not support this speculation. Relative lengths of these chromosomes are similar in both cytotypes (Table 4.1), and their G-banding sequences are directly homologous (Fig. 4.4b). Capanna *et al.* (1989:5 and 8) were mistaken also in claiming that pair 17 is telocentric in the 2n = 34 cytotype, and that the apparent equal sizes but different centromeric indices of pairs 3 and 7 of 2n = 30 and 2n = 34 cytotypes "..are easily explained by pericentric inversions". Pair 17 in the 2n = 34 cytotype has a distinct short arm (Fig. 4.1), and the euchromatic sequences of the long arms of chromosomes 3 and 7 are identical in the respective cytotypes, so pericentric inversions could not have occurred. Furthermore, Capanna *et al.* (1989:5) claimed that one of the NORs in the *A. hottentotus* 2n = 30 cytotype is located on the long arm of pair 8 (their no. 9), whereas my data unequivocally demonstrate that the NOR in question is located on the short arm. These discrepancies can be attributed to the small samples (n = 4 and n = 1 for the 2n = 30 and 2n = 34 cytotypes, respectively) analysed by Capanna *et al.* (1989), and their reliance on non-differentially stained karyotypes which do not allow accurate determination of genetic homology or the type and number of chromosomal rearrangements that may have occurred (Baker *et al.* 1987).

The long arms of pair 1 in *C. obtusirostris* apparently correspond directly with those of *C. asiatica* and *C. trevelyani*, but with only the proximal euchromatic sequences in *Amblysomus* and *Chlorotalpa*. Since C-bands are located pericentromerically in *Amblysomus* and both outgroups (Fig. 4.4), differences between the long arms of these taxa cannot be ascribed to heterochromatic additions. This implies that euchromatic additions to pair 1 have occurred during the karyotypic evolution of *Amblysomus* and *Chlorotalpa*. The precise arrangements involved, however, cannot be ascertained from the limited banding data available.

The proximal sequences of the short arm of pair 1 in *Calcochloris obtusirostris* correspond with those in other taxa, but the distal sequences match those of the small acrocentric (pair 14) observed in *A. h. hottentotus* (Fig. 4.5b). This suggests that the reduced 2n, and submetacentric morphology of pair 1 in *C. obtusirostris* arose by the tandem fusion of pairs 1 and 14, which are subtelocentric and telocentric respectively in the other species. Good G-band homology is evident for the major portion of the long arm of pair 3 in *Calcochloris obtusirostris*, but the proximal portion adjacent to the centromere and its short arm differ from the other taxa, apparently as a result of a pericentric inversion (Fig. 4.5b).

4.3.3 Taxonomic implications

Capanna *et al.* (1989), who first reported the karyotypes of the 2n = 30 and 2n = 34 cytotypes in *A. hottentotus*, erroneously referred the 2n = 34 cytotype to the taxon *Amblysomus iris*, despite J. Meester's (*in litt.*) warning that positive identification of the single skull available was not possible because these species are cranially indistinguishable. Although the 2n = 34 cytotype occurs at Wakkerstroom, the type locality of *A. i. septentrionalis* Roberts, 1913, morphometric analyses unequivocally indicate that *A. iris* is a purely coastal taxon whose range does not extend inland to the southern Mpumalanga highveld (Chapter 5). All of the *Amblysomus* collected at Wakkerstroom during the present study have 2n = 34, and associate with the types of both *A. h. drakensbergensis* Roberts, 1946, and *A. i. septentrionalis* in multivariate morphometric analyses, indicating that they represent the same species. Roberts (1913, 1946), therefore, was mistaken in referring *Amblysomus* from this region to two different species.

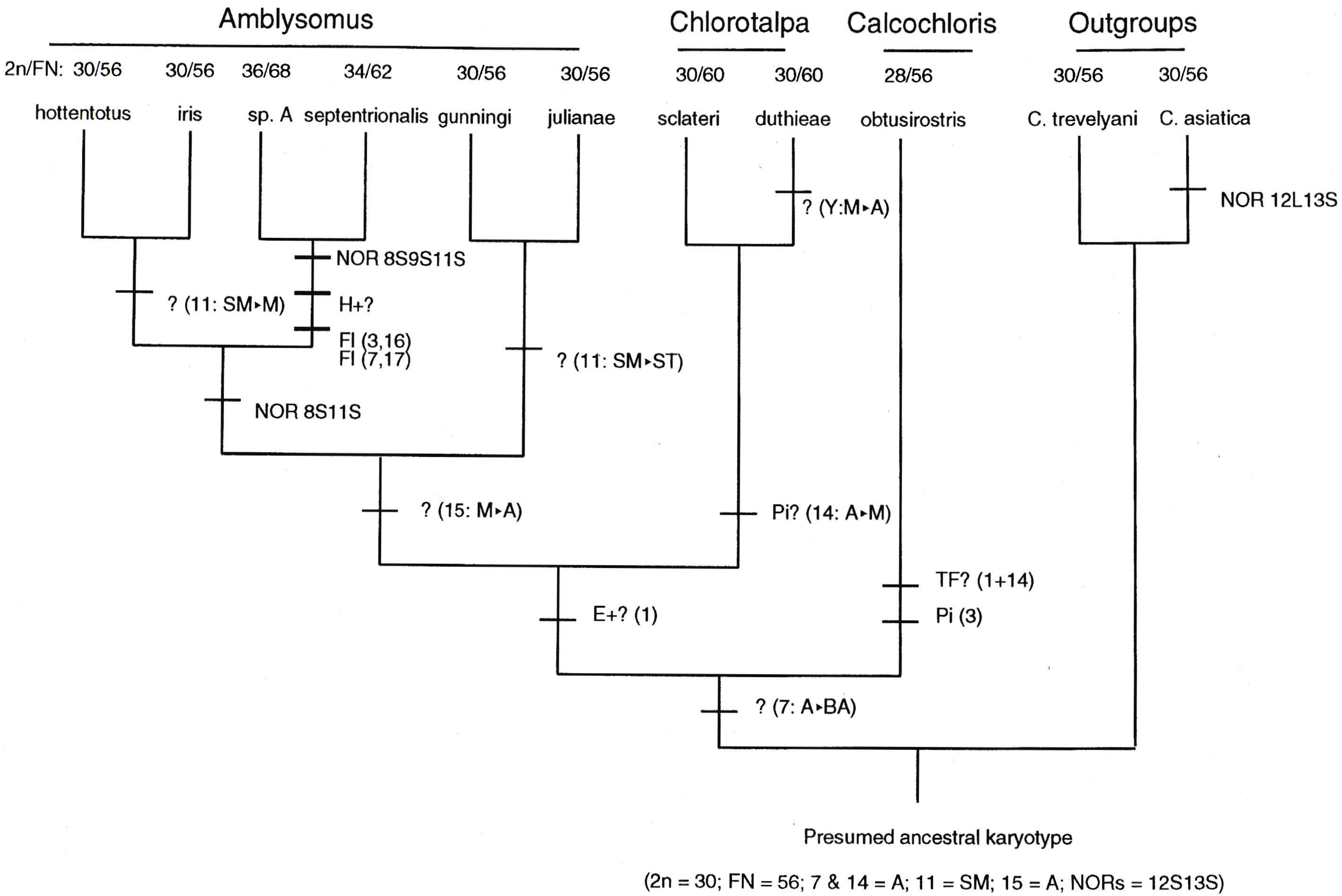
Given the apparent lack of intraspecific karyotypic variation in most of the taxa analysed, the existence of three geographical cytotypes in *A. hottentotus* is taxonomically important. The rearrangements which have occurred during the differentiation of these cytotypes cannot, however, necessarily be regarded as having caused speciation. The role of chromosomal rearrangements in speciation in evolution is controversial, and it is becoming increasingly apparent that such changes often do not have severe negative heterotic effects (Baker 1981; Sites and Moritz 1987; Yates and Moore 1990). However, the differences in the number and locations of the nucleolar organizer regions in the 2n = 30 and 2n =34/36 cytotypes strongly suggest functional genome divergence. Nucleolar organizer regions correspond with clusters of rRNA cistrons, which play an important role in the inner organization of chromosomes; thus, NOR differentiation probably affects gene expression and plays an active role in species divergence (Yoshida 1983).

The karyotypic differences between the cytotypes are correlated with morphological and ecological differences. Overall size increases markedly with the change from the 2n = 30 to 2n = 34 and 2n = 36 karyotypes. This variation is associated with increasing altitude and vegetation differences. The 2n = 30 cytotype occurs in a variety of forest and grassland habitats at lower altitudes (0 - 1200 m) in southeastern Africa, and shows a clinal pattern of size increase in relation to altitude in KwaZulu-Natal. The other cytotypes are known from only "Near-Highland Sourveld" (veld type 57b of Acocks, 1988) at altitudes of 1600 - 1800 m on the eastern escarpment (2n = 34), or altitudes of 2000-2150 m in the Mpumalanga highveld (2n = 36; Section 5.3.2.2). Multivariate craniometric analyses indicate that the three cytotypes also differ diagnostically in skull configuration, to the extent that there is no overlap of discriminant score ranges along the first two canonical variate axes, and individuals are assigned to their correct *a priori* groups with 100% accuracy (Section 5.3.2.3). The three cytotypes thus differ phenotypically, ecologically, and cytogenetically, and can be considered to represent cryptic but distinct biological species. The 2n = 34 cytotype, which Capanna *et al.* (1989) referred to *A. iris*, thus represents the species *Amblysomus septentrionalis*. This name has priority over *drakensbergensis*, which becomes the first synonym. No published name is yet available for the new species represented by the 2n = 36 cytotype, which is hereafter referred to as *Amblysomus Species A*.

Cladistic analyses of karyotypic properties distinguish six groupings within the chrysochlorids studied (Table 4.2, Fig. 4.6), of which three correspond with recognized genera, whereas the others are members of *Amblysomus*. The chromosomal data presented, although equivocal, clearly differentiate *Amblysomus* from *Chlorotalpa* and *Calcochloris*. Karyotypic data thus support Meester's (1974) recognition of *Chlorotalpa* and *Calcochloris* as discrete genera, in contrast to the classifications of Ellerman *et al.* (1953), Petter (1981) and Simonetta (1968) which treated these taxa as synonyms of *Amblysomus*. Chromosomal data also are congruent with hyoid data (Section 3.4) in suggesting that *A. gunningi* and *A. julianae* should be distinguished taxonomically (in the subgenus *Neamblysomus*) from other *Amblysomus*.

The relatively greater karyotypic variability of *Amblysomus* is correlated with a richer diversity of species which, although cranially similar, are characterized by quite

Fig. 4.6. Possible cladistic relationships among the chrysochlorid taxa studied, based on chromosomal data, with *Chrysochloris asiatica* and *Chrysospalax trevelyani* used as outgroups. Owing to the poor banding data for some taxa, rearrangements identified should be regarded as only tentative. A - acrocentric; ST - subtelocentric; SM - submetacentric; M - metacentric; E+ - euchromatic addition; Pi - pericentric inversion; H+ - heterochromatin addition; TF - tandem fusion; FI - centric fission; NOR - location of the nucleolar organizer regions on the long (L) or short (S) arms of chromosomes. Question marks denote unidentified rearrangements which have led to changes in standard karyotypes; broken lines represent branching patterns that are not fully resolved by karyotypic data.


Amblysomus
Chlorotalpa
Calcochloris
Outgroups
2n/FN: 30/56
30/56
36/68
34/62
30/56
30/56
30/60
30/60
28/56
30/56
30/56
hottentotus
iris
sp. A
septentrionalis
gunningi
julianae
sclateri
duthieae
obtusirostris
C. trevelyani
C. asiatica
? (Y:M▸A)
NOR 12L13S
NOR 8S9S11S
? (11: SM▸M)
H+?
FI (3,16)
FI (7,17)
? (11: SM▸ST)
NOR 8S11S
? (15: M▸A)
Pi? (14: A▸M)
TF? (1+14)
E+? (1)
Pi (3)
? (7: A▸BA)
Presumed ancestral karyotype
(2n = 30; FN = 56; 7 & 14 = A; 11 = SM; 15 = A; NORs = 12S13S)

marked differences in size and colour. This genus exhibits many advanced karyotypic and morphological features, suggesting that it is still in the process of diverging from other chrysochlorid taxa (Broom 1907a; Roberts 1951).

4.3.4 Comparison with other Insectivora

Capanna *et al.* (1989) remarked that the nondifferentially stained karyotypes of golden moles resemble those of certain Madagascan Tenrecidae, which are often regarded as being the closest extant relatives of chrysochlorids. However, standard karyotypes do not allow accurate assessment of genetic homology (Baker *et al.* 1987), and there is no unequivocal morphological evidence favouring a close relationship between tenrecs and chrysochlorids (MacPhee and Novacek 1993). Until G-banded karyotypes of both families are available for comparison, the degree of chromosomal conservatism and cytotaxonomic affinity among these taxa will not be decisively addressed.

Although only a few chromosomal rearrangements have been identified here, it appears that centric fissions, tandem fusions, pericentric inversions, and alterations in the number and location of the NORs may have all played a role in the chromosomal evolution of chrysochlorids. As in the Talpidae, there does not appear to be any overt pattern to the fixation of rearrangements whereby the occurrence of one type of change affects the likelihood of the same kind of mutation occurring in a particular lineage again (see Yates and Moore 1990). Chromosomal variability in the Chrysochloridae, although sufficient marked to be taxonomically useful, is similar in extent and nature to that in the karyotypically conservative talpids (Yates and Moore 1990), and does not appear to be the result of chain processes involving multiple changes of a particular kind. This is in contrast to the chromosomal diversity and prominent role of karyotypic orthoselection characterizing many fossorial rodents (Patton and Sherwood 1983; White 1978).

APPENDIX 4.1

SPECIMENS EXAMINED

All specimens were karyotyped within 24 hours of capture, and were prepared as skin, skull and/or skeleton voucher specimens, and deposited in the Transvaal Museum Mammal collection. Taxonomic designations follow Meester *et al.* (1986).

Amblysomus gunningi, *n* = 2. NORTHERN PROVINCE: De Hoek State Forest, Magoebaskloof, 2,4 km N and 13,6 km W Tzaneen, 23°50'S, 30°02'E.

Amblysomus hottentotus devilliersi, *n* = 3. WESTERN CAPE PROVINCE: Grootvadersbosch Forest Reserve, 5,5 km N and 10 km W Heidelberg, 34°01'S, 20°47'E; Jonkershoek Nature Conservation Headquarters, 6,4 km S and 6,5 km E Stellenbosch, 34°00'S, 18°58'E.

Amblysomus hottentotus hottentotus, *n* = 33. EASTERN CAPE PROVINCE: Palm Springs Resort, Kidds Beach, 20 km S and 15 km W East London, 33°09'S, 27°42'E; KWAZULU-NATAL: Balgowan, Michaelhouse Golf Course, 29°24'S, 30°03'E; Botanic Gardens, University of Natal sports grounds, and Durban Country Club, central Durban, 29°50'S, 31°01'E; Dukuduku Forest Reserve, 7,5 km N and 15 km W Mtubatuba, 28°22'S, 32°21'E; Umtamvuma Nature Reserve, 9 km N and 9 km W Port Edward, 31°02's, 30°12'E; Wyford Farm, 4 km S and 4,8 km E Van Reenen, 28°24'S, 29°25'E; MPUMALANGA: Ermelo Dam, 7 km W Ermelo, 26°28'S, 28°57'E; Graskop town, 24°56'S, 30°50'E; Tafelkop Farm, 7,2 km N and 12 km E Wakkerstroom, 27°21'S, 30°09'E; Verloren-Vallei Nature Reserve, 26,4 km N and 3,2km E Dullstroom, 25°13'S, 30°08'E.

Amblysomus hottentotus marleyi, *n* = 1. KWAZULU-NATAL: Goudhoek Farm, 10 km N and 10 km W Babanango, 28°17'S, 30°54'E.

Amblysomus iris iris, n = 6. KWAZULU-NATAL: Hazelmere Dam, 6 km N and 2 km W Verulam, 29°36'S, 31°01'E; Dukuduku Forest Reserve, 7,5 km N and 15 km W Mtubatuba, 28°22'S, 32°21'E.

Amblysomus iris corriae, *n* = 3. WESTERN CAPE PROVINCE: Natures Valley Township, 33°59's, 23°33'E; Saasveld Forest Research Station, 6 km E George, 33°58'S, 22°31'E.

Amblysomus julianae, *n* = 11. NORTHERN PROVINCE: Nylsvley Nature Reserve, 14,4 km S and 2,4 km W Naboomspruit, 24°40'S, 28°43'E; MPUMALANGA: Pretoriuskop Rest Camp, Kruger National Park, 25°11'S, 31°17'E; GAUTENG: Shere and Tierpoort smallholdings, 15,2 km S and 20 km E Pretoria, 25°45'S, 28°24'E.

Chlorotalpa duthieae, *n* = 3. WESTERN CAPE PROVINCE: Natures Valley Township, 33°59'S, 23°33'E.

Chlorotalpa sclateri, *n* = 6. WESTERN CAPE PROVINCE: Mountain View Camp, Karoo National Park, 14 km N and 4 km W Beaufort West, 32°15'S, 22°32'E; FREE STATE: Agricultural Showgrounds, Ficksburg, 28°53'S, 27°53'E.

Calcochloris obtusirostris chrysillus, *n* = 11. KWAZULU-NATAL: Kwazulu Department of Health Camp, Kosi Lake, 26°57'S, 32°49'E; Lalanek Inspection Quarters, 6 km N and 4,5 km E Manzengwenya, 27°13'S, 32°46'E.

Chrysochloris asiatica, *n* = 6. WESTERN CAPE PROVINCE: Kirstenbosch Gardens, Cape Town, 33°58'S, 18°28'E; Jonkershoek Nature Conservation Headquarters, 6,4 km S and 6,5 km E Stellenbosch, 34°00'S, 18°58'E; Algeria Forest, 21 km S and 16 km E Clanwilliam, 32°22'S, 19°02'E.

Chrysospalax trevelyani, *n* = 5. EASTERN CAPE PROVINCE: Nqadu Forest, 19 km N and 2,5 km W Umtata, Transkei, 31°26'S, 28°46'E; Kologha Forest, 5 km N and 6 km W Stutterheim, 32°32'S, 27°15'E.

PART III

REVISION OF DESCRIBED SPECIES

CHAPTER 5

CRANIOMETRIC VARIATION IN THE HOTTENTOT GOLDEN MOLE, *Amblysomus hottentotus*

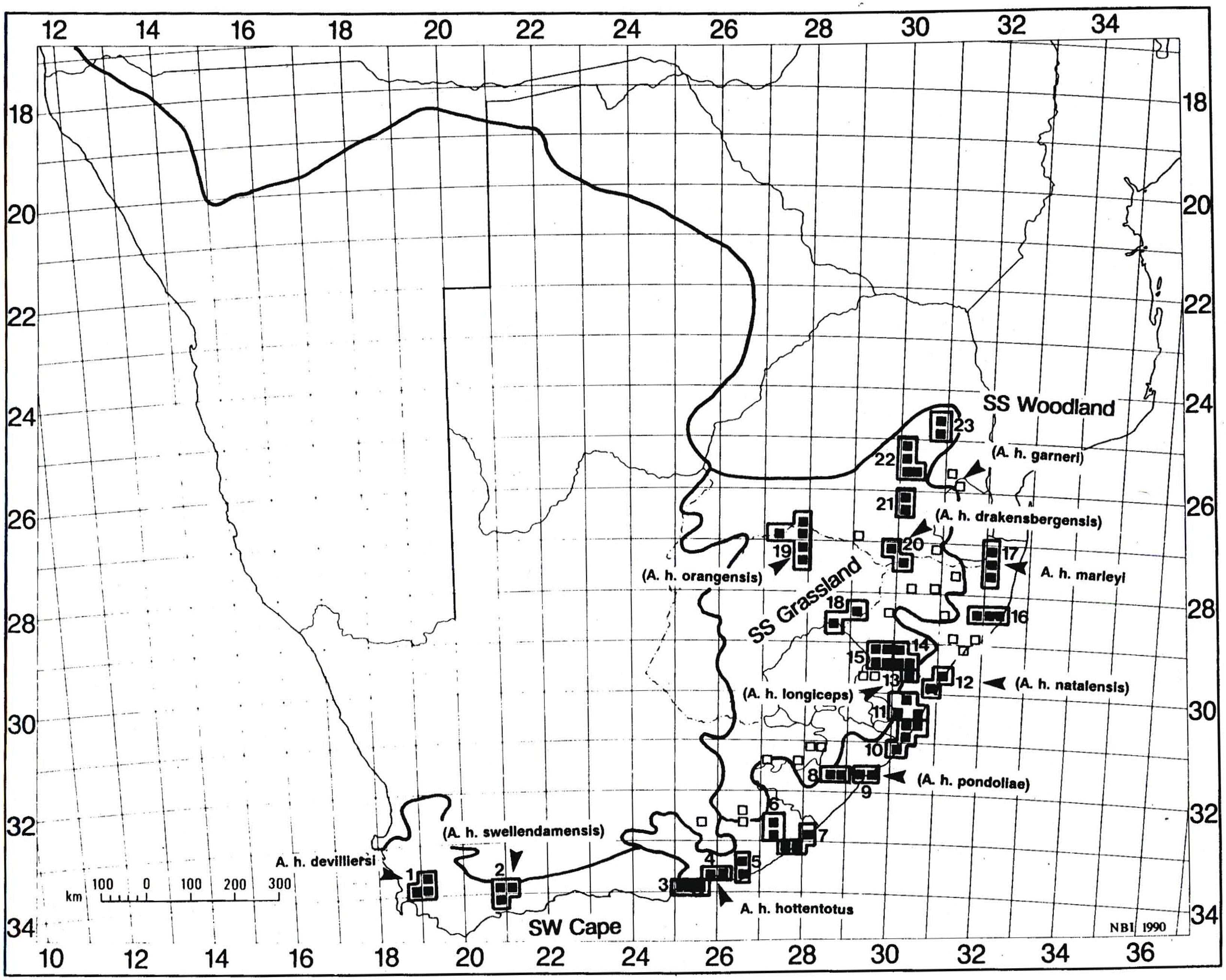
5.1 INTRODUCTION

Amblysomus hottentotus is the most widespread chrysochlorid species in southern Africa, and occurs in the mesic parts (> 500mm rainfall p.a.) of South Africa, from Stellenbosch (34°00'S, 18°58'E) in the Western Cape Province to the Graskop district (24°56'S, 30°50'E) of Mpumalanga (Fig. 5.1). Within this range it inhabits a wide altitudinal and climatic spectrum of subterrestrial habitats. These include coastal forests, woodland savanna and inland mist forests of the Southern Savanna Woodland biotic zone, temperate grasslands and montane moors in the Southern Savanna Grassland zone, and fynbos of the South-West Cape biotic zone (Kuyper 1985; Meester 1965; Meester *et al.* 1986; Rautenbach 1978). Its distribution is not continuous, however, owing to this species' requirement for friable soils with an abundance of earthworms and insect prey (Roberts 1951).

Perhaps as the result of stabilizing selection acting on localized populations of individuals with low vagility, considerable geographic variation exists in the size and colouration of *A. hottentotus* (Roberts 1951). Metabolic rate and other physiological properties of this species also vary geographically in relation to body size (Kuyper 1985), while local demes display marked intra-populational variation in fur colour and sexual size dimorphism (Broom 1907a). This variability has led to the description of more than 10 subspecies, of which only three (*A. h. hottentotus*, *A. h. marleyi* and *A. h. devilliersi*) are currently recognized (Hutterer 1993; Meester 1974; Meester *et al.* 1986).

Previous taxonomic revisions of chrysochlorids (Forcart 1942; Meester 1974; Petter 1981; Simonetta 1968; amongst others) were largely intuitive, or based on elementary statistical evaluation of relatively few specimens. They focused mainly on inter-specific and generic relationships, with the result that intra-specific variation in taxa was not adequately assessed. The existence of significant geographic variation in

Fig. 5.1. The distribution of *A. hottentotus* in the different biotic zones of Southern Africa (Rautenbach 1982), plotted by quarter-degree squares and pooled as population samples (see Table 5.1). Open squares denote localities not included in analyses (owing to small sample sizes) or literature records. Arrows indicate type localities, with the names of taxa described from there. Current synonyms are given in parentheses.


SS Woodland
SS Grassland
SW Cape
A. h. devilliersi
(A. h. swellendamensis)
A. h. hottentotus
(A. h. pondoliae)
(A. h. longiceps)
(A. h. natalensis)
A. h. marleyi
(A. h. orangensis)
(A. h. drakensbergensis)
(A. h. garneri)
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the size of the hyoid apparatus (Section 3.3.3), and karyotypic properties (Section 4.3.1), of *A. hottentotus* points to the need for more detailed examination of morphological variation in this species.

5.2 MATERIALS AND METHODS

Six hundred and fifteen specimens from various museums (Section 2.1) were examined and measured. Only two population samples (Durban and King Williams Town) were sufficiently large for meaningful statistical study of intra-population variation. Data for specimens belonging to toothwear class 5 (TW5) were excluded owing to very small sample sizes.

Geographic variation was assessed by comparing data suites of 23 locality and/or pooled samples from throughout the range of the species (Fig 5.1), for each measurement individually, and for combinations of measurements simultaneously. Numbers given in square brackets ([]) in the text refer to operational taxonomic units (OTUs) designated in Table 5.1.

Colourimetric analyses were limited to comparisons of selected groups of OTUs. Individual colour measurements were taken mid-dorsally, mid-ventrally, and on the right flank in the abdominal region, using "Standard Revised Munsell Soil Colour Charts" (Oyama *et al.* 1967). Scoring of colour was done under standard conditions (natural light from an east-facing window), with the fur brushed forwards to reduce the iridescence which may impart a green, bronze or violet lustre to the pelage.

Colour names, when given, are followed by a standard Munsell notation detailing hue, value and chroma. This is necessary because colour names do not adequately express delicate differences in shades, and the same colour name may have several Munsell designations. For example, reddish-black is designated by 10R 1,7/1 (hue = 10R, value = 1,7, chroma = 1), 2,5YR 2/1 or 7,5R 1,7/1.

Increasing hue co-ordinates indicate a change in the position on the visible spectrum, from 0 (red) through the five major colours to red-purple (100), and thus a decrease in the dominant spectral wavelength. Value co-ordinates indicate the tone or relative lightness of a colour, and range from 0 (dark) - 10 (light). Chroma co-ordinates indicate the saturation or vividness of a colour, and increase as a colour becomes richer.

Table 5.1.

Localities pooled as Operational Taxonomic Units (OTUs) for analysis of geographic variation in *A. hottentotus*. The first column gives OTU numbers referred to in Fig. 5.1, the second gives names by which OTUs are referred to in the text. For males, OTUs 9 and 10, and 13 and 14, were pooled to increase sample sizes. See the Gazetteer for more details of individual localities.

OTU No.	OTU Name	Localities
1	Stellenbosch	Stellenbosch, Town and Jonkershoek Research Station; Paarl, La Motte; Worcester, Haweqwas Forest.
2	Grootvadersbosch	Heidelberg, Grootvadersbosch State Forest; Riversdale, Garcia State Forest.
3	Port Elizabeth	Port Elizabeth, Walmer, Van Stadens Wildflower Reserve; Uitenhague, Groendal Wilderness; Coega.
4	Alexandria	Alexandria, Alexandria Forest Station, Groenkop & Lidney Farms; Paterson.
5	Albany	Grahamstown; Bathurst; Port Alfred; Seymour; Somerset East.
6	King Williams Town	King Williams Town district; Ciskei, Berlin district.
7	East London	East London; Gonubie; Kidds Beach.
8	Umtata	Umtata.
9	Port St Johns	Port St Johns; Nqeleni.
10	Oribi Gorge	Oribi Gorge Nature Reserve; Ixopo, Cornhill Farm; Port Edward, Umtavuma Nature Reserve; Bizana; Hibberdene.
11	Umdoni	Scottburgh, Umdoni Golf Course; Vernon Crookes Nature Reserve.
12	Durban	Durban, University of Natal campus, Durban Country Club, Bluff, Glenwood.
13	Pietermaritzburg	Pietermaritzburg, Prestbury, Sweetwaters, Town Bush.
14	Karkloof	Karkloof forest; Howick; Hilton; Dargle, Kilgobbin Farm.
15	Estcourt	Estcourt, Petchange; Mooi River, De Hoek; Rosetta; Elandslaagte.
16	St. Lucia	St. Lucia; Mtubatuba, Dukuduku Forest; Ngoye forest; Charters Creek; Umfolozi Nature Reserve; Hluhluwe Nature Reserve; Mtunzini Nature Reserve.
17	Ubombo	Zululand, Ubombo and Ingwavuma.
18	Golden Gate	Golden Gate National Park; Harrismith, Summerslie and Waterfall farms; Clarens.
19	Heilbron	Heilbron, Vaalbank Farm; Parys, Roseberry Plain; Viljoensdrift, Kruisementfontein and Zandfontein farms.
20	Wakkerstroom	Wakkerstroom, Town and Tafelkop Farm (=Kastrol Nek); Amersfoort, Begin der Lyn.
21	Ermelo	Ermelo district, Municipal Nature Reserve; Carolina; Vlakfontein farm.
22	Belfast	Belfast, Palmer vlei, Swartkoppies and Wemmershuis farms; Dullstroom, Verloren-Vallei Nature Reserve.
23	Graskop	Graskop; Mariepskop.

5.3 RESULTS AND DISCUSSION

5.3.1 Non-geographic variation

5.3.1.1 Sex ratios

Golden moles are difficult to sex by external observation or manipulation, as both sexes have a single urogenital opening, and in males the penis is short while the testes are abdominal (Dobson 1882). It is thus possible that collectors in the past may have sexed individuals incorrectly, with a bias towards females. To test for such possible errors, I used 74 *A. hottentotus* collected in Durban during a two-year study of reproductive seasonality (Bernard *et al.* 1994). As reproductive tracts of these specimens were preserved, sexes could be determined with certainty. The sex ratio (male:female) of this sample was 1:0,85, which did not deviate significantly from parity ($X^2 = 0{,}500$; $p = 0{,}479$). Sex ratios for museum specimens originating from King Williams Town (1:0,82: $X^2 = 1{,}12$; $p = 0{,}290$; $n = 109$) and East London (1:0,8: $X^2 = 0{,}472$; $p = 0{,}492$; $n=36$) also did not deviate significantly from a 1:1 ratio. This suggests that the magnitude of error made by past collectors is negligible, that sex ratios in *A. hottentotus* are not skewed significantly in favour of either sex, and probably also do not vary markedly on a geographical basis.

5.3.1.2 Qualitative dental characters

Seventy of the 81 *A. hottentotus* specimens from Durban, and 115 of the 118 specimens from the King Williams Town district, display similar dental morphology, as follows:

I2 morphology - sectorial, with one main high cusp. A posterior accessory cusp is sometimes present in younger individuals (TW1-2), but is not apparent in older specimens (TW3-5), suggesting that its presence depends on the extent of toothwear. Simonetta's (1968:33) claim that this is a critical taxonomic character in chrysochlorids must thus be rejected.

Canine morphology - sectorial, with one high anterior cusp and a posterior, sloping cutting edge. Accessory cusplets are sometimes present in younger (TW2) specimens, but are eroded away in older individuals (TW4-5), and thus are of no taxonomic significance.

P1 morphology - sectorial, with a high paracone (P^1) or protoconid (P_1), and a sloping posterior edge for cutting. The parastyle/paraconid and mesostyle/metaconid are sometimes present, but poorly-developed. Teeth play mainly a cutting role, although in older individuals (TW4-5) where the paracone or protoconid is heavily eroded, a crushing function is probably also served.

P2 - M2 morphology - molariform, with the protoconid, metaconid and paraconid connected by well-developed crests to form a high, crushing trigonid basin. Talonids are present, and well-developed.

M3 - absent in all quadrants.

Twelve specimens from Durban display anomalous character states. In one female (TM39246, TW3), M3 are present and similar in morphology to other molars, although noticeably smaller. The upper right canine is unerupted in one male (TM40873, TW4), whereas four individuals show premolars and/or canines in the process of erupting whilst also having erupted and worn second molars. Two females (TM39423, TW3; TM40869, TW4) show heavy toothwear but lack M2 on either the left or right side, thus confirming the unusual sequence of tooth replacement in chrysochlorids. Five specimens (3 ♂: TM5274, TW3; TM39203, TW3; TM40868, TW3; 1 ♀: TM39423, TW3; Unknown sex: TM12516, TW2) have P1 that are pseudo-molariform or semi-molariform, with four distinct cusps (although a high trigon/trigonid basin is not formed). But, it is often difficult to distinguish these character states from the sectorial condition, since there is appreciable intergradation that may be attributed, in part, to differential toothwear.

Only three specimens from King Williams Town display unusual dental morphology. In one male (KM992, TW3), the first upper premolar and canine in one quadrant are teratologically fused to form a single, large tooth. Two other individuals (TM39457, female, TW4; KM1003, male, TW5) have premolars in the process of being replaced while the second molars are erupted with heavy toothwear.

This variability lends support to the observation, made with respect to *Amblysomus gunningi* by Ellerman *et al.* (1953), that dental characters in chrysochlorids show a high degree of plasticity, and that caution must be exercised when using these characters as taxonomic indicators. Dental variation is substantial in the Durban population (14,8% of specimens), but negligible in the King Williams Town sample (2,5% of specimens). This suggests that certain populations are more variable than others. Almost twice as many males as females exhibit anomalies in the Durban population, which further suggests a sexual trend in dental variability. Comparative analyses of larger population samples from throughout the range of *A. hottentotus* are required to establish whether this trends is real, or merely the result of sampling error.

5.3.1.3 Intra-population craniometric variation

Durban population

Two-way analyses of variance of 22 external and cranial measurements of males and females collected in the greater Durban area, and belonging to TW2-4 (Table 5.2), indicated significant ($p \leq 0{,}05$) sexual dimorphism in 17 (77%) of the characters, and significant age-related variation in four (18%) variables. Normality and homoscedasticity criteria were satisfied by the data.

Multivariate analysis of variance (MANOVA) of a selected subset of 11 cranial variables (reduced suite to increase sample sizes = ARB: anterior rostral breadth; MIO: mid inter-orbital breadth; ZMB: zygomatic breadth; IOW: infra-orbital width; GSL: greatest skull length; GSH: greatest skull height; IPG: interpterygoid width; PPL: post-palatal length; CPL: coronoid process length; APW: ascending process width; MDL: mandible length) indicated that the sex-toothwear groups differed significantly in size ($F_{(70,213)} = 1{,}91$; $p < 0{,}001$). MANOVA of males and females separately revealed that toothwear groups within each sex did not differ significantly (♂: $F_{(28,34)} = 1{,}49$; $p = 0{,}132$; ♀: $F_{(28,28)} = 1{,}26$; $p = 0{,}271$), but MANOVA of TW3 males and females indicated significant sexual dimorphism ($F_{(14,15)} = 3{,}05$; $p = 0{,}02$).

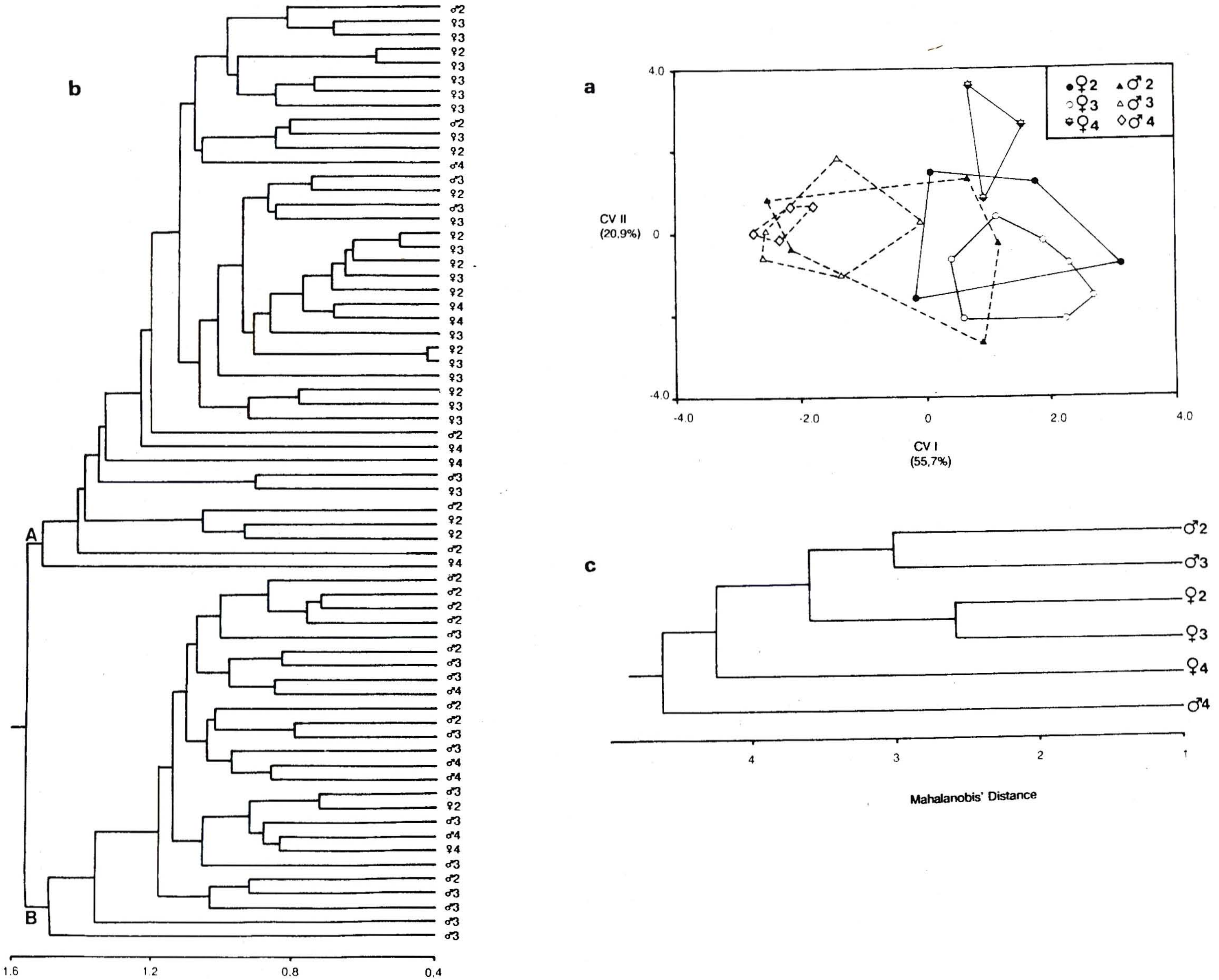
A six group discriminant function analysis produced a 71% overall *a posteriori* classification (♂: TW2(n = 13) - 62%, TW3(n = 15) - 80%, TW4(n = 5) - 80%; ♀: TW2(n = 10) - 70%, TW3(n = 15) - 53%, TW4 (n = 5) - 80%). Most misidentifications involved TW2 male and TW3 female specimens. In scattergrams of canonical variates I and II (Trace = 77%; Fig. 5.2a), males and females tended to plot

Table 5.2

Summary statistics and results of two-way analyses of variance to test for sexual dimorphism and age variation (toothwear classes 2-4) in *A. hottentotus* from Durban, KwaZulu-Natal. $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size; $^{\#}$ and * denote significance of *F* values at $p \leq 0{,}05$ and $p \leq 0{,}01$ respectively.

OTU	STAT	TL	HF	M	BCW	ARB	MIO	ZMB	IOW	GSL	GSH	P@P	PBM	PAL	MTL	IPG	PPL	EAM	BBW	FML	CPL	APW	MDL
♂ TW2	$\bar{x}$	124,3	16,0	55,2	5,07	4,85	8,35	16,59	7,28	26,69	12,81	7,56	4,91	13,37	6,68	2,35	8,92	1,38	11,76	4,66	7,21	4,41	16,77
	sd	11,6	1,0	12,8	0,36	0,29	0,40	0,73	0,28	0,93	0,40	0,24	0,25	0,73	0,28	0,17	0,44	0,11	0,64	0,23	0,32	0,26	0,78
	n	11	13	10	12	13	13	13	13	13	13	13	11	12	13	13	13	12	13	13	13	13	13
♂ TW3	$\bar{x}$	127,6	15,31	57,09	5,33	5,05	8,31	17,00	7,50	27,00	13,04	7,70	4,96	13,61	6,74	2,37	8,95	1,35	11,94	4,65	7,29	4,61	17,14
	sd	9,9	1,3	8,5	0,26	0,18	0,28	0,53	0,26	0,65	0,27	0,20	0,31	0,36	0,23	0,17	0,33	0,14	0,45	0,26	0,32	0,22	0,45
	n	14	13	11	13	15	15	15	15	15	15	13	14	14	14	15	15	10	12	15	15	15	15
♂ TW4	$\bar{x}$	133,5	16,2	59,4	5,33	5,10	8,41	17,32	7,58	26,82	13,21	7,66	4,93	13,58	6,57	2,34	8,97	1,31	12,12	4,66	7,15	4,66	17,19
	sd	10,0	14,8	7,6	0,34	0,29	0,31	0,69	0,20	0,94	0,52	0,33	0,19	0,62	0,14	0,11	5,24	0,12	0,39	0,18	0,27	0,18	0,67
	n	6	5	5	5	5	5	5	5	5	5	5	4	5	4	5	5	5	5	5	5	5	5
♀ TW2	$\bar{x}$	120,9	15,0	44,0	4,78	4,75	8,26	16,16	7,16	25,90	12,57	7,40	4,91	12,92	6,60	2,27	8,71	1,33	11,44	4,49	7,04	4,20	16,64
	sd	7,8	1,8	9,0	0,33	0,23	0,31	0,42	0,24	0,48	0,27	0,16	0,27	0,30	0,20	0,14	0,18	0,08	0,49	0,16	0,27	0,21	0,43
	n	11	11	7	10	11	11	11	11	10	11	11	11	11	11	11	11	11	10	11	11	11	11
♀ TW3	$\bar{x}$	123,0	15,1	44,6	4,71	4,86	8,25	16,19	7,22	25,93	12,56	7,42	4,93	12,89	6,47	2,31	8,64	1,39	11,44	4,58	6,92	4,20	16,37
	sd	8,3	0,8	3,1	0,14	0,17	0,26	0,43	0,20	0,56	0,25	0,21	0,20	0,35	0,27	0,16	0,26	0,13	0,42	0,21	0,24	0,22	0,48
	n	15	14	11	14	16	16	16	16	16	16	16	16	16	15	16	16	15	15	15	16	16	16
♀ TW4	$\bar{x}$	124,5	14,7	46,8	4,65	4,89	8,37	16,25	7,43	26,20	12,62	7,16	4,63	13,02	6,30	2,27	8,93	1,34	11,55	4,50	7,12	4,44	16,79
	sd	14,0	1,5	4,6	0,31	0,14	0,30	0,58	0,11	0,40	0,26	0,26	0,38	0,23	0,19	0,19	0,25	0,11	0,33	0,25	0,21	0,08	0,44
	n	6	6	6	6	5	6	6	6	5	6	6	4	5	5	6	5	4	5	6	6	6	6
SEX	*F*	3,72	5,72*	25,63*	46,68*	7,61*	0,738	25,89*	10,37*	26,71*	13,24*	24,32*	0,71	26,04*	10,94*	3,27	8,24*	0,01	12,05*	4,37$^{\#}$	12,27*	31,24*	11,82*
TW	*F*	1,57	0,52	0,26	0,40	4,20$^{\#}$	0,48	1,63	5,44*	0,23	3,88$^{\#}$	2,11	1,22	0,35	2,92	0,26	0,95	0,26	0,70	0,15	0,16	4,36$^{\#}$	0,93
INT	*F*	0,33	1,19	0,12	2,85	0,33	0,02	1,56	0,79	0,61	3,26$^{\#}$	2,35	0,95	0,57	1,16	0,02	0,72	0,37	0,38	0,47	1,74	1,88	2,29

Fig. 5.2. Intrapopulation phenetic relationships among specimens of male and female *A. hottentotus* from Durban, and belonging to three toothwear classes (TW 2-4), as indicated by: a) pairwise comparison of the first two canonical variate axes from a six-group discriminant functions analysis; b) a distance phenogram based on single standardized data (co-phenetic correlation = 0,821); and c) cluster analysis (UPGMA) of Mahalanobis' distances between group centroids in multidimensional discriminant space.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0
-4.0
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-2.0
0
2.0
4.0
CV I
(55,7%)
c
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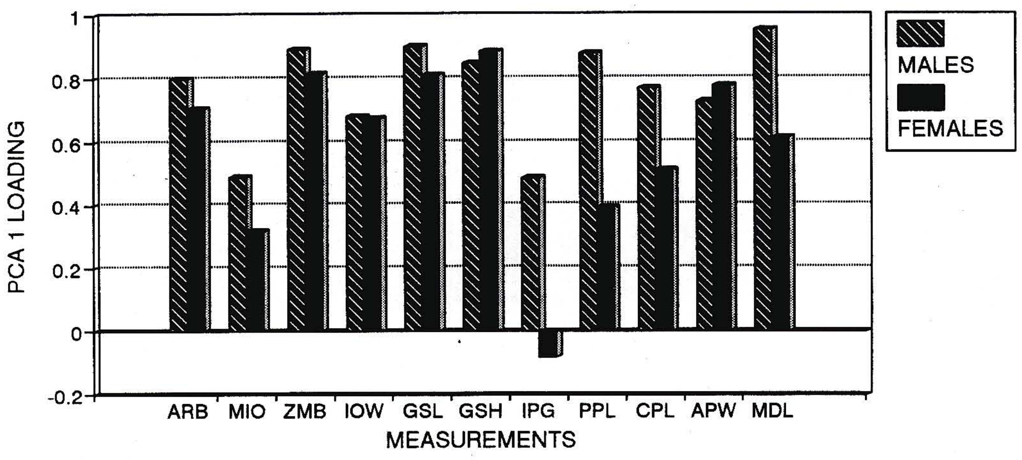
♀2
♀3
♀4
♂4
4
3
2
1
Mahalanobis' Distance

apart, but the toothwear groups within each sex overlapped broadly. A similar result was evident in a scattergram comparing the first three principal component axes (not illustrated).

Cluster analysis of all specimens with a complete suite of 19 cranial characters, and based on average taxonomic distances, divided the specimens into two major phena (Fig. 5.2b). The one major phenon (Cluster A, $n = 40$) contained 78% ($^{31}/_{40}$) of all female specimens, and the other (Cluster B, $n = 26$) contained 73% ($^{24}/_{33}$) of all male specimens. Sex ratios within and between clusters differed significantly from parity ($X^2 = 27{,}99$; $p < 0{,}001$), but the number of TW2-4 specimens between the two major clusters did not deviate significantly from a 1:1:1 ratio ($X^2 = 0{,}39$; $p = 0{,}82$). No detectable sub-clustering on the basis of toothwear was evident. Cluster analysis of group centroids from discriminant functions analysis, based on Mahalanobis' distances, resulted in the TW2 and TW3 classes clustering together for each sex, whereas the male and female TW4 classes separated from the other groups at high distances exceeding 4,0 (Fig. 5.2c).

Male and female *A. hottentotus* from Durban thus differ in cranial length (PAL, GSL, PPL, MTL), width (ARB, IOW, ZMB, P@P, BBW) and height (GSH), mandible robustness (CPL, APW, MDL) and claw size (BCW), with males being larger. Differences between males and females are not purely isometric, however, since there are subtle differences in the relative proportions of some parts of the skull regardless of size. Scrutiny of eigenvector coefficients from the PCA analyses (Fig. 5.3) showed that the first component (which explains 49,8% of the phenetic variation in males, and 56,3% in females) was an overall size component, as indicated by the high, positive loadings for most variables. But, this vector also reflected shape differences between males and females in the orofacial frontal and oral subunits, as indicated by the low and/or negative loadings for MIO and IPG. IPG and MIO are similar in magnitude in both sexes (Table 5.2), in contrast to other measurements which are significantly larger in males than females. Male specimens are thus characterized by slightly narrower interpterygoid widths (IPG:ZMB), and significantly smaller inter-orbital widths (MIO:ZMB) than females (Table 5.3). In the second (male) and third (female) components, IPG was contrasted with MIO, which reflects proportional differences between the sexes with the ratio of IPG:MIO being slightly (but not significantly)

Fig. 5.3. Within-group eigenvector coefficients for the first three principal component axes, based on 11 measurements of male and female *A. hottentotus* samples (TW 2 - 4 combined) from Durban.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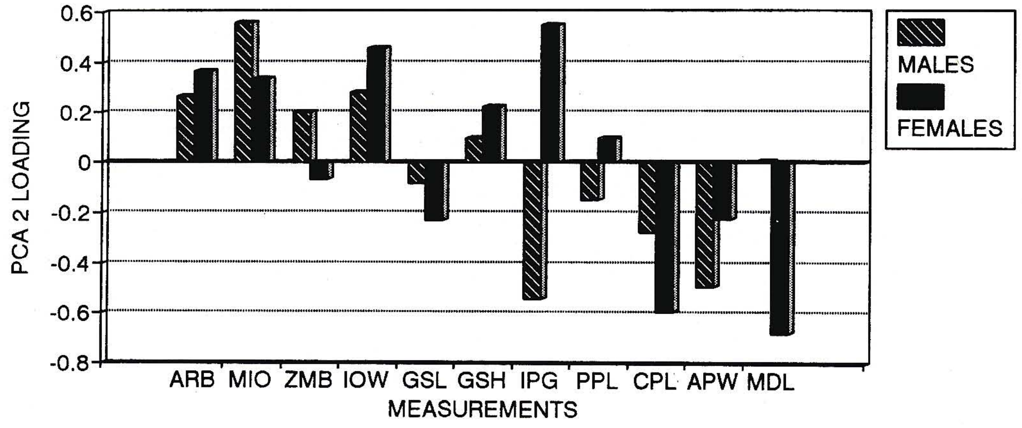
MEASUREMENTS
MALES
FEMALES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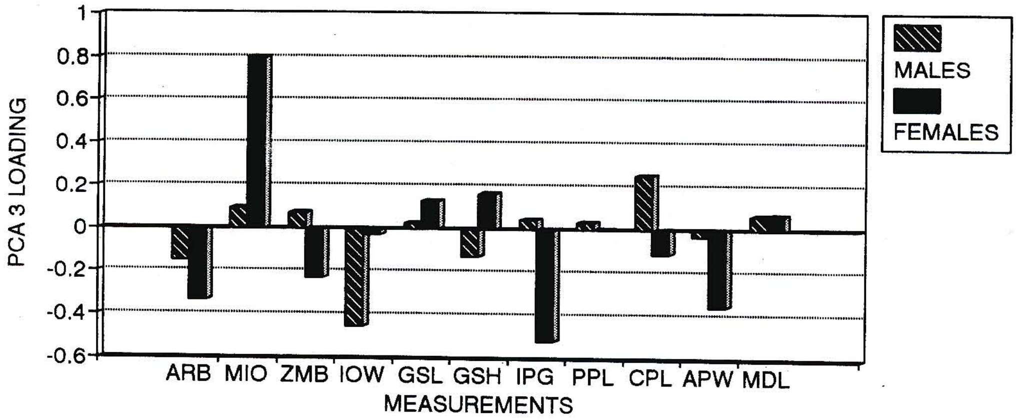
PCA 2 LOADING
ARB MIO ZMB IOW GSL GSH IPG PPL CPL APW MDL
MEASUREMENTS
MALES
FEMALES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PCA 3 LOADING
ARB MIO ZMB IOW GSL GSH IPG PPL CPL APW MDL
MEASUREMENTS
MALES
FEMALES

Table 5.3

Selected cranial ratios (expressed as percentages) and results of *t*-tests for male and female *A. hottentotus* (TW 2 - 4 combined) from Durban, KwaZulu-Natal. *n* = sample size; $\overline{x}$ = arithmetic mean; *sd* = standard deviation; *t* = Student's *t* statistic; *p* = probability.

			STATISTICS				
RATIO	SEX	*n*	$\overline{x}$	*sd*	RANGE	*t*	*p*
MIO/ZMB	M	33	49,4	1,8	44,7-53,8		
	F	29	51,1	2,1	46,5-54,7	3,415	<0,01
IPG/ZMB	M	33	14,0	1,0	11,9-15,8		
	F	30	14,2	1,0	12,1-16,5	0,759	0,451
IOW/ZMB	M	33	44,0	1,3	41,1-46,7		
	F	33	44,7	1,3	42,1-47,0	2,297	<0,05
IPG/MIO	M	33	28,3	2,2	24,2-33,6		
	F	33	27,6	2,0	23,4-32,5	1,229	0,223
APW/MDL	M	33	26,7	1,1	24,5-28,6		
	F	33	25,7	1,0	23,5-27,3	3,980	<0,01

greater in males than females. Similarly, differences in the loading patterns for IOW and mandible characters (APW, CPL, MDL) on the second and third principal components emphasized the existence of subtle sexual differences in shape, with males exhibiting significantly narrower rostra (IOW:ZMB) and more robust mandibular rami (APW:MDL) than females (Table 5.3).

Sexual variation in the cranial dimensions of *A. hottentotus* from Durban thus involves mainly dimorphism, complemented by subtle allometric differences in cranial shape, particularly in the facial and mandibular regions.

Age-related variation in Durban *A. hottentotus* is less marked than sexual dimorphism, and the toothwear groups within each sex do not differ markedly in most individual measurements, or in combinations of measurements. Age related changes involve mainly a slight increase in cranial width (ARB, IOW) and height (GSH), and also mandible size (APW), without any significant change in shape. The tendency for MTL to become smaller with age in both sexes is the direct result of the reduction in medial-distal length of the cheekteeth with increasing occlusal attrition, and thus is an artefact of the ageing regime employed.

King Williams Town population

Two-way analyses of variance of 22 external and cranial variables for TW2-4 specimens indicated significant sexual dimorphism in nine (40%) measurements (Table 5.4), and significant differences between the toothwear classes in four (18%) of measurements. MANOVA using the reduced suite of 11 measurements (see above) indicated that differences between the sex-toothwear groups were not significant ($F_{(55,197)} = 1{,}28$; $p = 0{,}12$). A six-group multiple discriminant function analysis produced an overall *a posteriori* classification of 58,3% (♂: TW2(n = 10) - 20%, TW3(n = 12) - 75%, TW4(n = 4) - 50%; ♀: TW2(n = 20) - 60%, TW3(n = 9) - 78%, TW4(n = 3) - 67%), indicating poor differentiation between the sex-age classes. Most mis-identifications involved male and female TW2 specimens. In scattergrams of principal components I and II (Trace = 79,7%; Fig. 5.4a), and canonical variates I and II (not illustrated), the sex-toothwear groups overlapped broadly.

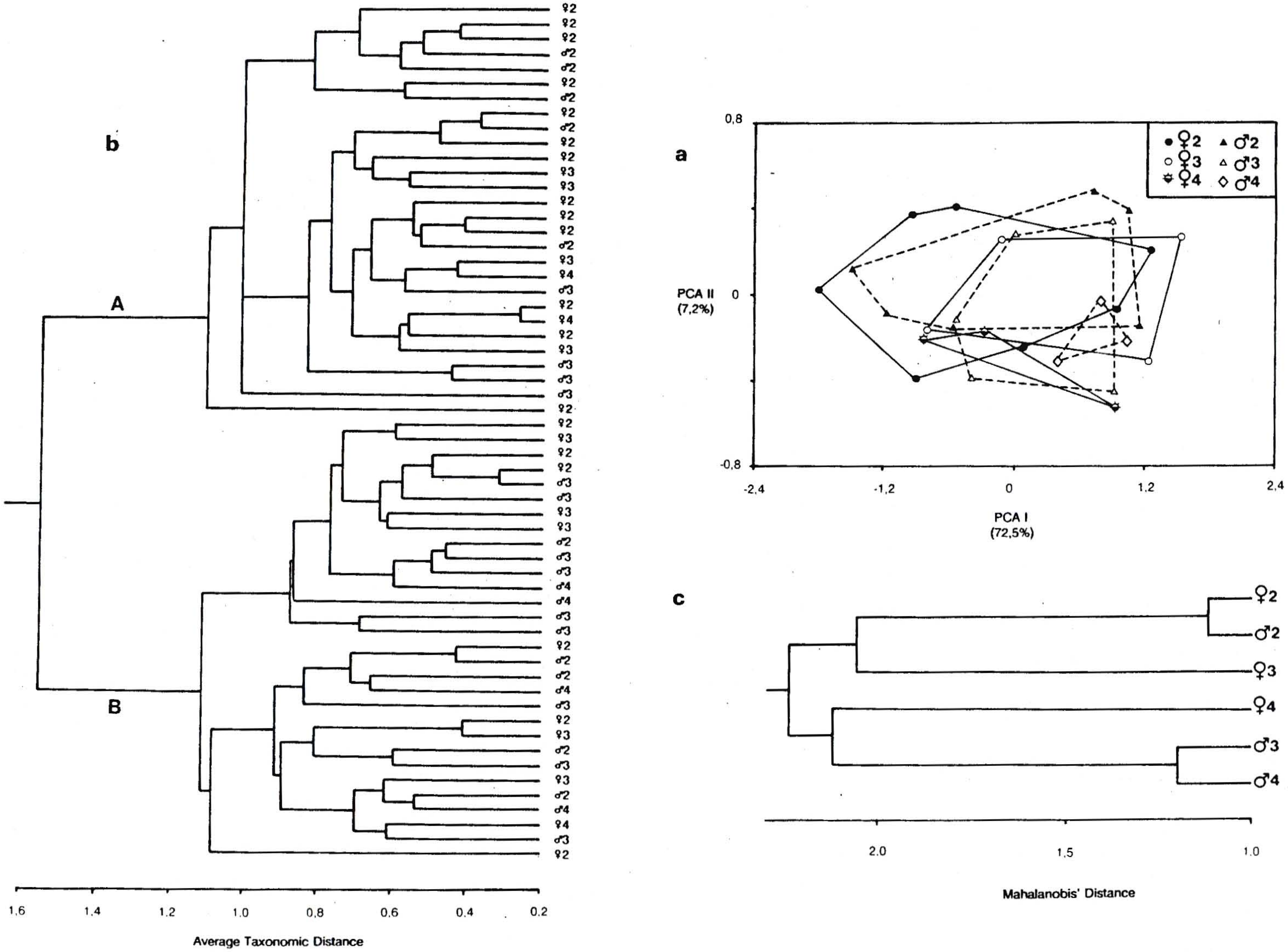
Cluster analysis of the King Williams Town specimens, based on average taxonomic distances, divided the specimens into two major phena (Fig. 5.4b). One of these (Cluster A, n = 28) contained 61% and 33% of all female and male specimens

Table 5.4

Summary statistics and results of two-way analyses of variance to test for sexual dimorphism and age variation (toothwear classes 2-4) in *A. hottentotus* from King Williams Town, Eastern Cape Province. Slashes indicate samples that were too small (n = 1) for the computation of statistics. $\overline{x}$ = arithmetic mean; *sd* = standard deviation; n = sample size; # and * denote significance of F values at $p \leq 0,05$ and $p \leq 0,01$ respectively.

OTU	STAT	TL	HF	BCW	ARB	MIO	ZMB	IOW	GSL	GSH	P@P	PBM	PAL	MTL	IPG	PPL	EAM	BBW	FML	CPL	APW	MDL
♂ TW2	$\overline{x}$	126,7	14,9	5,48	5,01	8,18	16,48	7,35	26,95	13,11	7,50	5,04	13,23	6,72	2,10	8,61	1,34	11,82	4,79	7,22	4,12	16,77
	sd	15,6	1,1	0,47	0,37	0,36	1,04	0,45	2,09	0,49	0,43	0,30	0,60	0,26	0,12	0,38	0,13	0,69	0,41	0,42	0,72	0,75
	n	10	10	16	17	17	18	18	18	18	18	15	18	15	18	18	10	17	11	17	16	18
♂ TW3	$\overline{x}$	123,1	14,1	5,67	5,16	8,29	16,84	7,53	26,96	13,32	7,55	5,01	13,41	6,49	2,16	8,62	1,39	12,26	4,81	7,17	4,57	16,91
	sd	5,4	1,2	0,34	0,18	0,34	0,54	0,34	0,79	0,38	0,31	0,24	0,51	0,18	0,14	0,29	0,19	0,52	0,22	0,32	0,34	0,48
	n	9	9	16	14	17	17	17	17	17	17	15	16	16	17	17	11	16	17	17	17	16
♂ TW4	$\overline{x}$	124,0	/	5,85	5,27	8,32	17,06	7,49	26,98	13,43	7,55	4,86	13,24	6,32	2,16	8,60	/	12,31	4,91	7,23	4,66	16,90
	sd	8,5	/	0,44	0,21	0,22	0,91	0,28	0,98	0,55	0,10	0,23	0,57	0,38	0,21	0,42	/	0,83	0,24	0,21	0,14	0,60
	n	2	/	4	4	5	5	5	5	5	5	5	5	5	5	5	/	5	5	5	5	5
♀ TW2	$\overline{x}$	115,9	13,8	5,32	4,92	8,14	16,26	7,07	26,59	12,94	7,27	4,85	13,03	6,40	2,14	8,54	1,35	11,56	4,81	7,07	4,43	16,46
	sd	8,3	1,7	0,31	0,30	0,32	0,88	0,43	1,07	0,47	0,38	0,43	0,61	0,29	0,18	0,41	0,10	0,82	0,25	0,47	0,42	0,71
	n	20	19	22	21	21	22	22	21	22	21	11	20	12	22	22	21	22	22	21	22	22
♀ TW3	$\overline{x}$	116,5	14,3	5,45	5,05	8,39	16,24	7,31	26,77	13,05	7,38	4,89	13,23	6,33	2,21	8,50	1,35	11,71	4,72	7,09	4,62	16,58
	sd	6,7	1,2	0,28	0,27	0,33	0,75	0,25	0,89	0,36	0,32	0,26	0,60	0,33	0,14	0,32	0,11	0,51	0,21	0,31	0,37	0,68
	n	13	12	13	12	12	13	13	12	13	13	8	11	9	13	13	11	12	13	13	13	13
♀ TW4	$\overline{x}$	110,8	/	5,38	5,11	8,21	16,69	7,45	24,46	13,01	7,32	4,80	12,88	6,29	2,27	8,77	/	12,04	4,73	7,18	4,50	16,71
	sd	13,0	/	0,12	0,36	0,39	0,93	0,33	0,80	0,33	0,21	0,31	0,53	0,20	0,16	0,43	/	0,57	0,09	0,47	0,32	0,43
	n	4	/	4	4	3	4	4	4	4	5	4	4	3	4	4	/	2	4	4	4	4
SEX	*F*	12,59*	1,49	8,36*	2,92	0,06	4,67#	9,05*	2,27	6,90#	6,83#	3,08	2,83	7,85*	1,50	0,58	0,22	7,52*	0,61	1,48	1,04	4,56#
TW	*F*	0,52	0,01	2,82	2,99	2,24	1,73	4,25#	0,16	2,05	0,73	0,68	1,26	3,88#	2,10	0,33	0,49	3,34#	0,21	0,13	3,69#	0,72
INT	*F*	0,43	2,45	0,71	0,07	0,56	0,47	0,49	0,15	0,38	0,10	0,16	0,12	1,13	0,23	0,51	0,36	0,54	0,57	0,11	1,32	0,07

Fig. 5.4. Intrapopulation phenetic relationships among specimens of male and female *A. hottentotus* belonging to three toothwear classes (TW 2 - 4), and originating from King Williams Town, as indicated by: a) pairwise comparison of the first two principal component axes (cophenetic correlation = 0,989); b) a phenogram based on average taxonomic distance coefficients computed from single standardized data (co-phenetic correlation = 0,703); and c) cluster analysis (UPGMA) of Mahalanobis' distance between group centroids in multidimensional discriminant space.


b
A
B
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♀2
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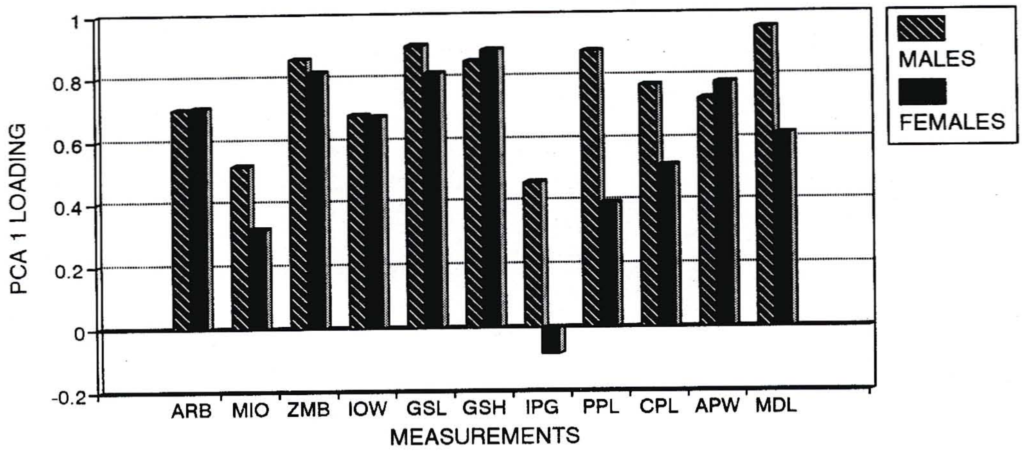
♂3
♀2
1,6
1,4
1,2
1,0
0,8
0,6
0,4
0,2
Average Taxonomic Distance
a
0,8
0
-0,8
PCA II
(7,2%)
-2,4
-1,2
0
1,2
2,4
PCA I
(72,5%)
● ♀2
○ ♀3
✡ ♀4
▲ ♂2
△ ♂3
◇ ♂4
c
♀2
♂2
♀3
♀4
♂3
♂4
2.0
1.5
1.0
Mahalanobis' Distance

Fig. 5.5. Within-group eigenvector coefficients for the first three principal component axes for male and female *A. hottentotus* samples (TW 2 - 4 combined) from King Williams Town, based on analyses of 11 measurements.


PCA 1 LOADING
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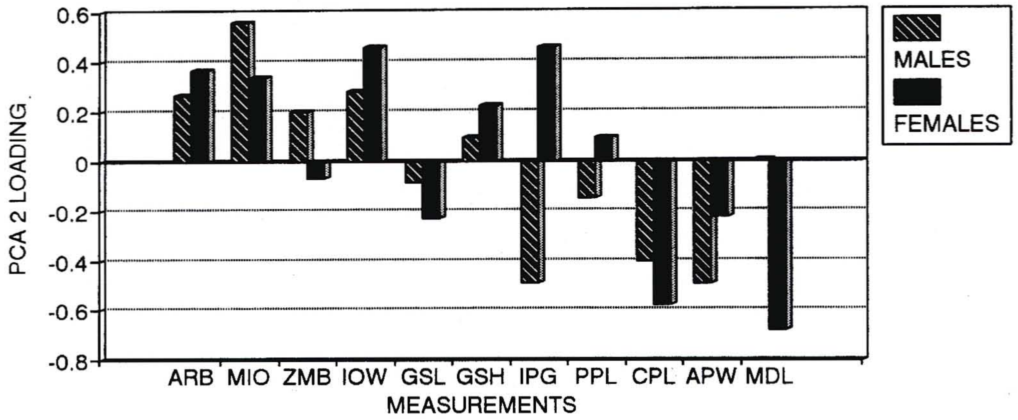
0.8
0.6
0.4
0.2
0
-0.2
ARB
MIO
ZMB
IOW
GSL
GSH
IPG
PPL
CPL
APW
MDL
MEASUREMENTS
MALES
FEMALES


PCA 2 LOADING
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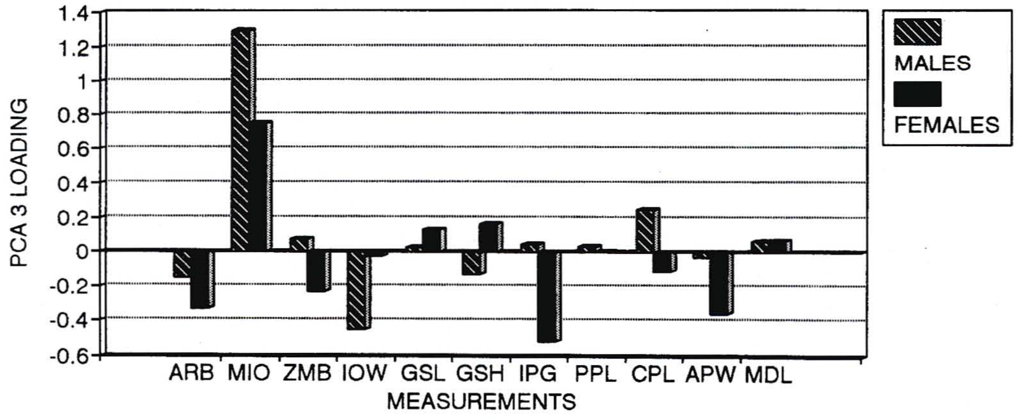
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
ARB
MIO
ZMB
IOW
GSL
GSH
IPG
PPL
CPL
APW
MDL
MEASUREMENTS
MALES
FEMALES


PCA 3 LOADING
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
ARB
MIO
ZMB
IOW
GSL
GSH
IPG
PPL
CPL
APW
MDL
MEASUREMENTS
MALES
FEMALES

vary geographically, shape differences between the sexes are less plastic, and subject to greater epigenetic constraint.

The existence of significant sexual size and shape dimorphism in *A. hottentotus* from both populations necessitated that the sexes be considered separately during analyses of geographic variation.

5.3.2 Geographic variation

5.3.2.1 Qualitative dental characters

In his key to the Chrysochloridae, Meester (1974) stated that there are normally only nine upper and lower teeth in each jaw half in *Amblysomus*, and that if a tenth tooth (M3) is present (as in *A. gunningi*), it differs in morphology from the other molars. Of the 615 *A. hottentotus* specimens examined, seven (1,1%) have either an M^3 and/or an M_3 that is similar to the other molars in morphology, although noticeably smaller. One specimen (NMB5242; TW5) has peg-like M3, but this appears to be the result of extremely heavy toothwear. Two specimens (TM6676, TM39246) possess M3 on both sides, while another three (TM5272, TM6675, TM20140) have M^3 on only one side. One specimen (TM41600) from Wakkerstroom has both M^3 but lacks M_3, whereas a specimen from Elliot (NMB5242) has an M^3 on the left side, and an M_3 on the right. When present, M3 are small and distinctly triconid, although in older individuals these teeth may be reduced to a stump by heavy toothwear.

The occurrence and morphology of a third molar is thus variable, not only between individuals, but also within the jaw quadrants of the same specimens. The seven specimens showing third molars emanate from six distant localities (Port Elizabeth, $n = 1$; Umtata, $n = 1$; Albany, $n = 2$; Durban, $n = 1$; East London, $n = 1$; Wakkerstroom, $n = 1$), indicating that the presence of this tooth is random, rather than the manifestation of any geographic pattern in dental variability.

The morphology of P1 has also been used for diagnostic purposes (Meester 1974), to distinguish *Calcochloris* (P1 molariform) from *Amblysomus* (P1 triconid and sectorial - see Section 2.2.3). Eighteen (2,9%) of the specimens examined (Durban, $n = 5$; Port Elizabeth, $n = 1$; St. Lucia, $n = 1$; Graskop, $n = 11$; all TW2-4) have first premolars that are pseudo-molariform, being elevated to nearly the height of the other premolars, with four distinct cusps and a small posterior occlusal basin.

However, a well-developed trigon/trigonid basin analogous to that in other cheekteeth is not formed, and a posteriorly-sloping cutting edge is present (Fig. 2.2). These teeth appear to play both a cutting and crushing role. Since such premolars are found within widely-separated populations, variability in this character is apparently the result of localized variation, rather than geographic differentiation.

Variation in the morphology of P1 may be due, at least partly, to variable toothwear. In the Graskop sample, seven specimens belonging to TW2 show semi-molariform P_1, whereas the remaining four specimens belong to TW3-4 and have sectorial P_1 owing to attrition of the paraconid and metaconid. Conversely, nine of the specimens in this sample have semi-molariform P^1, and two show the pseudo-molariform condition, but these differences are not correlated with toothwear class, and thus cannot be attributed to dental attrition. Furthermore, there does not appear to be any direct correlation between P^1 and P_1 morphology, if toothwear is taken into account. Of the three Graskop specimens belonging to TW3, one has pseudo-molariform P^1 and semi-molariform P_1, one displays pseudo-molariform P^1 but sectorial P_1, while the third has semi-molariform P^1 and sectorial P_1. This implies that while toothwear may modify the appearance of $P^1{}_1$, other factors also underlie the apparent plasticity of this character. These could include the unusual sequence of tooth replacement found in chrysochlorids, so that deciduous and permanent premolars with differing morphologies may occur together in the same individual (Broom 1916b), and scoring difficulty owing to appreciable intergradation between the three character states. Variation in P1 morphology within *A. hottentotus* is, therefore, of little systematic importance, and the preponderance of pseudo- or semi-molariform first premolars in the Graskop sample is not taxonomically significant.

Eleven (1,8%) specimens have canines or premolars in the process of erupting, whilst also having second molars with considerable toothwear. These specimens originated from six widely-separated localities (Alexandria, $n = 2$; King Williams Town, $n = 2$; Albany, $n = 1$; Oribi, $n = 1$; Durban, $n = 4$; Belfast, $n = 1$). The atypical sequence of tooth replacement previously demonstrated in the Durban and King Williams Town OTUs (Section 5.3.1.2) thus occurs in other samples as well, and probably exists to a greater or lesser extent is all populations.

Lundholm (1955) noted that the occurrence of protocones on $P^{2\text{-}3}$ is variable in *A. h. marleyi* from Ubombo and Ingwavuma. Of the 15 specimens examined from these localities, 12 have distinct protocones on P^2 and P^3 (TW2 *n* = 3, TW3 *n* = 6, TW4 *n* = 3), while two specimens, including the holotype (TM5578, TW2), lack protocones on P^2. One individual (TM5583, TW2) lacks protocones on the P^3 as well. The holotype of *A. h. marleyi* is thus teratological. All of the other (603 = 98%) specimens examined have well-developed protocones on $P^{2\text{-}3}$, so intra-specific variability in this character is restricted to the Ubombo and Ingwavuma populations.

With regard to the presence of talonids on the lower cheekteeth, Lundholm (1955:287) noted that talonids are sometimes weakly-developed, or absent, in *Amblysomus*. The majority of specimens examined have well-developed talonids on the lower premolars and molars. Only three individuals (TM40781, TM40790, TM42131) show feeble talonids, and these originated from Graskop at the extreme north of the species' range.

Two other specimens display unique dental anomalies. In KM992 (♂ TW3), the first upper premolar and canine in one quadrant are fused to form a single large tooth, while TM8995 from Grootvadersbosch lacks erupted teeth altogether, but has the cranial dimensions of an adult. These specimens are clearly teratological.

Dental variability in *A. hottentotus* therefore appears to be randomly determined and localized rather than geographic in nature, and is negligible in that very few individuals (0,5% - 2,2%) show anomalies when specimens from across its range are considered. With the exception of the Graskop and Ubombo OTUs, more than 95% of specimens have dental characters that are typical for the species. Since no other golden mole species are known to occur at either Graskop or Ubombo, dental characters can be used with confidence for diagnostic purposes.

5.3.2.2 Univariate analyses

Summary statistics and the results of one-way analyses of variance for 19 measurements of male and female *A. hottentotus* from 23 OTUs are given in Tables 5.5 and 5.6. In both sexes, all measurements differed significantly ($p < 0{,}001$) among the OTUs, and were characterized by broadly-overlapping non-significant subsets. This indicates that size variation is gradual, rather than discontinuous.

Table 5.5

Summary statistics of one external (BCW) and 18 cranial measurements in 23 pooled locality samples of female *A. hottentotus*, and *F* statistics from single-classification ANOVA of OTU means. p = significance of F values; $\overline{x}$ = sample mean; *sd* = standard deviation; n = sample size. Vertical lines denote maximally non-significant subsets indicated by SNK multiple comparisons tests.

BCW ($F = 20{,}117$; $p < 0{,}001$)

Loc	$\overline{x} \pm sd\ (n)$	Range
17	3,91±0,17(7)	3,70-4,20
16	4,41±0,22(8)	4,11-4,77
12	4,72±0,24(31)	4,06-5,41
2	4,97±0,30(4)	4,72-5,35
5	4,98±0,26(8)	4,62-5,46
4	4,98±0,41(8)	4,05-5,37
9	5,05±0,45(7)	4,66-5,97
1	5,12±0,27(5)	4,78-5,38
11	5,12±0,13(5)	4,89-5,23
3	5,14±0,38(7)	4,43-5,66
8	5,16±0,24(5)	4,85-5,52
23	5,19±0,24(3)	4,97-5,52
7	5,26±0,31(14)	4,59-5,69
19	5,28±0,17(5)	4,99-5,42
6	5,38±0,29(42)	4,79-5,93
10	5,61±0,39(9)	5,29-6,58
13	5,72±0,49(6)	4,89-6,27
20	5,72±0,27(10)	5,21-6,10
14	5,73±0,30(8)	5,51-6,17
18	5,77±0,29(5)	5,45-6,22
21	5,77±0,49(5)	5,41-6,31
15	5,81±0,33(6)	5,34-6,17
22	5,88±0,27(14)	5,26-6,19

Table 5.5 (cont.)

FML ($F = 7{,}651$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
16	4,35±0,17(7)	4,19-4,64
17	4,40±0,14(7)	4,18-4,61
2	4,52±0,08(3)	4,48-4,99
12	4,54±0,21(32)	4,22-4,92
11	4,63±0,09(5)	4,49-4,73
1	4,64±0,13(5)	4,43-4,78
5	4,64±0,24(8)	4,29-5,11
8	4,65±0,24(7)	4,37-5,04
3	4,67±0,25(7)	4,32-4,99
10	4,68±0,23(10)	4,29-5,09
4	4,68±0,12(9)	4,47-4,83
6	4,77±0,23(39)	4,19-5,22
19	4,84±0,17(5)	4,70-5,08
9	4,86±0,19(5)	4,64-5,15
7	4,87±0,20(12)	4,49-5,19
15	4,87±0,25(6)	4,55-5,14
18	4,88±0,36(5)	4,58-5,51
20	4,92±0,21(15)	4,47-5,28
23	4,93±0,09(3)	4,85-5,05
14	4,98±0,20(7)	4,70-5,24
22	4,99±0,17(14)	4,63-5,27
21	5,01±0,29(8)	4,53-5,05
13	5,04±0,34(9)	4,75-5,66

ARB ($F = 6{,}705$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	4,23±0,23(7)	3,87-4,51
1	4,60±0,28(5)	4,29-4,98
16	4,64±0,20(8)	4,43-5,01
3	4,65±0,24(7)	4,27-4,87
23	4,71±0,20(3)	4,51-4,99
5	4,78±0,17(8)	4,51-5,04
8	4,80±0,15(7)	4,61-5,02
11	4,81±0,09(5)	4,71-4,95
10	4,83±0,26(10)	4,56-5,39
12	4,83±0,19(34)	4,26-5,23
19	4,84±0,20(5)	4,55-5,04
4	4,86±0,27(9)	4,33-5,22
2	4,87±0,24(4)	4,68-5,17
21	4,89±0,36(5)	4,61-5,23
7	4,96±0,35(11)	4,41-5,55
6	4,98±0,30(37)	4,42-5,58
20	5,04±0,22(15)	4,65-5,44
14	5,10±0,19(7)	4,85-5,38
22	5,12±0,23(14)	4,75-5,50
18	5,17±0,30(5)	4,64-5,34
15	5,17±0,23(6)	4,91-5,49
13	5,23±0,30(9)	4,77-5,68
9	5,30±0,20(5)	5,00-5,51

MIO ($F = 15{,}763$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	6,82±0,31(7)	6,51-7,19
2	7,74±0,22(4)	7,52-8,03
3	7,88±0,27(7)	7,60-8,33
5	7,89±0,28(8)	7,43-8,14
16	8,00±0,23(8)	7,70-8,36
1	8,01±0,17(5)	7,75-8,15
8	8,09±0,32(7)	7,61-8,41
4	8,09±0,34(9)	7,75-8,75
23	8,19±0,28(3)	7,86-8,55
6	8,20±0,33(37)	7,62-8,90
10	8,20±0,34(10)	7,82-8,90
7	8,26±0,54(12)	7,04-8,78
12	8,27±0,28(35)	7,47-8,75
11	8,29±0,38(5)	7,71-8,77
9	8,38±0,14(5)	7,82-8,90
14	8,76±0,28(7)	8,39-9,04
15	8,82±0,51(6)	8,35-9,76
19	8,88±0,26(5)	847-9,08
13	8,94±0,69(9)	8,12-9,79
21	8,96±0,26(5)	8,48-8,99
20	9,01±0,32(15)	8,47-9,56
18	9,05±0,55(5)	8,21-9,57
22	9,15±0,36(14)	8,21-9,63

ZMB ($F = 9{,}935$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	14,43±0,54(7)	13,91-15,48
2	15,22±0,04(3)	15,19-15,26
1	15,44±0,15(5)	15,29-15,63
5	15,64±0,42(8)	15,11-16,23
16	15,80±0,61(7)	15,26-17,11
3	15,98±0,77(7)	15,13-17,11
12	16,20±0,45(35)	15,48-17,35
11	16,24±0,42(5)	15,62-16,56
23	16,24±0,21(3)	15,97-16,49
7	16,29±0,74(12)	14,96-17,60
6	16,29±0,82(39)	14,60-18,02
10	16,33±0,83(9)	15,46-17,99
4	16,36±0,58(9)	15,67-17,44
8	16,39±0,35(7)	15,82-16,77
19	16,58±0,35(5)	16,09-16,96
14	17,00±0,67(6)	16,44-18,06
9	17,12±0,08(5)	17,00-17,20
13	17,12±0,99(9)	16,20-19,07
20	17,16±0,73(15)	16,16-18,95
15	17,17±0,37(6)	16,68-17,65
18	17,31±0,63(5)	16,59-18,24
22	17,56±0,56(14)	16,60-18,24
21	17,60±0,75(4)	16,93-18,36

IOW ($F = 6{,}299$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	6,70±0,37(7	6,23-7,22
8	6,90±0,21(7)	6,55-7,14
11	7,08±0,28(5)	6,78-7,47
2	7,10±0,39(4)	6,61-7,54
7	7,17±0,38(12)	6,63-7,70
6	7,17±0,37(39)	6,34-8,08
16	7,20±0,37(8)	6,79-7,83
1	7,23±0,24(5)	7,06-7,63
10	7,23±0,39(10)	6,69-7,71
5	7,24±0,18(8)	7,05-7,55
23	7,26±0,18(3)	7,11-7,51
12	7,27±0,26(35)	6,51-7,95
3	7,32±0,25(7)	6,93-7,63
9	7,38±0,09(5)	7,24-7,47
4	7,44±0,28(9)	6,98-7,99
15	7,50±0,33(6)	7,11-7,96
14	7,52±0,36(7)	7,20-8,19
19	7,58±0,31(5)	7,16-7,95
20	7,63±0,26(15)	7,29-8,10
18	7,68±0,44(5)	7,09-8,27
21	7,78±0,09(4)	7,65-7,81
13	7,82±0,47(9)	7,30-8,68
22	7,86±0,34(14)	7,25-8,34

GSL ($F = 24{,}617$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	23,37±0,77(7)	22,40-24,76
16	25,09±0,80(8)	24,25-26,80
5	25,56±0,64(8)	24,60-26,39
3	25,85±0,47(7)	25,30-26,74
12	25,98±0,49(33)	25,01-26,93
11	26,00±0,28(5)	25,59-26,28
8	26,17±0,40(7)	25,63-26,63
4	26,23±0,74(9)	25,34-27,68
2	26,31±0,06(3)	26,27-26,38
7	26,45±0,78(11)	25,13-27,51
1	26,55±0,66(5)	25,70-27,29
6	26,58±0,84(37)	24,90-28,38
19	26,64±0,34(5)	26,19-27,12
10	26,88±1,01(10)	25,89-28,64
23	26,93±0,24(3)	26,59-27,14
9	26,96±0,57(5)	26,49-27,92
15	28,05±0,56(6)	27,52-28,87
13	28,19±1,15(9)	27,04-29,91
14	28,22±0,29(7)	27,79-28,52
18	28,44±1,20(5)	26,62-29,72
20	28,51±0,88(15)	26,55-29,95
22	28,85±0,77(14)	27,21-29,67
21	28,96±0,64(4)	27,87-29,14

GSH ($F = 21{,}142$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	11,21±0,39(7)	1067-11,70
16	11,86±0,35(8)	11,52-12,48
2	12,28±0,23(3)	12,02-12,46
5	12,43±0,54(8)	11,55-13,45
3	12,44±0,22(7)	12,23-12,78
23	12,55±0,14(3)	12,37-12,72
11	12,56±0,27(5)	12,26-13,00
12	12,57±0,26(35)	12,03-12,97
1	12,61±0,28(5)	12,24-12,93
4	12,66±0,54(9)	12,06-13,62
10	12,82±0,37(10)	12,39-13,48
6	12,97±0,38(39)	12,23-13,83
8	12,98±0,19(7)	12,76-13,25
7	12,99±0,35(12)	12,39-13,70
19	13,21±0,29(5)	12,94-13,67
9	13,34±0,31(5)	12,94-13,72
21	13,35±0,30(5)	12,93-13,52
20	13,47±0,44(15)	12,79-14,43
18	13,50±0,38(5)	13,10-13,92
13	13,61±0,64(9)	12,83-14,56
15	13,62±0,28(6)	13,15-13,87
14	13,64±0,41(7)	13,15-14,35
22	13,69±0,28(14)	13,09-14,08

P@P ($F = 4{,}927$; p < 0,001)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	6,56±0,40(7)	6,10-7,20
10	7,04±0,28(8)	6,51-7,52
23	7,09±0,10(3)	6,96-7,19
11	7,10±0,33(5)	6,76-7,52
8	7,20±0,31(7)	6,69-7,56
2	7,20±0,24(3)	6,94-7,40
1	7,21±0,17(5)	6,95-7,42
5	7,23±0,39(7)	6,79-7,88
16	7,28±0,28(8)	6,79-7,78
6	7,29±0,32(38)	6,63-8,10
7	7,35±0,37(10)	6,85-7,94
3	7,35±0,55(7)	6,29-7,97
15	7,37±0,24(5)	7,02-7,67
12	7,37±0,22(35)	6,80-7,87
9	7,38±0,11(5)	7,23-7,49
14	7,40±0,29(7)	7,10-7,94
19	7,51±0,09(5)	7,37-7,59
13	7,55±0,45(9)	7,03-8,42
20	7,57±0,38(15)	6,67-8,21
21	7,62±0,23(5)	7,31-7,70
4	7,69±0,22(9)	7,24-8,06
18	7,74±0,44(5)	7,05-8,21
22	7,75±0,37(14)	7,24-8,27

PBM ($F = 2{,}603$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	4,47±0,25(7)	4,10-4,74
2	4,53±0,16(3)	4,38-4,70
1	4,63±0,22(5)	4,39-4,88
3	4,69±0,43(7)	4,35-5,63
4	4,69±0,26(7)	4,38-5,02
5	4,70±0,29(7)	4,30-5,17
8	4,74±0,35(7)	4,23-5,41
16	4,75±0,16(6)	4,52-4,98
19	4,78±0,31(5)	4,36-5,13
11	4,81±0,30(5)	4,50-5,23
6	4,82±0,28(23)	4,39-5,26
23	4,85±0,25(3)	4,56-5,16
20	4,86±0,30(15)	4,37-5,47
7	4,86±0,29(8)	4,40-5,32
12	4,87±0,26(33)	4,38-5,39
10	4,88±0,13(4)	4,76-5,01
15	4,89±0,27(3)	4,58-5,04
22	5,02±0,29(14)	4,59-5,60
13	5,04±0,24(4)	4,76-5,24
21	5,06±0,35(4)	4,76-5,25
9	5,10±0,18(5)	4,90-5,34
18	5,14±0,20(4)	4,87-5,32
14	5,16±0,18(7)	4,89-5,36

Table 5.5 (cont.)

PAL ($F = 14{,}693$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	11,51±0,49(7)	10,78-12,25
16	12,60±0,53(8)	12,10-13,66
5	12,74±0,45(8)	11,94-13,33
12	12,91±0,31(34)	12,23-13,47
3	12,94±0,26(6)	12,63-13,41
10	13,04±0,68(10)	12,45-14,56
6	13,04±0,51(35)	12,03-14,29
11	13,04±0,42(5)	12,34-13,45
7	13,08±0,62(11)	12,08-14,17
8	13,09±0,48(7)	12,28-13,65
2	13,17±0,80(4)	12,15-14,09
19	13,21±0,21(5)	12,86-13,36
23	13,29±0,22(3)	12,98-13,47
4	13,30±0,45(9)	12,59-14,14
1	13,35±0,64(4)	12,67-13,92
9	13,55±0,42(5)	13,12-14,24
15	13,82±0,21(6)	13,55-14,09
14	14,11±0,24(6)	13,73-14,47
13	14,15±0,79(8)	13,23-15,21
20	14,25±0,53(14)	12,86-14,91
22	14,34±0,51(14)	13,04-14,98
18	14,35±1,00(5)	12,68-15,25
21	14,46±0,28(8)	14,18-14,73

MTL ($F = 8{,}253$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	5,65±0,28(7)	5,32-6,11
2	6,12±0,18(3)	5,92-6,27
1	6,28±0,21(5)	6,05-6,56
8	6,28±0,12(7)	6,13-6,45
7	6,35±0,23(10)	6,00-6,67
6	6,36±0,29(24)	5,98-7,01
5	6,38±0,32(8)	6,00-7,04
9	6,41±0,18(5)	6,24-6,63
16	6,43±0,26(7)	5,99-6,60
3	6,46±0,27(7)	6,22-6,86
12	6,48±0,25(33)	5,99-6,91
11	6,52±0,27(5)	6,20-6,92
23	6,62±0,21(3)	6,38-6,90
10	6,62±0,24(4)	6,33-6,88
13	6,65±0,21(8)	6,43-7,00
19	6,68±0,24(5)	6,38-6,95
14	6,69±0,21(7)	6,36-6,97
15	6,69±0,12(4)	6,54-6,83
4	6,74±0,31(9)	6,15-7,11
18	6,84±0,46(5)	6,05-7,18
20	6,88±0,22(15)	6,54-7,17
22	6,90±0,31(14)	6,01-7,32
21	6,92±0,07(5)	6,84-6,96

IPG ($F = 3{,}493$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
3	2,00±0,17(7)	1,88-2,36
17	2,02±0,08(6)	1,91-2,17
1	2,08±0,17(5)	1,94-2,28
8	2,08±0,16(7)	1,89-2,30
2	2,10±0,17(4)	1,92-2,27
5	2,11±0,14(8)	1,94-2,33
23	2,12±0,10(3)	1,98-2,22
11	2,12±0,20(5)	1,91-2,45
4	2,14±0,14(9)	1,86-2,28
7	2,14±0,19(12)	1,86-2,58
6	2,17±0,16(39)	1,85-2,50
16	2,21±0,12(8)	2,10-2,47
21	2,22±0,03(8)	2,16-2,21
20	2,22±0,12(15)	2,05-2,52
19	2,23±0,10(5)	2,11-2,39
14	2,25±0,18(7)	2,00-2,46
15	2,26±0,16(6)	2,02-2,45
13	2,26±0,18(9)	1,95-2,59
9	2,26±0,14(5)	2,08-2,41
10	2,28±0,11(10)	2,06-2,44
12	2,29±0,14(35)	1,96-2,56
22	2,31±0,11(14)	2,07-2,50
18	2,44±0,17(5)	2,25-2,64

PPL ($F = 8{,}627$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	7,80±0,31(7)	7,35-8,27
16	8,08±0,37(7)	7,74-8,84
5	8,28±0,34(8)	7,83-8,89
11	8,30±0,30(5)	7,79-8,53
8	8,31±0,20(7)	7,96-8,53
3	8,32±0,29(7)	7,78-8,64
4	8,40±0,44(9)	7,59-9,21
19	8,45±0,22(5)	8,07-8,61
7	8,45±0,30(12)	7,98-9,17
6	8,54±0,35(39)	7,96-9,22
1	8,61±0,25(4)	8,47-8,99
2	8,64±0,48(4)	8,39-9,37
23	8,69±0,02(3)	8,67-8,71
12	8,70±0,25(34)	8,11-9,12
9	8,71±0,25(5)	8,44-9,00
21	8,76±0,27(8)	8,57-9,10
10	8,78±0,42(10)	8,21-9,40
15	8,97±0,26(6)	8,59-9,30
20	8,97±0,29(15)	8,49-9,38
14	9,04±0,20(7)	8,79-9,38
18	9,14±0,49(5)	8,37-9,62
13	9,15±0,39(9)	8,72-9,65
22	9,16±0,39(14)	8,69-9,61

EAM ($F = 2{,}946$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	1,13±0,11(6)	1,04-1,35
20	1,14±0,08(12)	1,04-1,31
19	1,15±0,15(5)	0,96-1,37
21	1,17±0,25(8)	0,96-1,46
8	1,19±0,09(5)	1,07-1,26
10	1,22±0,07(6)	1,15-1,33
18	1,22±0,08(4)	1,11-1,30
23	1,24±0,14(3)	1,05-1,38
4	1,25±0,13(7)	1,07-1,41
5	1,26±0,14(8)	1,04-1,44
22	1,26±0,12(11)	1,08-1,41
9	1,26±0,22(4)	0,96-1,48
3	1,28±0,11(6)	1,11-1,41
14	1,31±0,10(6)	1,15-1,41
16	1,33±0,09(7)	1,18-1,43
6	1,34±0,10(34)	1,11-1,55
7	1,34±0,20(9)	1,11-1,63
12	1,34±0,22(32)	1,10-2,38
1	1,35±0,07(4)	1,26-1,41
13	1,41±0,17(7)	1,21-1,72
2	1,47±0,08(3)	1,41-1,56
11	1,48±0,15(3)	1,33-1,62
15	1,50±0,17(4)	1,30-1,70

BBW ($F = 4{,}522$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	10,52±0,45(7)	10,05-11,33
2	11,00±0,10(3)	10,91-11,11
23	11,12±0,33(3)	10,76-11,55
5	11,22±0,36(8)	10,89-11,87
16	11,22±0,57(7)	10,67-12,17
1	11,34±0,39(5)	10,88-11,70
11	11,37±0,69(5)	10,83-12,57
12	11,48±0,43(33)	10,60-12,39
3	11,52±0,70(7)	10,74-12,66
10	11,53±0,54(10)	10,80-12,20
19	11,55±0,43(5)	10,84-11,89
6	11,60±0,64(36)	10,46-12,95
7	11,65±0,75(9)	10,83-13,16
21	11,69±0,79(8)	11,32-12,71
4	11,70±0,21(8)	11,03-12,08
8	11,80±0,30(5)	11,38-12,17
15	11,93±0,24(6)	11,60-12,14
13	12,12±0,63(8)	11,43-13,19
22	12,14±0,74(12)	10,95-13,23
20	12,15±0,56(15)	11,07-12,95
14	12,20±0,44(7)	11,56-12,70
18	12,40±0,52(5)	11,66-12,91
9	12,47±0,40(4)	12,12-12,88

CPL ($F = 9{,}497$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	6,38±0,29(7)	5,87-6,79
16	6,46±0,44(8)	5,91-7,08
8	6,78±0,20(7)	6,54-7,07
5	6,79±0,23(8)	6,52-7,16
11	6,85±0,26(5)	6,63-7,15
4	6,86±0,37(9)	6,34-7,44
3	6,92±0,28(7)	6,62-7,46
12	6,98±0,26(35)	6,56-7,43
6	7,07±0,36(38)	6,49-7,70
10	7,11±0,43(10)	6,54-8,11
19	7,14±0,19(5)	6,81-7,31
7	7,17±0,40(12)	6,62-7,83
1	7,21±0,19(5)	7,03-7,44
2	7,24±0,35(4)	7,04-7,76
23	7,42±0,34(3)	6,73-7,55
21	7,43±0,30(8)	7,17-7,76
9	7,47±0,51(5)	6,93-8,31
13	7,50±0,38(9)	6,93-7,98
18	7,52±0,47(5)	6,80-7,95
15	7,55±0,23(6)	7,28-7,89
20	7,59±0,43(15)	6,50-8,33
22	7,59±0,23(14)	7,24-7,96
14	7,66±0,24(7)	7,43-8,07

APW ($F = 9{,}170$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
16	3,83±0,45(8)	3,28-4,53
17	4,00±0,28(7)	3,68-4,51
12	4,26±0,21(35)	3,75-4,60
5	4,32±0,27(8)	3,92-5,43
11	4,35±0,20(5)	4,11-4,60
3	4,35±0,30(7)	4,05-4,95
8	4,38±0,16(7)	4,18-4,62
4	4,39±0,20(9)	4,14-4,79
6	4,49±0,38(39)	3,78-5,27
19	4,49±0,19(5)	4,25-4,71
1	4,52±0,25(5)	4,17-4,83
2	4,53±0,36(4)	4,25-5,06
23	4,55±0,24(3)	4,29-4,87
10	4,57±0,33(10)	4,19-5,35
7	4,58±0,30(12)	4,08-5,21
18	4,75±0,23(5)	4,53-5,12
15	4,78±0,17(6)	4,61-5,00
21	4,80±0,43(5)	4,41-5,21
22	4,80±0,23(14)	4,35-5,14
14	4,81±0,20(7)	4,48-5,06
9	4,84±0,35(5)	4,53-5,43
20	4,98±0,29(15)	4,43-5,43
13	5,03±0,33(9)	4,58-5,44

MDL ($F = 15{,}124$; $p < 0{,}001$)

Loc	$\bar{x} \pm sd\ (n)$	Range
17	14,62±0,54(7)	13,88-15,65
16	15,57±0,72(8)	14,68-16,91
5	16,17±0,49(8)	15,60-16,94
3	16,31±0,37(7)	15,82-16,70
8	16,36±0,34(7)	15,90-16,72
1	16,38±0,25(5)	16,21-16,81
11	16,39±0,47(5)	15,80-16,87
19	16,40±0,32(5)	15,91-16,76
6	16,51±0,65(39)	15,15-17,88
12	16,54±0,46(35)	15,56-17,46
4	16,63±0,68(9)	16,04-18,23
7	16,64±0,69(12)	15,57-17,62
2	16,65±0,56(3)	16,21-17,28
10	16,69±0,86(10)	15,76-18,46
23	16,78±0,34(3)	16,40-17,23
9	17,11±0,47(5)	16,72-17,83
15	17,45±0,35(6)	17,03-17,88
21	17,52±0,61(8)	16,96-18,17
14	17,66±0,35(7)	17,04-18,18
13	17,71±0,79(9)	16,58-18,71
20	17,72±0,52(15)	16,39-18,69
18	17,87±0,99(5)	16,46-18,80
22	18,08±0,45(14)	17,47-18,87

Table 5.6

Summary statistics of one external (BCW) and 18 cranial measurements in 23 pooled locality samples of male *A. hottentotus*, and *F* statistics from single-classification ANOVAs of OTU means. *p* = significance of *F* values; $\overline{x}$ = sample means; *sd* = standard deviation; *n* = sample size. Vertical lines denote maximally non-significant subsets from SNK multiple comparisons tests.

BCW (F = 4,945; p < 0,001)

Loc	$\overline{x} \pm sd$ *(n)*				Range
17	4,25±0,10(4)	│			4,12-4,37
8/9	4,91±0,26(11)	│		│	4,85-5,70
16	5,10±0,47(5)	│		│	4,70-5,87
2	5,19±0,13(3)	│	│	│	5,04-5,29
23	5,25±0,08(8)	│	│	│	5,20-5,43
12	5,26±0,33(35)	│	│	│	4,45-5,92
3	5,29±0,35(7)	│	│	│	4,74-5,77
5	5,30±0,32(10)	│	│	│	4,73-5,67
11	5,44±0,26(6)	│	│	│	4,98-5,76
4	5,50±0,18(7)	│	│	│	5,27-5,73
10	5,74±0,38(5)	│	│	│	5,29-6,14
7	5,59±0,34(18)	│	│	│	5,07-6,23
6	5,61±0,41(50)	│	│	│	4,41-6,58
19	5,69±0,28(4)	│	│	│	5,29-5,89
13	5,95±0,36(12)		│	│	5,42-6,57
21	6,05±0,65(5)		│	│	5,39-6,63
15	6,13±0,33(6)		│	│	5,55-6,37
20	6,23±0,35(8)		│	│	5,51-6,61
18	6,33±0,31(3)		│	│	5,98-6,57
22	6,81±0,28(7)		│		6,49-7,19

Table 5.6 (cont.)

FML ($F = 7,077$; $p < 0,001$)

Loc	$\bar{x} \pm sd$ (n)	Range
17	4,25±0,04(3)	4,22-4,29
16	4,35±0,22(6)	4,02-4,71
4	4,62±0,19(7)	4,40-4,91
5	4,63±0,22(10)	4,36-5,11
3	4,64±0,22(5)	4,28-4,82
2	4,66±0,04(4)	4,61-4,71
12	4,66±0,23(37)	4,12-5,21
23	4,67±0,15(6)	4,45-4,81
1	4,67±0,15(3)	4,58-4,84
10	4,75±0,16(5)	4,60-4,99
19	4,80±0,10(4)	4,67-4,91
11	4,81±0,12(6)	4,66-4,95
6	4,82±0,27(39)	4,07-5,50
8/9	4,83±0,17(8)	4,49-5,03
21	4,85±0,30(5)	4,42-5,08
7	4,86±0,18(16)	4,55-5,15
18	5,02±0,15(3)	4,85-5,13
20	5,05±0,33(8)	4,52-5,43
22	5,10±0,38(6)	4,47-5,50
15	5,11±0,17(7)	4,92-5,36
13	5,26±0,13(9)	5,06-5,39

ARB ($F = 6,325$; $p < 0,001$)

Loc	$\bar{x} \pm sd$ (n)	Range
17	4,56±0,11(4)	4,47-4,71
23	4,66±0,16(6)	4,44-4,84
16	4,81±0,08(6)	4,71-4,96
3	4,82±0,28(5)	4,41-5,03
1	4,89±0,03(3)	4,86-4,91
5	4,95±0,26(9)	4,67-5,43
2	4,99±0,13(4)	4,89-5,18
12	5,00±0,25(38)	4,32-5,37
21	5,01±0,39(5)	4,53-5,45
10	5,06±0,20(5)	4,84-5,37
11	5,11±0,15(6)	4,86-5,22
6	5,12±0,30(41)	4,25-5,67
20	5,19±0,28(9)	4,75-5,60
13	5,19±0,30(9)	4,76-5,71
19	5,21±0,19(4)	5,01-5,44
4	5,22±0,15(7)	4,98-5,38
7	5,24±0,30(19)	4,76-5,71
8/9	5,36±0,19(7)	5,03-5,63
18	5,49±0,13(3)	5,39-5,63
15	5,50±0,36(7)	5,08-5,96
22	5,66±0,16(7)	5,43-5,89

MIO ($F = 19,875$; $p < 0,001$)

Loc	$\bar{x} \pm sd$ (n)	Range
17	7,11±0,26(4)	6,88-7,48
1	7,94±0,08(3)	7,89-8,31
23	7,95±0,12(6)	7,76-8,04
3	8,00±0,18(5)	7,84-8,28
2	8,08±0,24(4)	7,76-8,31
5	8,12±0,32(10)	7,79-8,63
7	8,19±0,44(19)	7,40-8,98
8/9	8,26±0,27(8)	7,83-8,61
6	8,29±0,32(44)	7,60-8,84
11	8,31±0,20(6)	8,00-8,52
12	8,39±0,34(38)	7,68-8,92
16	8,46±0,56(6)	7,60-9,32
4	8,47±0,13(7)	8,37-8,73
10	8,63±0,20(5)	8,43-8,87
13	8,91±0,37(9)	8,20-9,34
21	8,98±0,38(4)	8,48-9,47
20	9,20±0,38(9)	8,48-9,69
15	9,36±0,50(7)	8,63-9,95
19	9,39±0,21(4)	9,11-9,55
18	9,42±0,15(3)	9,30-9,59
22	9,80±0,35(7)	9,57-10,56

ZMB ($F = 10,422$; $p < 0,001$)

Loc	$\bar{x} \pm sd$ (n)	Range
17	15,32±0,59(4)	14,75-16,00
2	16,01±0,41(4)	15,64-16,59
1	16,18±0,25(3)	16,03-16,47
23	16,21±0,25(6)	16,04-16,71
5	16,24±0,59(10)	15,30-16,79
3	16,27±0,36(5)	15,95-16,79
16	16,43±0,80(6)	15,72-17,94
11	16,74±0,58(6)	16,12-17,82
6	16,75±0,82(45)	14,62-18,27
7	16,85±0,76(19)	15,33-18,19
12	16,93±0,67(38)	15,33-18,00
4	17,25±0,34(7)	16,74-17.68
10	17,31±0,53(5)	16,43-17,75
13	17,33±0,64(9)	16,30-18,26
21	17,42±0,58(3)	16,93-18,36
8/9	17,87±0,81(8)	16,67-19,33
19	17,98±0,37(4)	17,53-18,35
20	18,12±0,75(9)	16,81-19,48
18	18,17±0,68(3)	17,41-18,69
15	18,27±0,90(7)	16,71-19,36
22	19,24±0,62(7)	18,60-20,43

IOW ($F = 5,217$; $p < 0,001$)

Loc	$\bar{x} \pm sd$ (n)	Range
17	6,92±0,15(4)	6,77-7,12
16	7,20±0,33(6)	6,64-7,65
11	7,26±0,32(6)	6,98-7,79
23	7,27±0,12(4)	7,16-7,44
2	7,31±0,17(4)	7,09-7,50
5	7,35±0,35(10)	6,73-7,88
7	7,40±0,35(19)	6,86-8,18
12	7,47±0,30(38)	6,80-8,17
6	7,50±0,39(50)	6,41-8,12
3	7,52±0,34(5)	7,14-7,85
8/9	7,52±0,24(8)	7,22-7,99
1	7,55±0,44(3)	7,13-8,01
10	7,57±0,17(5)	7,43-7,85
13	7,62±0,34(9)	6,99-8,03
21	7,71±0,23(5)	7,40-8,07
4	7,79±0,24(7)	7,51-8,15
18	7,82±0,13(3)	7,70-7,96
15	7,91±0,35(7)	7,45-8,26
20	7,95±0,26(9)	7,47-8,31
19	7,99±0,36(4)	7,60-8,44
22	8,28±0,28(7)	7,95-8,67

GSL ($F = 18,535$; $p < 0,001$)

Loc	$\bar{x} \pm sd$ (n)	Range
17	23,94±0,69(4)	23,06-24,58
3	25,90±0,67(5)	25,00-26,80
16	26,03±0,94(6)	25,09-27,60
5	26,35±0,64(10)	25,00-27,00
12	26,92±0,80(37)	25,03-28,19
11	26,94±0,88(6)	25,51-28,06
6	27,01±0,88(45)	25,51-28,92
7	27,13±1,00(16)	25,68-28,75
1	27,21±0,27(3)	26,90-28,75
4	27,22±0,75(7)	25,60-27,70
10	27,45±0,81(5)	26,20-28,32
23	27,70±0,57(6)	27,12-28,59
2	27,73±0,41(4)	27,30-28,20
8/9	28,00±0,74(7)	27,07-29,40
13	28,39±0,75(9)	26,95-29,32
21	28,43±1,26(5)	26,57-29,81
19	28,73±0,70(4)	27,78-29.36
20	29,23±0,80(9)	27,56-30,48
15	29,46±1,09(9)	27,32-30,84
18	29,59±0,68(3)	28,82-30,11
22	30,87±0,64(7)	29,92-31,96

GSH ($F = 13,311$; $p < 0,001$)

Loc	$\bar{x} \pm sd$ (n)	Range
17	11,63±0,43(3)	11,25-12,09
16	12,35±0,56(6)	11,83-13,38
23	12,60±0,15(6)	12,41-12,76
3	12,80±0,38(5)	12,44-13,37
1	12,81±0,14(3)	12,67-12,94
5	12,89±0,36(10)	12,16-13,36
2	12,91±0,24(4)	12,65-13,22
11	12,98±0,22(6)	12,71-13,24
12	13,01±0,38(38)	12,27-13,71
10	13,12±0,49(5)	12,36-13,60
4	13,13±0,21(7)	12,79-13,43
6	13,28±0,46(45)	12,13-14,03
7	13,29±0,45(19)	12,48-14,12
21	13,56±0,89(5)	12,26-14,19
8/9	13,67±0,41(8)	13,10-14,35
13	13,73±0,41(9)	13,13-14,35
18	13,87±0,29(3)	13,54-14,05
19	13,96±0,15(4)	13,86-14,17
20	13,97±0,45(9)	13,00-14,72
15	14,04±0,46(7)	13,40-14,75
22	14,69±0,41(7)	14,26-15,26

P@P ($F = 5,184$; $p < 0,001$)

Loc	$\bar{x} \pm sd$ (n)	Range
17	6,67±0,27(4)	6,34-6,93
2	7,13±0,34(4)	6,68-7,42
16	7,29±0,27(6)	6,92-7,61
10	7,47±0,28(5)	7,08-7,87
5	7,47±0,29(10)	7,08-7,88
13	7,50±0,43(9)	6,46-7,91
6	7,51±0,38(45)	6,53-8,24
11	7,52±0,24(10)	7,31-7,96
23	7,53±0,18(6)	7,33-7,76
21	7,57±0,50(5)	7,04-8,10
7	7,64±0,44(18)	7,03-8,75
3	7,64±0,39(5)	7,11-8,12
12	7,67±0,25(36)	7,09-8,12
8/9	7,71±0,18(8)	7,43-7,99
15	7,73±0,21(4)	7,52-8,00
20	7,73±0,40(9)	6,95-8,25
19	8,06±0,29(4)	7,69-8,30
4	8,06±0,32(6)	7,57-8,42
22	8,22±0,24(7)	7,80-8,523

PBM ($F = 4,089$; $p < 0,001$)

Loc	$\bar{x} \pm sd$ (n)	Range
3	4,45±0,29(5)	4,04-4,79
17	4,46±0,32(4)	4,19-4,79
23	4,51±0,19(6)	4,32-4,81
5	4,61±0,23(6)	4,31-4,87
16	4,65±0,30(6)	4,32-5,15
21	4,66±0,24(5)	4,37-4,96
2	4,78±0,21(3)	4,54-4,92
10	4,84±0,23(5)	4,58-5,11
12	4,94±0,26(34)	4,55-5,65
20	4,95±0,16(9)	4,67-5,16
11	4,99±0,21(6)	4,75-5,27
6	5,00±0,27(40)	4,43-5,67
7	5,02±0,46(13)	4,25-5,72
4	5,02±0,34(6)	4,60-5,45
13	5,02±0,19(9)	4,70-5,34
18	5,04±0,20(3)	4,84-5,24
8/9	5,07±0,19(9)	4,79-5,34
19	5,11±0,23(4)	4,83-5,30
22	5,18±0,26(6)	4,79-5,18
15	5,30±0,54(3)	4,70-5,75

Table 5.6 (cont.)

PAL (F = 13,527; p < 0,001)

Loc	$\bar{x} \pm sd$ (n)	Range
17	11,81±0,60(4)	11,07-12,41
16	12,93±0,82(5)	11,70-13,76
3	12,99±0,58(5)	12,13-13,76
5	13,27±0,52(10)	12,08-13,87
11	13,28±0,56(6)	12,77-14,12
6	13,32±0,60(45)	11,79-14,75
10	13,43±0,49(5)	12,63-13,83
12	13,55±0,53(36)	12,25-14,63
7	13,67±0,56(19)	12,96-14,76
4	13,93±0,53(7)	12,84-14,36
8/9	13,93±0,56(7)	12,95-14,75
1	13,95±0,04(3)	13,92-14,00
2	13,96±0,46(4)	13,37-14,39
13	14,19±0,40(9)	13,71-14,86
21	14,32±0,60(4)	13,24-14,79
23	14,35±0,39(5)	13,81-14,75
19	14,47±0,24(4)	14,12-14,67
15	14,58±0,62(7)	13,32-15,31
20	14,74±0,50(9)	13,78-15,62
18	14,94±0,24(3)	14,67-15,10
22	15,65±0,42(7)	15,06-16,16

MTL (F = 8,527; p < 0,001)

Loc	$\bar{x} \pm sd$ (n)	Range
17	5,81±0,37(4)	5,38-6,23
1/2	6,31±0,35(4)	5,81-6,72
16	6,41±0,23(6)	6,20-6,81
8/9	6,49±0,10(8)	6,33-6,59
7	6,51±0,33(18)	6,00-7,15
3	6,52±0,26(5)	6,17-6,87
6	6,55±0,33(42)	5,77-7,13
11	6,58±0,29(6)	6,27-7,01
5	6,58±0,30(8)	6,20-7,16
10	6,59±0,15(4)	6,45-6,79
23	6,62±0,22(6)	6,33-6,87
12	6,71±0,23(36)	6,24-7,12
13	6,75±0,19(9)	6,43-6,99
21	6,76±0,46(5)	6,23-7,29
15	6,80±0,29(4)	6,43-7,06
18	6,98±0,16(2)	6,82-7,18
4	6,99±0,19(6)	6,69-7,21
20	7,07±0,27(9)	6,59-7,43
19	7,21±0,16(4)	7,02-7,39
22	7,41±0,18(6)	7,14-7,58

IPG (F = 5,940; p < 0,001)

Loc	$\bar{x} \pm sd$ (n)	Range
3	1,99±0,08(5)	1,87-2,07
5	2,01±0,19(10)	1,77-2,34
21	2,04±0,09(5)	1,93-2,13
1	2,06±0,15(3)	1,96-2,23
16	2,09±0,18(6)	1,76-2,22
17	2,09±0,08(4)	2,00-2,19
23	2,14±0,09(6)	2,05-2,28
6	2,16±0,14(45)	1,85-2,57
7	2,16±0,15(17)	1,75-2,36
4	2,16±0,07(4)	2,03-2,24
11	2,19±0,13(6)	2,03-2,32
2	2,21±0,10(4)	2,13-2,35
8/9	2,22±0,11(8)	2,02-2,22
13	2,26±0,20(9)	1,96-2,60
10	2,27±0,18(5)	1,99-2,49
15	2,33±0,14(7)	2,15-2,55
20	2,34±0,14(9)	2,16-2,60
19	2,34±0,13(4)	2,15-2,43
22	2,34±0,12(7)	2,22-2,59
12	2,36±0,15(38)	2,05-2,65
18	2,37±0,07(3)	2,31-2,44

PPL (F = 8,563; p < 0,001)

Loc	$\bar{x} \pm sd$ (n)	Range
17	7,80±0,30(4)	7,48-8,16
3	8,28±0,18(5)	8,07-8,55
23	8,45±0,18(6)	8,25-8,68
5	8,59±0,34(10)	7,97-9,01
1	8,62±0,21(3)	8,47-8,86
6	8,63±0,35(45)	7,82-9,19
4	8,72±0,11(7)	8,57-8,85
7	8,72±0,29(17)	8,24-9,32
16	8,73±0,30(6)	8,39-9,26
11	8,77±0,36(6)	8,43-9,23
2	8,90±0,21(4)	8,73-9,20
12	8,97±0,37(38)	8,14-9,50
8/9	9,00±0,47(8)	8,42-9,76
18	9,05±0,39(3)	8,68-9,45
10	9,07±0,54(5)	8,11-9,38
20	9,08±0,31(9)	8,40-9,48
21	9,13±0,74(5)	8,45-10,10
13	9,13±0,38(9)	8,64-9,71
19	9,23±0,40(4)	8,67-9,62
15	9,43±0,33(7)	9,04-9,96
22	9,77±0,30(7)	9,33-10,10

EAM (F = 2,664; p < 0,001)

Loc	$\bar{x} \pm sd$ (n)	Range
17	1,07±0,11(3)	1,00-1,19
20	1,10±0,10(8)	1,00-1,21
3	1,24±0,13(5)	1,11-1,41
21	1,24±0,16(5)	0,96-1,46
19	1,24±0,12(4)	1,11-1,40
5	1,27±0,16(8)	1,07-1,52
23	1,28±0,15(6)	1,11-1,46
4	1,30±0,15(7)	1,04-1,48
22	1,31±0,15(7)	1,11-1,56
15	1,32±0,12(7)	1,21-1,51
10	1,33±0,28(4)	1,04-1,71
13	1,33±0,07(8)	1,22-1,41
8/9	1,34±0,14(8)	1,11-1,48
16	1,34±0,11(6)	1,19-1,47
12	1,36±0,13(31)	1,11-1,63
6	1,36±0,15(22)	1,11-1,78
11	1,37±0,10(6)	1,26-1,51
7	1,42±0,15(14)	1,19-1,63

BBW (F = 5,359; p < 0,001)

Loc	$\bar{x} \pm sd$ (n)	Range
17	10,84±0,57(4)	10,23-11,56
23	11,45±0,28(6)	11,12-11,80
16	11,51±0,71(6)	10,52-12,63
1	11,54±0,63(3)	10,83-12,03
5	11,55±0,43(10)	10,66-12,06
2	11,60±0,57(3)	10,98-12,10
11	11,79±0,57(6)	11,03-12,45
3	11,85±0,58(5)	11,25-12,54
7	11,98±0,75(15)	10,89-13,56
12	11,99±0,59(35)	10,59-13,24
6	12,06±0,65(44)	10,70-13,51
13	12,27±0,75(9)	11,30-13,66
4	12,37±0,57(7)	11,30-12,99
21	12,38±0,80(4)	11,55-13,13
10	12,48±0,72(5)	11,64-13,31
19	12,51±0,49(4)	11,93-13,11
20	12,73±0,63(9)	11,24-13,28
15	12,84±0,63(7)	12,07-13,81
8/9	12,93±0,55(7)	12,24-13,90
22	13,25±0,49(7)	12,81-14,07

CPL (F = 9,198; p < 0,001)

Loc	$\bar{x} \pm sd$ (n)	Range
16	6,82±0,38(6)	6,34-7,51
17	6,85±0,34(4)	6,45-7,27
3	6,87±0,27(5)	6,49-7,12
4	6,99±0,29(10)	6,59-7,43
11	7,15±0,22(6)	6,80-7,43
6	7,19±0,37(44)	6,37-7,85
12	7,27±0,33(38)	6,73-8,23
23	7,32±0,25(6)	7,00-7,67
7	7,36±0,36(19)	6,83-8,02
4	7,39±0,23(7)	6,94-7,65
1	7,52±0,04(3)	7,48-7,55
10	7,55±0,33(5)	7,03-7,87
21	7,69±0,75(5)	6,90-8,52
18	7,70±0,12(3)	7,56-7,78
8/9	7,71±0,44(8)	7,21-8,51
13	7,76±0,46(9)	7,13-8,31
19	7,95±0,33(4)	7,46-8,18
2	7,96±0,35(4)	7,51-8,35
20	7,98±0,45(9)	6,93-8,52
15	8,00±0,44(7)	7,23-8,60
22	8,31±0,18(7)	8,04-8,51

APW (F = 6,354; p < 0,001)

Loc	$\bar{x} \pm sd$ (n)	Range
16	4,26±0,36(6)	3,67-4,66
17	4,27±0,24(4)	4,09-4,59
3	4,31±0,36(5)	3,78-4,68
6	4,39±0,54(45)	3,03-5,37
5	4,46±0,18(10)	4,08-4,73
11	4,55±0,29(6)	4,21-4,82
12	4,56±0,25(38)	3,99-5,07
7	4,72±0,31(19)	4,39-5,39
4	4,78±0,22(6)	4,36-5,01
23	4,78±0,32(6)	4,43-5,18
1	4,87±0,04(3)	4,83-4,90
10	4,88±0,33(5)	4,43-5,25
8/9	4,93±0,42(8)	4,21-5,64
13	4,98±0,46(9)	4,23-5,44
21	5,04±0,45(5)	4,53-5,45
18	5,13±0,34(3)	4,55-5,15
2	5,14±0,09(4)	5,05-5,27
19	5,18±0,30(4)	4,73-5,37
20	5,36±0,44(9)	4,60-5,95
15	5,37±0,48(7)	4,50-5,96
22	5,44±0,28(7)	5,12-5,79

MDL (F = 12,654; p < 0,001)

Loc	$\bar{x} \pm sd$ (n)	Range
17	15,20±0,64(4)	14,39-15,72
16	16,32±0,64(6)	15,76-17,57
3	16,35±0,58(5)	15,76-17,02
11	16,57±0,47(6)	15,68-16,98
5	16,65±0,58(10)	15,51-17,56
6	16,84±0,62(45)	15,55-18,32
23	17,06±0,32(6)	16,65-17,38
12	17,08±0,64(38)	15,55-18,21
7	17,08±0,56(19)	16,27-18,08
1	17,10±0,10(3)	16,99-17,17
10	17,19±0,45(5)	16,43-17,63
4	17,46±0,62(7)	16,19-18,11
8/9	17,58±0,53(8)	16,73-18,51
21	17,59±0,94(5)	16,16-18,52
2	17,60±0,43(4)	17,00-17,96
13	17,61±0,52(9)	16,59-17,61
19	17,89±0,55(4)	17,08-18,31
20	18,23±0,60(9)	16,99-18,92
18	18,27±0,20(3)	18,04-18,42
15	18,40±0,79(7)	16,95-19,55
22	19,32±0,40(7)	18,96-19,32

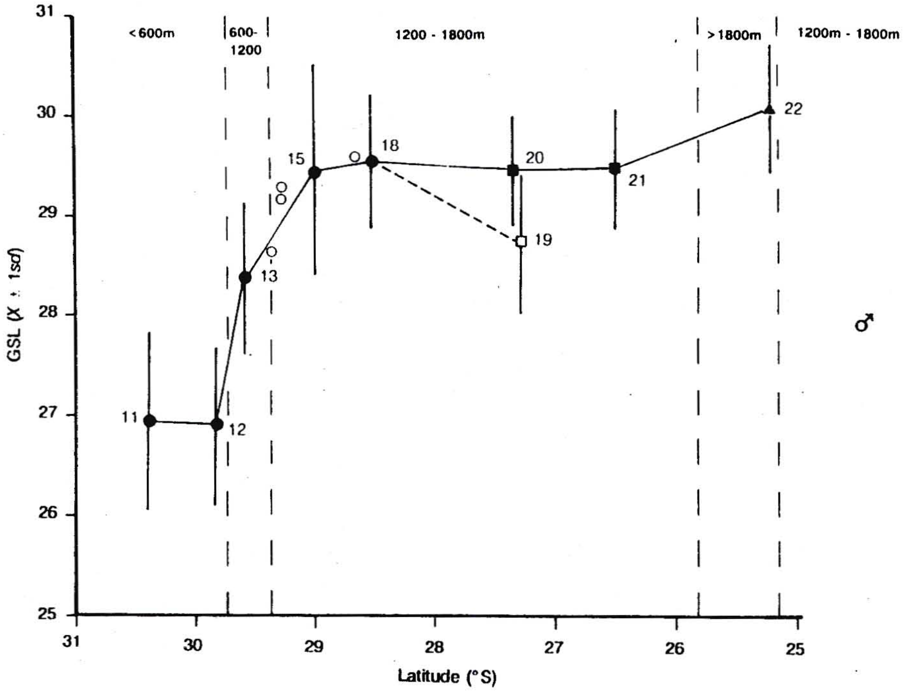
No overt clinal pattern of variation in relation to latitude and longitude was evident across the entire range of the species, for either sex. However, the order of ranked means was similar in most measurements of both sexes. This reflects a regular pattern of variation whereby OTUs from Zululand (Ubombo [17] and St. Lucia [16]) are smallest in most measurements, while those from the KwaZulu-Natal uplands (Pietermaritzburg [13] and/or Karkloof [14], Estcourt 15]), Free State (Golden Gate [18], Heilbron [19]) and Mpumalanga (Wakkerstroom [20], Ermelo [21], Belfast [22]) are largest. The coastal OTUs [1-12], representing populations from the Western Cape eastwards and northwards through to southern KwaZulu-Natal (Durban), were intermediate in size in most measurements. Males and females from Graskop [23] are significantly smaller than other Mpumalanga OTUs [20-22] in all measurements, and resemble the coastal OTUs in size.

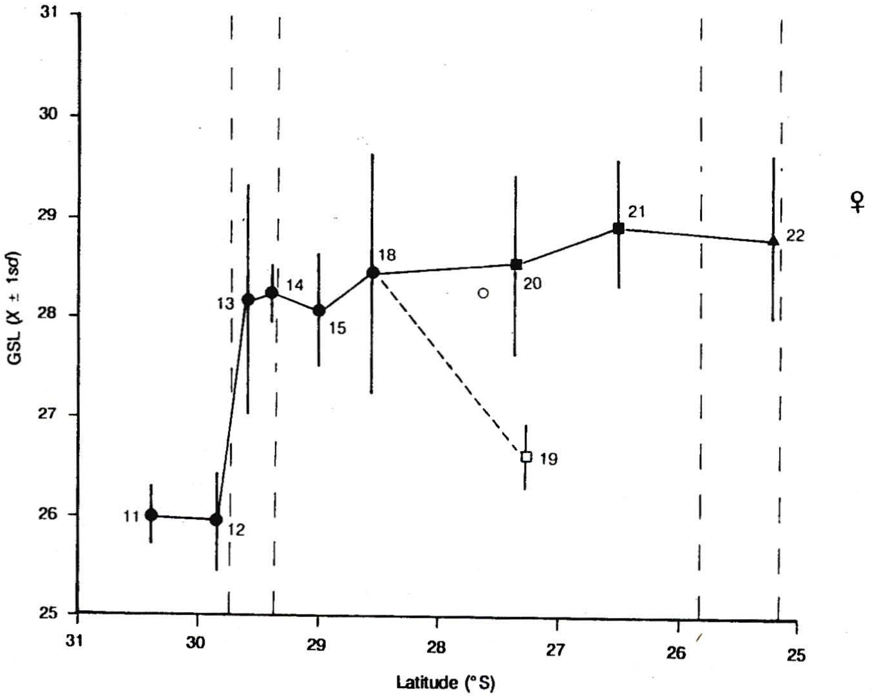
Only one measurement - EAM - showed a different pattern of geographic variation, with OTUs from the uplands of KwaZulu-Natal [13-15], Free State [18-19] and Mpumalanga [20-22] generally being smaller than the coastal OTUs.

The only OTUs differentiated by truly unique means (*i.e.* means not included in any particular subsets; see Pimentel and Smith 1990) were Ubombo [17] and Belfast [22]. The Ubombo OTU was significantly smaller than other OTUs in six measurements of both sexes (MIO, GSL, GSH, PAL, MTL, PPL, MDL), and a further three variables (P@P, ARB, BCW) in females. The Belfast OTU [22] was largest in 18 variables of males and six variables of females, but was significantly differentiated by only two measurements (GSL, MDL) in males. None of the measurement means at this locality were truly unique in females, suggesting that a greater extent of size variation was manifest in the male sample. Whether this reflects a real phenomenon whereby geographic variation in males is more pronounced than in females, or merely an artefact of small sample sizes, could not be ascertained from available data.

If one considers only the OTUs from KwaZulu-Natal (excluding Zululand), Free State and the Mpumalanga highveld, a distinct cline in overall size (as reflected by GSL in particular) in relation to latitude is evident (Fig. 5.6). This gradient exists in a northerly direction from southern KwaZulu-Natal [11,12] inland through the KwaZulu-Natal uplands [13-15] to Golden Gate [18], and thence northeastwards to Wakkerstroom [20], Ermelo [21] and Belfast [22]. The cline is stepped between Durban [12] and

Fig. 5.6. Variation in greatest skull length (GSL ± 1*sd*) in relation to latitude, altitude and karyotype among male and female samples of *A. hottentotus* from KwaZulu-Natal, Free State and Mpumalanga. Numbers next to each point indicate OTU or pooled locality samples detailed in Table 5.1. Symbols denote: (●) - 2n=30; (■) - 2n=34; (▲) - 2n=36; (□) - 2n=? (Heilbron); (○) - individual specimens (with 2n=30) from other localities in the uplands of KwaZulu-Natal.


31
30
29
28
27
26
25
GSL (X ± 1sd)
<600m
600-1200
1200 - 1800m
>1800m
1200m - 1800m
11
12
13
15
18
19
20
21
22
♂
31
30
29
28
27
26
25
Latitude (° S)


31
30
29
28
27
26
25
GSL (X ± 1sd)
11
12
13
14
15
18
19
20
21
22
♀
31
30
29
28
27
26
25
Latitude (° S)

Pietermaritzburg/Karkloof [13-14]. This coincides with a sudden increase in altitude from less than 100m at the coast, to elevations of about 600m a.s.l. in the southern, lower lying parts of Pietermaritzburg, and to approximately 1100m a.s.l. in the vicinity of Hilton, Howick and Karkloof. Thereafter, the cline is more continuous, with size increasing gradually as one progresses northwestwards until reaching the Golden Gate area [18] on the rim of the Great Escarpment formed by the Drakensberg Mountains. Size then tends to remain the same (males) or increase slightly (females) as one progresses northeastwards along the edge of the plateau formed by the Low Berg, to the Wakkerstroom [20] and Ermelo [21] samples, which are characterized by 2n = 34. Between Ermelo and Belfast [22], size increases quite markedly again in males, but stays relatively constant in females. This again corresponds with a marked increase in altitude, from 1600 - 1800m a.s.l., to greater than 2100m a.s.l. in the Steenkampsberge near Dullstroom. This size increase is also associated with a change in karyotype, from 2n = 34 at Ermelo to 2n = 36 at Belfast.

Overall size decreases from the Golden Gate [18] district to Heilbron [19], and this is associated with a decrease in altitude to about 1500m a.s.l. The Heilbron sample may represent a relict population, however, as there are no museum records of intermediate localities. A cline in body size thus cannot be inferred.

The clinal pattern described above may be the result of altitudinal changes in climate and vegetation. Size and altitude are strongly and significantly correlated in both sexes (Table 5.7). Moreover, size in both sexes is strongly and negatively correlated with mean annual temperature and mean annual minimum temperature. The changes in altitude and climate between coastal and inland KwaZulu-Natal are associated with major vegetation changes from Southern Savanna Woodland to Southern Savanna Grassland (Acocks 1988; Meester 1965; Rautenbach 1978). The clinal size variation in *A. hottentotus* from this region is thus associated with increasing altitude, changing vegetation and decreasing environmental temperature, and is consistent with Bergmann's Rule.

Fielden *et al.* (1990b) and Withers (1978) demonstrated that golden moles have high thermal conductances and poor thermoregulatory abilities. Kuyper (1985) also noted that moles from higher altitudes are larger, with lower mass-specific metabolic

Table 5.7

Pearson's product-moment correlation coefficients and associated probabilities for the association between overall size, as reflected by mean skull length (GSL), and three environmental variables in male and female *A. hottentotus* from OTUs in the uplands of KwaZulu-Natal, Free State and the Mpumalanga highveld. All environmental variables satisfied Kolmogorov-Smirnov tests of normality.

Variable	Male GSL		Female GSL	
	r	*p*	*r*	*p*
Altitude	0,885	0,004	0,795	0,018
Mean annual min. temp.	-0,965	0,003	-0,927	0,005
Mean annual temp.	-0,953	0,004	-0,936	0,007

rates. The tendency for *A. hottentotus* to become larger with increasing altitude may, therefore, be an adaptive physiological response to minimize heat loss and thermoregulatory energy requirements as ambient temperatures decrease geographically. This suggests that overall size may be strongly influenced by environmental parameters, implying that it has limited systematic value. The existence of karyotypic variation associated with increasing size indicates, however, that larger body size may also be genetically determined, and thus that size variation should not be excluded from taxonomic consideration entirely.

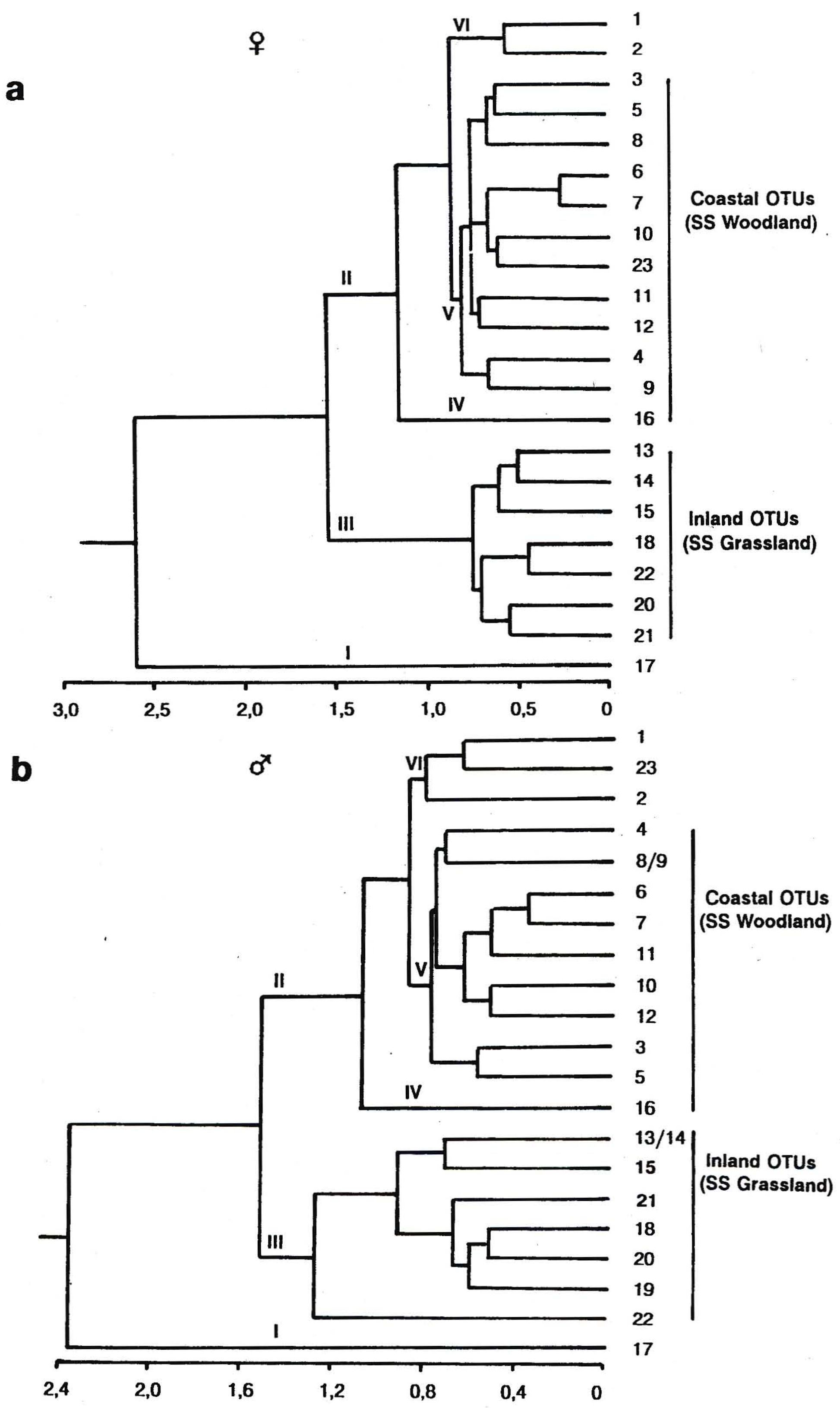
5.3.2.3 Multivariate analyses

Multivariate analyses of variance using 18 variables (EAM excluded to increase sample sizes) indicated highly significant differences between the 23 OTUs represented in both the female ($F_{(336,1710)} = 3{,}34$; $p < 0{,}001$) and male ($F_{(304,1581)} = 3{,}48$; $p < 0{,}001$) *A. hottentotus* data suites.

Cluster analyses of OTU means for 18 measurements based on average taxonomic distances (ATD), which tend to reflect overall size (Sneath and Sokal 1973), showed the existence of three discrete geographical phena in both sexes (Phena I - III in Fig. 5.7). In each sex, Phenon I separated from the other OTUs at high distances (exceeding 2,3), and comprised a single sample [17] from Ubombo, where specimens are markedly smaller than other *A. hottentotus*. Phenon II included all coastal OTUs ([1-12, 16], from Stellenbosch in the Western Cape to St. Lucia in Zululand), as well as a single OTU (Graskop, [23]) from the Mpumalanga escarpment. In both sexes, three further sub-divisions within Phenon II were evident by virtue of their separation at ATDs of 0,80 - 0,86: subphenon IV, consisting of only the St. Lucia OTUs [16]; subphenon VI, including Stellenbosch [1] and Grootvadersbosch [2] in the Western Cape; and subphenon V, comprising intermediately located coastal OTUs from the Eastern Cape and KwaZulu-Natal. Phenon III in both sexes included OTUs from the Southern Savanna Grassland biome, where individuals are considerably larger than coastal *A. hottentotus*.

Correlation phenograms, which tend to reflect shape differences rather than overall size (Sneath and Sokal 1973), divided the OTUs for each sex into two major

Fig. 5.7. Average taxonomic distance phenograms based on cluster analysis of single-standardized data for OTU samples of: a) female (co-phenetic correlation = 0,874); and b) male *A. hottentotus* (co-phenetic correlation = 0,765). OTU numbers refer to pooled locality samples indicated in Table 5.1.


a
♀
VI
II
V
IV
III
I
1
2
3
5
8
6
7
10
23
11
12
4
9
16
13
14
15
18
22
20
21
17
Coastal OTUs
(SS Woodland)
Inland OTUs
(SS Grassland)
3,0
2,5
2,0
1,5
1,0
0,5
0
b
♂
VI
II
V
IV
III
I
1
23
2
4
8/9
6
7
11
10
12
3
5
16
13/14
15
21
18
20
19
22
17
Coastal OTUs
(SS Woodland)
Inland OTUs
(SS Grassland)
2,4
2,0
1,6
1,2
0,8
0,4
0

phena (Fig. 5.8). Whereas most of the coastal localities (Phenon I, [1-12, 23]) separated from inland OTUs (Phenon II, [13-15, 18-22]) in both sexes, the female Pietermaritzburg [13] and Estcourt [15] samples grouped with the coastal OTUs, while the Umtata [8] and Oribi [10] samples clustered with the inland OTUs. In Phenon I, OTUs from the Western Cape ([1,2]; subphenon III) separated from the other coastal samples, which clustered into two groups (subphena IV and V) with differing OTU compositions in males and females. The Ubombo [17] samples grouped with the coastal localities in females, but with OTUs from the KwaZulu-Natal uplands [13,15] in males.

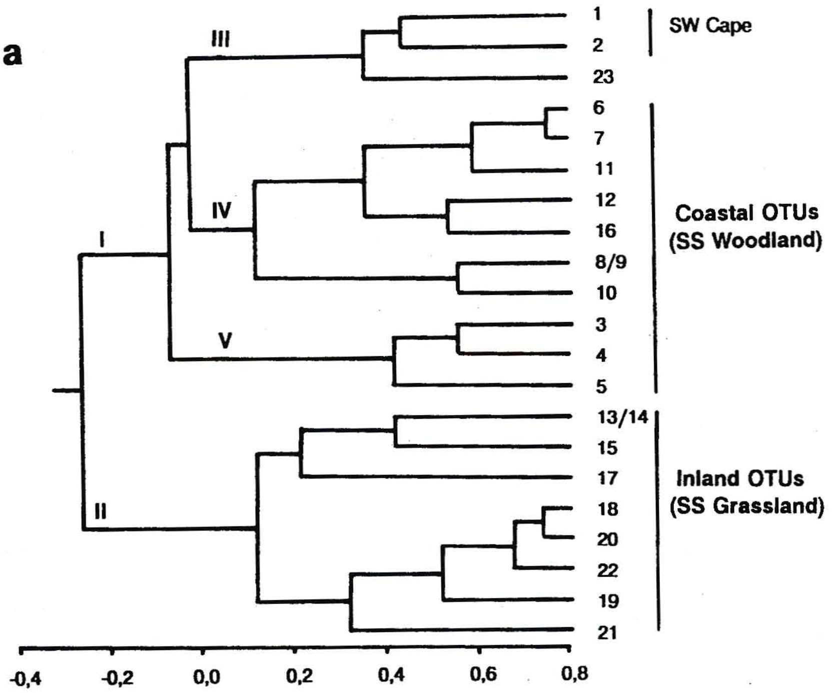
Correlation phenograms thus indicated that while the Ubombo OTU is well differentiated in terms of size, there are no marked differences in cranial shape which distinguish this OTU from from other *A. hottentotus*. In contrast, the correspondence of major phena in the correlation and distance phenograms for each sex shows that coastal OTUs from the South-West Cape and Southern Savanna Woodland biotic zones are distinguished from those in the Southern Savanna Grasslands by differences in both cranial size and shape. Shape differences between these phena are, however, less overt than size variation, with the result that shape discrimination between them is equivocal.

The separation of the St. Lucia OTU(s) [16] in a distinct subphenon in distance phenograms, but not in correlation phenograms, indicated that while this OTU is slightly (but not significantly) smaller than other coastal samples from the Eastern Cape and southern KwaZulu-Natal, cranial shape differences between them are negligible. Conversely, the tendency for the Stellenbosch [1] and Grootvadersbosch [2] OTUs to separate from other coastal OTUs in both the correlation and distance phenograms indicates that the OTUs from the South-West Cape biotic zone differ in both skull size and shape from those in Southern Savanna Woodland.

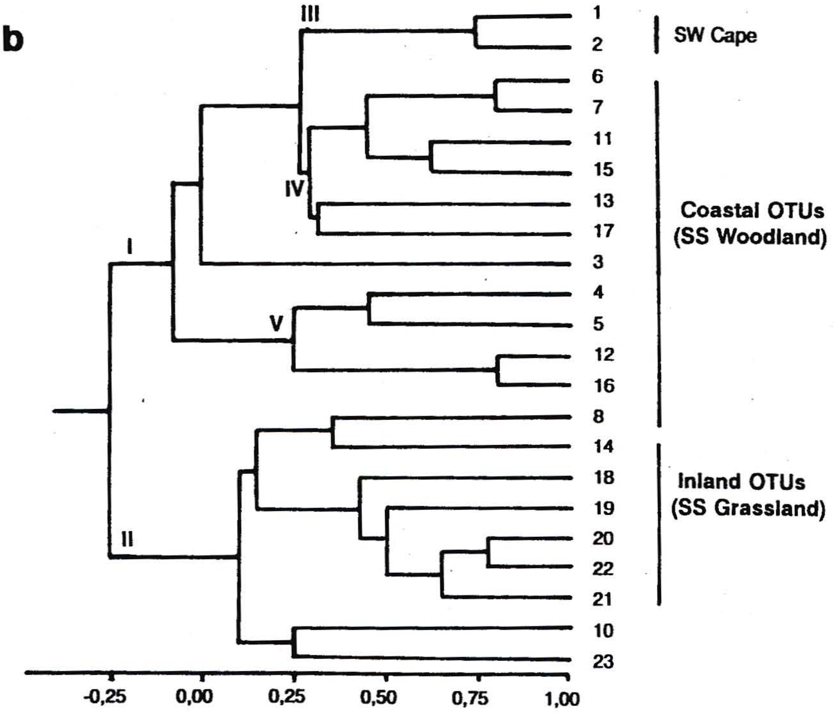
The OTUs characterized by 2n = 34 (Wakkerstroom [20] and Ermelo [21]) and 2n = 36 (Belfast [22]) grouped apart from those with 2n = 30 [13-15] in both the distance and correlation phenograms. This indicated that the 2n = 30 OTUs from the KwaZulu-Natal uplands are distinguished from the other cytotypes in Southern Savanna Grassland by differences in both cranial size and shape. In contrast, the 2n = 34 and 2n = 36 OTUS grouped together in correlation and distance phenograms, and in close association with those from Free State. This implied that shape differences between

Fig. 5.8. Phenograms based on correlation coefficients computed from single-standardized data for OTU samples of: a) male (co-phenetic correlation = 0,715); and b) female *A. hottentotus* (co-phenetic correlation = 0,728). OTU numbers refer to pooled locality samples indicated in Table 5.1.

a


III
IV
I
V
II
1
2
23
6
7
11
12
16
8/9
10
3
4
5
13/14
15
17
18
20
22
19
21
SW Cape
Coastal OTUs
(SS Woodland)
Inland OTUs
(SS Grassland)
-0,4
-0,2
0,0
0,2
0,4
0,6
0,8

b


III
IV
I
V
II
1
2
6
7
11
15
13
17
3
4
5
12
16
8
14
18
19
20
22
21
10
23
SW Cape
Coastal OTUs
(SS Woodland)
Inland OTUs
(SS Grassland)
-0,25
0,00
0,25
0,50
0,75
1,00

the 2n = 34 and 2n = 36 OTUs are subtle, and that variation in overall size is gradual.

Principal components analyses confirmed the existence of three major phena delimited mainly on the basis of size, and several geographical subgroups of OTUs distinguished mainly by shape differences (Fig. 5.9). Regardless of sex, the Ubombo sample plotted to the top left, inland OTUs to the bottom right, and coastal OTUs between. In females, the St. Lucia OTU separated from other coastal samples along the second component axis, whereas in males this OTU associated closely with the coastal OTUs. In males, the Heilbron sample grouped with the coastal OTUs, and the 2n = 34 OTUs from Mpumalanga separated from the 2n = 36 Belfast OTU along both axes. Conversely, the female OTUs from Mpumalanga formed a tight cluster that included the Heilbron [19] sample.

The first component was a general size vector, as indicated by the high, positive loadings for all variables (Table 5.8). Separation along this axis reflects an increase in size, from left to right. This component accounted for over 80% of the sample variance in both sexes, indicating that craniometric variation in *A. hottentotus* is dominated by overall skull size. The second component accounted for only about 5% of sample variance in each sex, and was a shape vector contrasting posterior palate width (IPG, PBM) with medial palate width (P@P) and maxilla length (MTL) in males. In females, this component contrasted mandibular ramus length (CPL, APW) with palate width (P@P, IPG) and maxilla length (MTL). The scatterplots thus indicate that as skull size increases, posterior width of the palate tends to become relatively narrower in males, while in females mandibular ramus lengths tend to be relatively shorter.

The differences between the scatterplots for male and female *A. hottentotus* reflected divergent patterns of variable participation in the second principal component. Examination of variable loadings (Table 5.8) showed that the third component in males contrasted mandibular ramus length (APW, CPL) with palate width (P@P), and thus resembled the second component of females. However, anterior rostral breadth (ARB) and bibullar width (BBW) also loaded highly and positively, whereas palatal length (PAL) loaded negatively. This suggests that the PC3 for males contrasted mandibular ramus length not only with palate width and length, but also with ventral skull widths

Fig. 5.9. Scatterplots of scores from principal components analyses of data for the sexes apart, and combined. a) pairwise comparison of the first two principal component axes, based on data for only female *A. hottentotus* (co-phenetic correlation = 0,991); b) pairwise comparison of the first two principal components axes, based on data for only male *A. hottentotus* (co-phenetic correlation = 0,998); c) pairwise comparison of the first two principal components axes, based on combined data following individual standardization of the sexes (c; co-phenetic correlation = 0,996); and d) pairwise comparison of the first and third principal components axes, based on combined data following individual standardization of the sexes. Capital letters denote clusters of OTUs discussed further in the text. Symbols: (●) - 2n=30; (■) - 2n=34; (▲) - 2n=36; (□) - 2n=? (Heilbron).

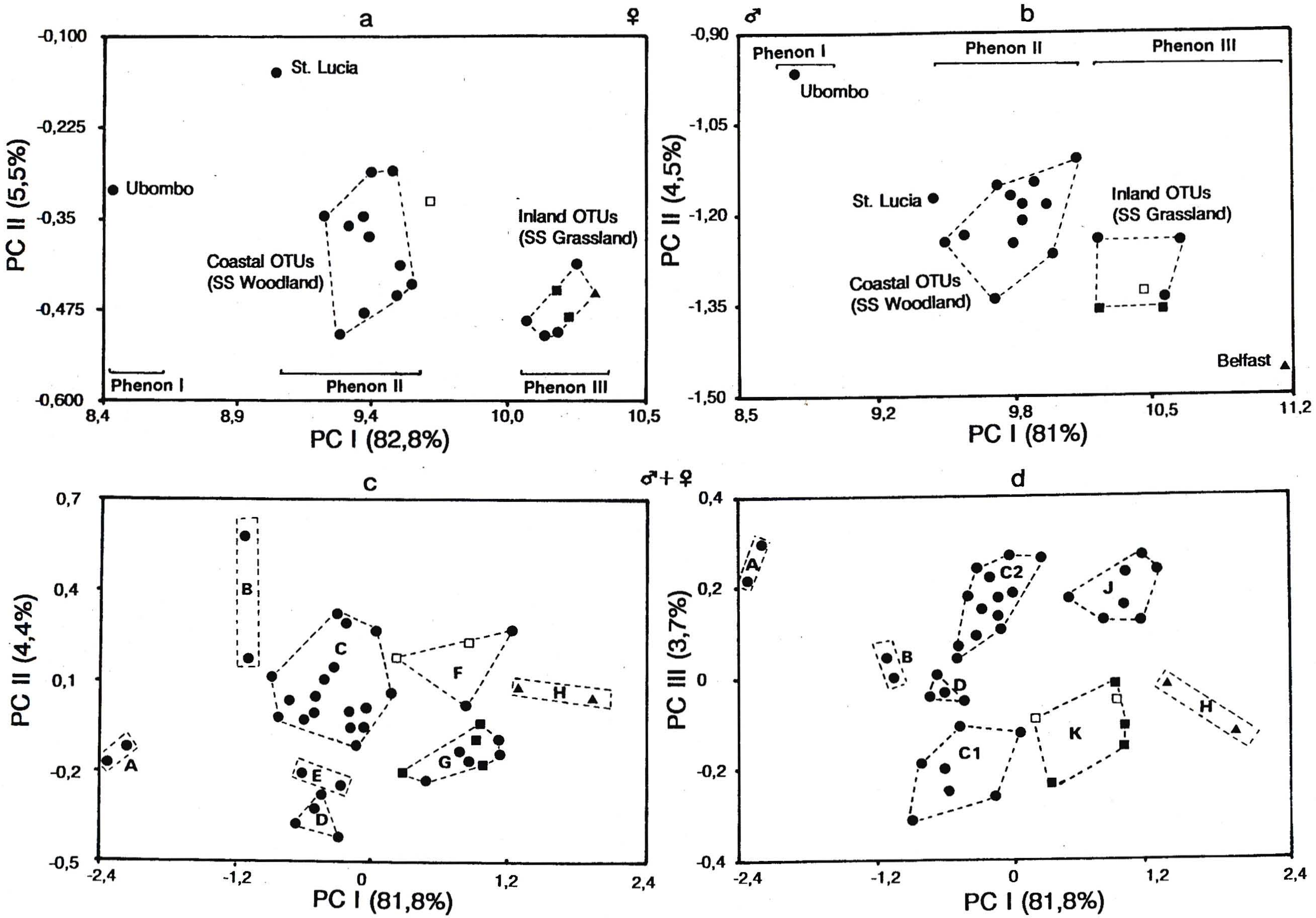

a
♀
-0,100
-0,225
-0,35
-0,475
-0,600
PC II (5,5%)
St. Lucia
Ubombo
Coastal OTUs
(SS Woodland)
Inland OTUs
(SS Grassland)
Phenon I
Phenon II
Phenon III
8,4
8,9
9,4
10,0
10,5
PC I (82,8%)
b
♂
-0,90
-1,05
-1,20
-1,35
-1,50
PC II (4,5%)
Phenon I
Phenon II
Phenon III
Ubombo
St. Lucia
Coastal OTUs
(SS Woodland)
Inland OTUs
(SS Grassland)
Belfast
8,5
9,2
9,8
10,5
11,2
PC I (81%)
c
♂+♀
0,7
0,4
0,1
-0,2
-0,5
PC II (4,4%)
A
B
C
D
E
F
G
H
-2,4
-1,2
0
1,2
2,4
PC I (81,8%)
d
0,4
0,2
0
-0,2
-0,4
PC III (3,7%)
A
B
C1
C2
D
H
J
K
-2,4
-1,2
0
1,2
2,4
PC I (81,8%)

Table 5.8

Factor matrix showing measurement loadings for the first three principal components computed for males and females individually, and for the sexes combined following individual standardization of data. Boldfaced loadings indicate strong variable participation in the respective axes.

	FACTOR LOADINGS								
	MALES			FEMALES			MALES + FEMALES		
Meas.	I	II	III	I	II	III	I	II	III
BCW	**0,888**	-0,234	0,012	**0,940**	-0,207	0,008	**0,915**	-0,150	-0,123
ARB	**0,891**	**0,265**	**0,230**	**0,905**	0,003	**-0,160**	**0,898**	0,080	**0,190**
MIO	**0,932**	-0,087	0,077	**0,959**	0,156	0,039	**0,946**	0,130	-0,045
ZMB	**0,949**	0,071	0,171	**0,948**	0,166	0,068	**0,949**	0,176	0,015
IOW	**0,932**	-0,198	0,123	**0,896**	0,178	**0,220**	**0,914**	0,144	**-0,216**
GSL	**0,972**	-0,066	-0,167	**0,976**	-0,119	0,028	**0,974**	-0,145	-0,044
GSH	**0,977**	0,013	0,099	**0,962**	-0,089	-0,003	**0,969**	-0,025	0,001
P@P	**0,831**	**-0,281**	**0,296**	**0,816**	**0,352**	**0,334**	**0,823**	**0,333**	**-0,336**
PBM	**0,783**	**0,447**	0,200	**0,871**	0,173	**-0,244**	**0,828**	0,164	**0,355**
PAL	**0,926**	-0,203	**-0,218**	**0,964**	-0,063	0,110	**0,946**	-0,125	-0,156
MTL	**0,895**	**-0,332**	0,090	**0,878**	**0,286**	**0,215**	**0,886**	**0,232**	**-0,270**
IPG	**0,744**	**0,413**	-0,142	**0,742**	**0,434**	**-0,461**	**0,743**	**0,288**	**0,453**
PPL	**0,932**	0,071	0,002	**0,921**	-0,156	**-0,228**	**0,926**	-0,095	0,133
BBW	**0,906**	0,090	**0,226**	**0,907**	0,125	-0,033	**0,906**	0,166	0,045
FML	**0,852**	0,126	-0,053	**0,881**	-0,270	0,135	**0,867**	-0,237	0,025
CPL	**0,890**	0,059	**-0,366**	**0,916**	**-0,309**	-0,077	**0,903**	**-0,323**	0,063
APW	**0,881**	0,032	**-0,420**	**0,887**	**-0,428**	0,008	**0,884**	**-0,401**	0,027
MDL	**0,975**	-0,054	-0,143	**0,977**	-0,103	-0,014	**0,976**	-0,114	-0,025

in general. Similarly, the third component in females contrasted posterior palate width (IPG, PBM) with palate width (P@P) and maxilla length (MTL), and was thus similar to the second component of males. But, post-palatal length (PPL) and anterior rostral breadth (ARB) also loaded highly and negatively, whereas anterior inter-orbital width (IOW) loaded positively. This indicates that the PC3 of females contrasted also maxilla length with post-palatal length, and rostral breadth with anterior inter-orbital width.

Patterns of variable interaction in the first three principal components were thus complex, and the differences between males and females may be attributed to both allometric variation associated with sexual dimorphism, and statistical noise associated with small samples available for some OTUs.

To clarify the nature of geographic variation in the cranial shape of *A. hottentotus*, Cheverud's (1982) method for eliminating sexual dimorphism was used. OTU means for each sex were standardized independently before data for the sexes were pooled and entered into a principal components analysis. Predictably, the first component separated the OTUs according to general size (Fig. 5.9c and 5.9d), and accounted for 81,8% of the pooled sample variance. The second component contrasted mandibular ramus length (APW, CPL) with palatal widths (IPG, P@P) and maxilla length (≡ palate length; MTL). Decreasing scores along this axis indicated a lengthening of the mandibular ramus (Table 5.9). The third component contrasted posterior palate widths (IPG, PBM) with medial palate width (P@P) and maxilla length, and rostral breadth (ARB) with anterior inter-orbital width (IOW). Decreasing scores along this axis reflected a relative narrowing in posterior palate width, and a comparative broadening of the rostrum (Table 5.9).

Pairwise comparison of the first two principal components axes (Fig. 5.9c) revealed the existence of three major groups of OTUs, separated mainly along the first axis. These corresponded with the three major size-delimited phena distinguished in distance phenograms when the sexes were analysed separately (Fig. 5.7), *viz.* Phenon I - Ubombo [17], Phenon II - coastal OTUs [1-12] and Graskop [23], and Phenon III - inland OTUs from Southern Savanna Grassland [13-15, 18-22]). Eight distinct sub-groups of OTUs (A - H in Fig. 5.9c) were evident within the three major phena discriminated mainly by size. Phenon A included only the Ubombo OTU(s) [17], which plotted well to the left of others along the first axis by virtue of their markedly smaller size. Within the coastal phenon, three subphena (B, C and D) separated from each other along primarily the second component axis. This reflects slight differences in cranial configuration, with a tendency for the St. Lucia OTUs ([16] - subphenon B) to have relatively shorter mandibular rami than those from the Eastern Cape and southern KwaZulu-Natal (subphenon C), while OTUs [1-2] from the Western Cape (subphenon D) have comparatively longer rami (Table 5.9). The Graskop samples [23] grouped together (subphenon E) between those from the Western Cape and more northern coastal OTUs, but with closer affinity to the former. This was consistent with the clustering pattern in distance and correlation phenograms for males (but not females).

Within the major inland phenon, three distinct subphena (F - H) were evident, but these did not correspond directly with the three cytotypes, or the subgroups in distance phenograms. OTUs from the Free State (subphenon F) separated from those in the uplands of KwaZulu-Natal and the Mpumalanga highveld (subphenon G), primarily along the second component. This reflected slight differences in the relative length of mandibular rami between these populations (Table 5.9). The Belfast OTUs (subphenon H) plotted to the right of other inland samples, by virtue of their larger size.

Pairwise comparison of the first and third principal components axes (Fig. 5.9d) confirmed the phenetic distinctness of the Ubombo, St. Lucia, Belfast and Western Cape OTUs (subphena A, B, D and H), and revealed the existence of two subgroups in the coastal cluster (subphenon C). One of these (subgroup C1) comprised OTUs [3-5] from the Eastern Cape (including the type locality), and plotted well below subgroup C2, which included samples [6-12] from further north. OTUs [1-2] from the Western Cape (subphenon D) plotted intermediately. Separation along PC3 reflected slight differences in the relative widths of the interpterygoid region and rostrum of the OTUS.

Within the inland phenon, two distinct subgroups of OTUs separated widely along the third axis, but these differed in constitution from those discriminated along the second axis. Subphenon J, containing 2n = 30 OTUs from the uplands of KwaZulu-Natal [13-15] and Golden Gate [18], plotted well above the 2n = 34 OTUs ([19, 20-21], which together formed subphenon K.

Table 5.9

Selected cranial ratios for subgroups of OTUs discriminated by pairwise comparisons of the first and second or third principal component axes in Figs. 5.9c and 5.9d.

PC	Subgroup	OTUs	CRANIAL	RATIOS
2			APW:P@P	APW:MTL
	B	16	55,5±4,1	63,1±4,9
	C	3-12	60,8±2,7	69,4±3,2
	F	18-19	61,8±2,3	70,4±2,7
	H	22	64,1±3,0	71,5±2,7
	G	13-15, 20-21	66,3±2,1	73,8±2,8
	A	17	62,5±2,1	72,2±1,9
	E	23	63,9±0,5	70,5±2,5
	D	1-2	65,9±5,4	74,4±2,6
3			IPG:P@P	ARB:IOW
	A	17	31,1±0,4	64,5±1,9
	B	16	29,7±1,1	65,6±1,7
	E	23	29,2±1,0	64,5±0,6
	D	1-2	29,6±1,1	66,3±2,5
	C1	3-5	27,3±1,1	65,4±1,3
	C2	6-12	29,8±1,2	68,9±1,9
	J	13-15,18	30,2±0,3	68,4±1,2
	K	19-21	29,0±1,1	64,7±1,1
	H	22	29,2±0,9	66,8±2,3

Principal components analyses thus indicated that while craniometric variation in *A. hottentotus* is dominated by overall size, subtle differences in cranial configuration distinguish nine geographic subgroups within the three major size-delimited phena. Within the inland phenon, the three subgroups (H, J, K) in Figure 5.9d corresponded with karyotypic groupings - evidence that the three cytotypes within *A. hottentotus* are characterized by differences in skull size and shape. Discrimination of the Heilbron OTU(s) from the Free State was, however, hampered by a lack of karyotypic data, and the craniometric intermediacy of sample(s). As a result, these OTUs grouped with Golden Gate ($2n=30$) in subphenon F when the first and second axes were compared, but associated with OTUs having $2n=34$ (Wakkerstroon and Ermelo; subphenon K) in scatterplots contrasting the first and third axes.

Multiple discriminant functions analyses based on individuals resulted in an overall *a posteriori* classification of 80% for females, and 81% for males (Table 5.10 and 5.11). Most OTUs showed quite high (>75%) percentages of correct specimen identification, indicating that local populations are well differentiated from each other. This is typical of subterrestrial mammals with limited vagility (Nevo 1979). Six OTUs (Ubombo [17], St. Lucia [16], Stellenbosch [1] and/or Grootvadersbosch [2], King Williams Town [6], Durban [12]) showed very high percentages (> 90%) of correct specimen classification in both sexes. A further five OTUs (♀ - Golden Gate [18], Belfast [22]; ♂ - Graskop [23], Ermelo [21] and Wakkerstroom [20]) showed high classification accuracy in either sex. These populations are thus particularly well differentiated from others. Within each sex, most mis-identifications involved specimens from adjacent OTUs, either along the coast [1-12], or on the escarpment in the Free State and Mpumalanga highveld [18-22]. The OTUs [13-15] from the uplands of KwaZulu-Natal showed relatively lower levels of classification accuracy, with misidentified specimens assigned to either the Wakkerstroom [20] and Belfast [22] samples from further inland, or to coastal OTUs [5,12]. This reflects the size and geographical intermediacy of these OTUs between the major coastal phenon and the OTUs from the Great Escarpment.

Table 5.10

A posteriori Geisser classification summary based on a 22 group discriminant functions analysis of female *A. hottentotus* samples, showing the percentage assignment of specimens to various OTUs. Samples characterized by very high (>90%) accuracy of specimen assignment to the correct *a priori* groups are underlined in boldface on the diagonal. The Port St. Johns OTU was excluded owing to small sample size. See Table 5.1 for a key to OTU numbers.

	% Specimens classified into each population																					
OTU	1	2	3	4	5	6	7	8	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	50	0	17	17	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0
4	0	0	0	88	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	14	0	43	29	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	**94**	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	40	60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	20	0	80	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	67	0	33	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	60	40	0	0	0	0	0	0	0	0	0	0	0
12	0	0	3	0	0	0	0	0	0	0	**97**	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	14	0	0	0	0	14	57	0	0	0	0	0	0	14	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	80	0	0	0	0	0	20	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	75	0	0	0	0	25	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	60	0	0	0	20	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	83	17	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	7	0	73	0	7	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	40	40	0
22	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	**92**	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0	67

Table 5.11

A posteriori Geisser classification summary based on a 19 group discriminant functions analysis of male *A. hottentotus* samples, showing the percentage assignment of specimens to the various OTUs. Samples characterized by very high (>90%) accuracy of specimen assignment to the correct *a priori* groups are shown in underlined boldface on the diagonal. The Karkloof and Golden Gate OTUs were excluded from analysis owing to small sample sizes, whereas specimens from Stellenbosch and Grootvadersbosch, and Port. St. Johns and Umtata, respectively, were pooled to increase sample sizes. See Table 5.1 for a key to OTU numbers.

	% Specimens classified into each population																		
OTU	1	3	4	5	6	7	8	10	11	12	13	15	16	17	19	20	21	22	23
1	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	60	0	20	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	83	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	14	71	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0
6	0	0	3	3	**90**	3	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	9	27	55	0	0	0	9	0	0	0	0	0	0	0	0	0
8	0	0	0	0	50	0	50	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	50	0	50	0	0	0	0	0	0	0	0	0
11	0	0	0	0	17	0	0	0	67	16	0	0	0	0	0	0	0	0	0
12	0	3	0	0	0	4	0	0	0	**93**	0	0	0	0	0	0	0	0	0
13	0	0	0	0	11	0	0	0	0	0	89	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	67	0	0	0	33	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	75	25	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	80	0
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**

In scatterplots of the first two canonical variate axes (Figure 5.10), three groups of OTUs were discernable. These corresponded with the major phena delimited by size in cluster and principal components analyses. Phenon I comprised only the Ubombo OTU [17]. Phenon II included coastal OTUs [1-12,16], as well as the Graskop OTU [23] from the eastern Drakensberg escarpment, while Phenon III consisted of inland OTUs [13-15, 18-22] from KwaZulu-Natal, Free State and the Mpumalanga highveld. There was, however, substantial overlap of scores between phena II and III along both axes, especially for the geographically intermediate OTUs from the uplands of KwaZulu-Natal.

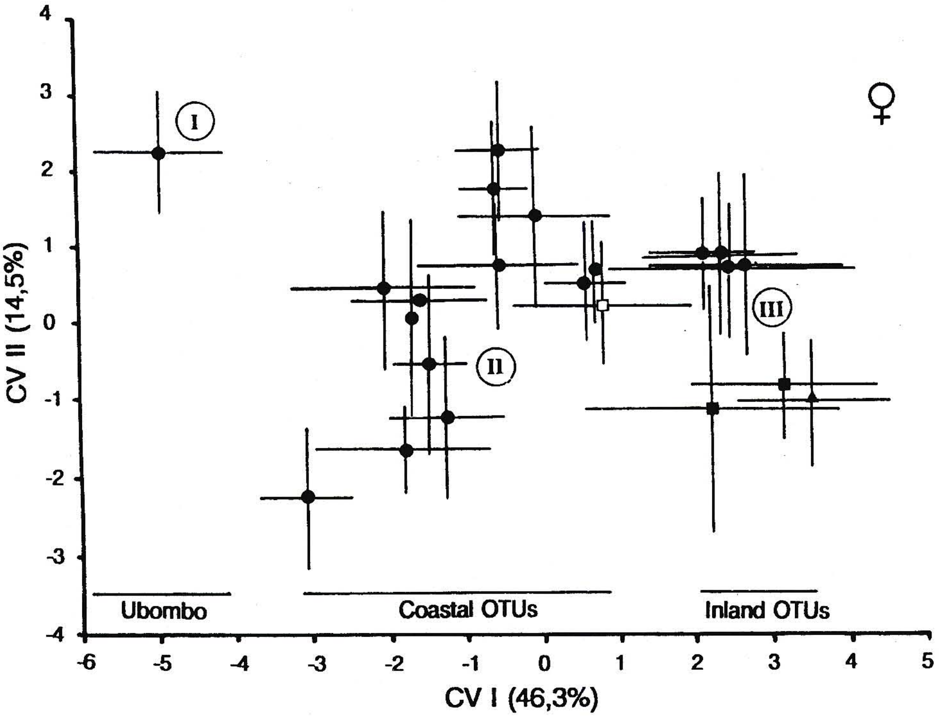
Assuming that hybrids are characterized by morphological intermediacy (Genoways and Choate 1972; George *et al.* 1981), then the overlap of discriminant scores between the coastal and inland phena suggests that interbreeding occurs in their zone of geographical contact (*viz.* Pietermaritzburg - Karkloof region). But, the assumption that hybrids are morphologically intermediate is not always justified, as known hybrids display varying degrees of intermediacy (Neff and Smith 1978).

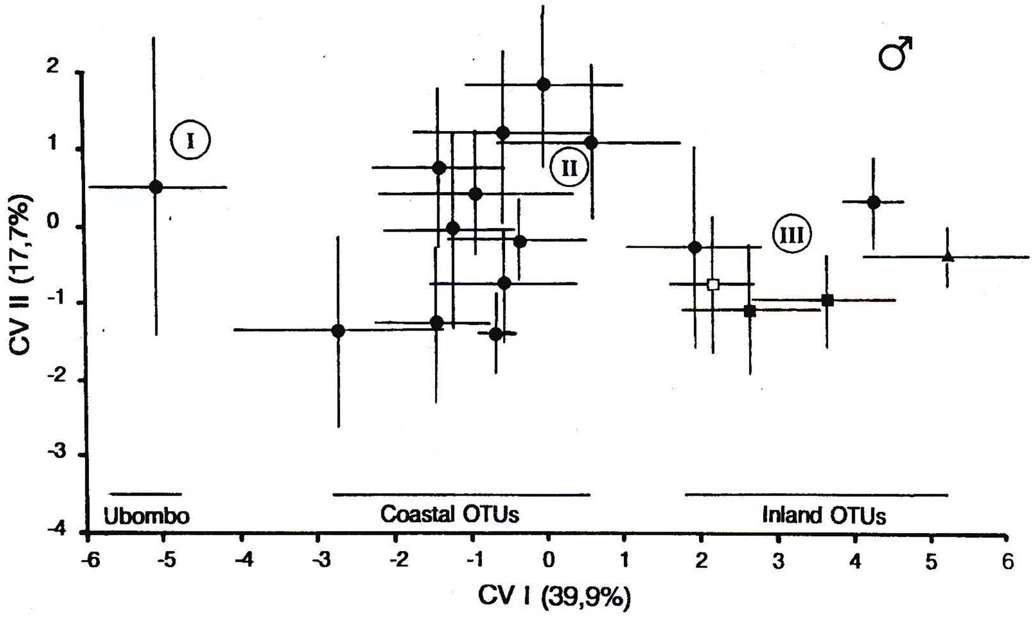
Neff and Smith (1978) pointed out that the statistical assumptions of discriminant functions analysis (*viz.* multivariate normality and equality of within-group covariance matrices) are more exacting than those of principal components analysis, so that the latter is more appropriate for evaluating whether or not hybrids are present between parapatric OTUs. Principal components analyses (Fig. 5.9) showed, however, that the major coastal and inland phena within *A. hottentotus* are well separated along the first component. But, since this component reflected mainly size, which appears to be susceptible to environmental influence, genetic discontinuity between the coastal and inland phena cannot necessarily be assumed.

Thorpe (1976) showed that when extreme groups are included in discriminant functions analysis, patterns of differentiation between phenetically similar subgroups may be obscured. The inclusion of the smaller-sized Ubombo [17] and St. Lucia [16] samples, and coastal OTUs from the Eastern Cape, in the discriminant functions analyses described above may, therefore, have obscured potential phenetic discontinuities between the coastal and inland phena in KwaZulu-Natal.

Since the resolution power of discriminant functions analysis increases as extreme groups are eliminated (Thorpe 1976), a further series of analyses targeting only one

Fig. 5.10. Plot of the mean and one standard deviation of specimen scores along the first two canonical variate axes for OTU samples of female and male *A. hottentotus*. Roman numerals denote major phena that are discriminated also in distance phenograms and principal components axes scattergrams (Figs. 5.7 - 9). Symbols indicate: (●) - 2n=30; (■) - 2n=34; (▲) - 2n=36; (□) - 2n-? (Heilbron).


♀
I
II
III
Ubombo
Coastal OTUs
Inland OTUs
CV II (14,5%)
CV I (46,3%)
4
3
2
1
0
-1
-2
-3
-4
-6
-5
-4
-3
-2
-1
0
1
2
3
4
5

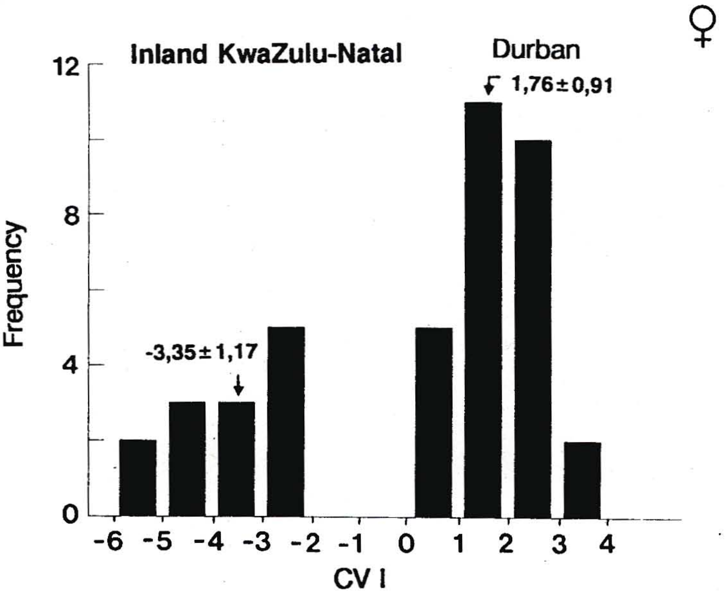

♂
I
II
III
Ubombo
Coastal OTUs
Inland OTUs
CV II (17,7%)
CV I (39,9%)
2
1
0
-1
-2
-3
-4
-6
-5
-4
-3
-2
-1
0
1
2
3
4
5
6

OTU (Durban [12]) of the coastal phenon in KwaZulu-Natal, and varying combinations of OTUs from the inland phenon, were performed. A two-group analysis of individuals representing OTUs with 2n = 30 showed that multivariate differences between the Durban and Pietermaritzburg/Karkloof/Estcourt OTUs [13-15] were highly significant (♀: $F_{(16,26)} = 10{,}95$; $p < 0{,}001$; ♂: $F_{(16,25)} = 17{,}72$; $p < 0{,}001$). Individuals were assigned to their correct *a priori* groupings with 100% accuracy, with no overlap of discriminant scores (Fig. 5.11). Similarly, multivariate differences between five groups of individuals representing the three different cytotypes (2n = 30: Durban [12], Pietermaritzburg/Karkloof/Estcourt [13-15]; 2n = ?: Heilbron [19]; 2n = 34: Wakkerstroom/Ermelo [20-21]; and 2n = 36: Belfast [22]) were highly significant (♀: $F_{(80,273)} = 4{,}77$; $p < 0{,}001$; ♂: $F_{(64,166)} = 4{,}99$; $p < 0{,}001$). Although the overall *a posteriori* classifications in this analysis were less accurate (♀ - 96%; ♂ - 94%), specimens from Durban (Cluster A) plotted well to the left of the inland OTUs (Clusters B-E) along the first canonical variate axis (Fig. 5.12), and were correctly classified with 100% accuracy. Most misidentifications involved specimens from the four inland OTUs, which tended to plot apart with minimal overlap along the second axis.

These results were congruent with those from principal component analyses (Fig. 5.9d), and suggested that there are no morphological intermediates (hybrids) between the Durban [12] and inland OTUs [13-15]. This implied that the major coastal and inland phena do not interbreed in their zone of parapatry. In contrast, the tendency for the inland OTU [13-15, 18-22] clusters to overlap slightly along the second axis (Fig. 5.12) suggested the existence of morphological intermediates, and thus interbreeding between the different cytotypes. But, size showed a clinal pattern of variation in relation to altitude and climate in this region, so it is again possible that the observed craniometric variation may have a strong environmental component which served to mask potential discontinuities between the cytotypes.

This possibility was supported by a further analysis in which the Durban specimens were excluded from analysis. This effectively removed most of the influence of clinal size variation (see Fig. 5.6), and presumably also reduced the environmental component of phenotypic variation, since the remaining specimens come from the same biotic zone with roughly similar climates and altitudes. Discriminant

Fig. 5.11. Frequency distribution plot of specimen scores along the first canonical variate axis for male (n = 42) and female (n = 43) *A. hottentotus* representing OTUs from Durban and Inland KwaZulu-Natal (Pietermaritzburg\Karkloof\Estcourt). Group centroids are indicated by arrows.


♀
Inland KwaZulu-Natal
Durban
1,76±0,91
-3,35±1,17
Frequency
12
8
4
0
-6 -5 -4 -3 -2 -1 0 1 2 3 4
CV I

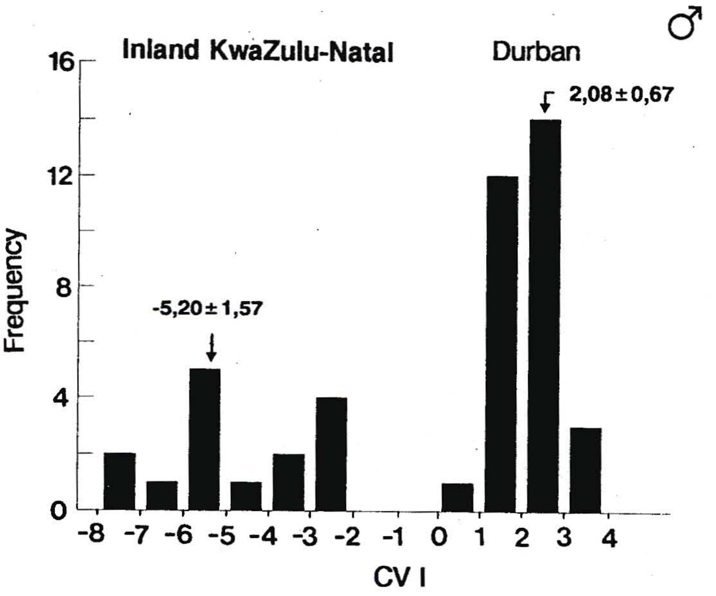
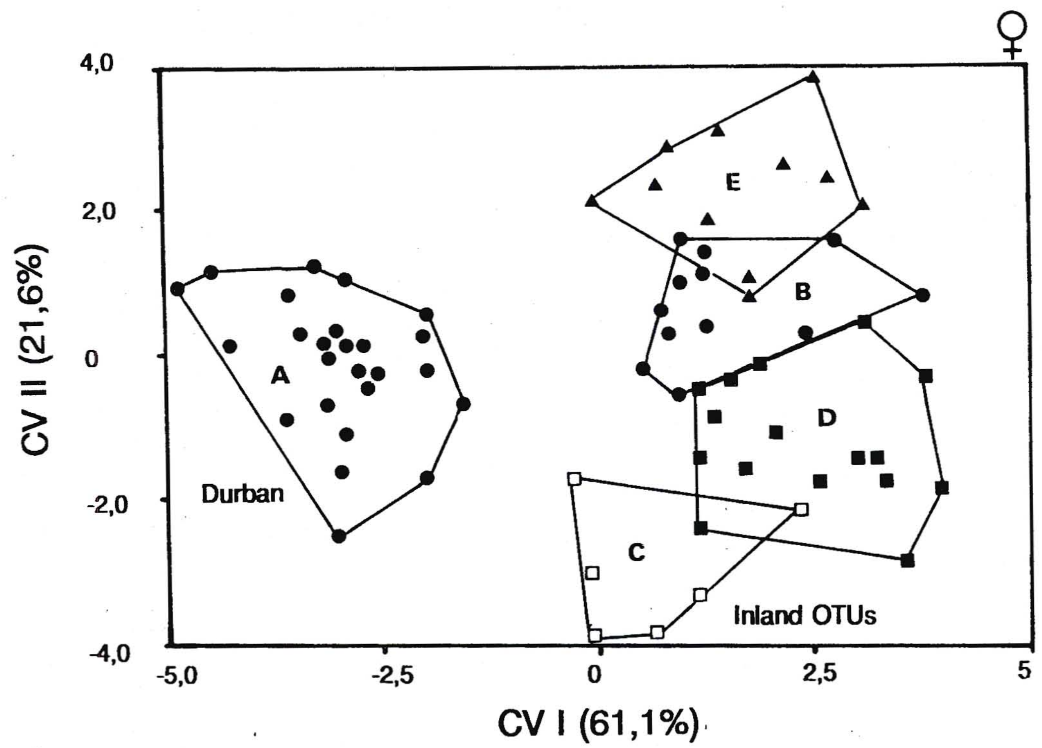
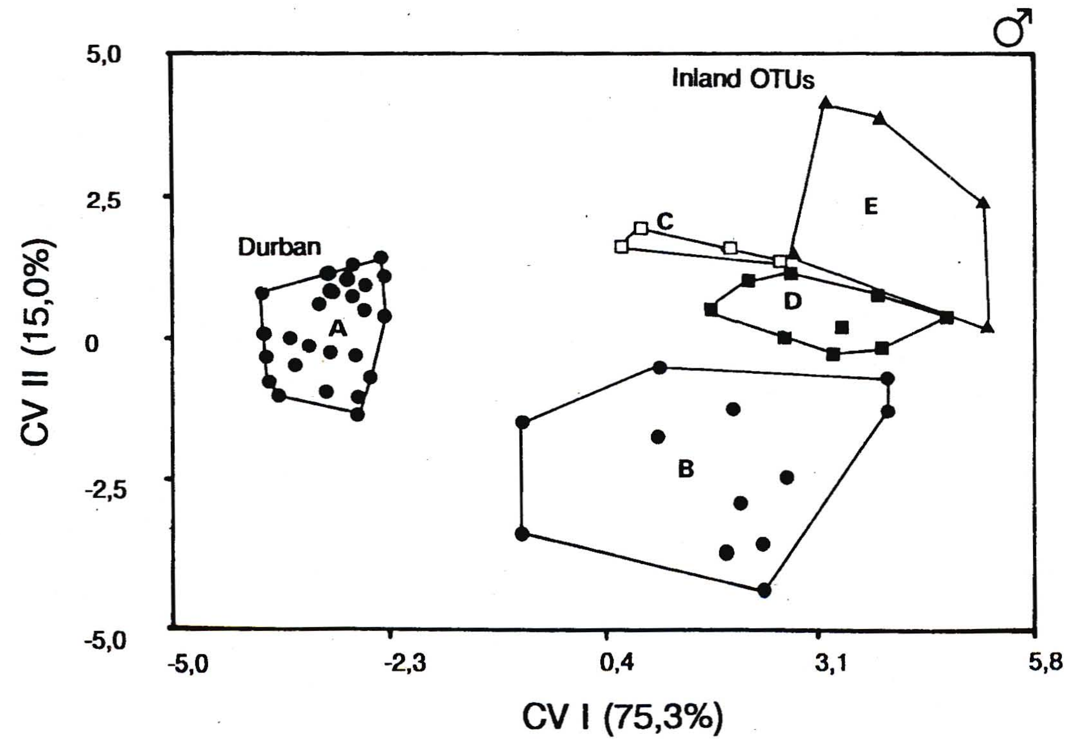

♂
Inland KwaZulu-Natal
Durban
2,08±0,67
-5,20±1,57
Frequency
16
12
8
4
0
-8 -7 -6 -5 -4 -3 -2 -1 0 1 2 3 4
CV I

Fig. 5.12. Pairwise comparisons of the first two canonical variate axes based on discriminant functions analyses of female and male *A. hottentotus* from five OTUs: A - Durban; B - inland KwaZulu-Natal (Pietermaritzburg, Karkloof, Estcourt); C - Heilbron; D - southern Mpumalanga (Wakkerstroom and Ermelo); and E - eastern Mpumalanga highveld (Belfast\Dullstroom). Symbols indicate: (●) - 2n=30; (■) - 2n=34; (▲) - 2n=36; (□) - 2n=?.

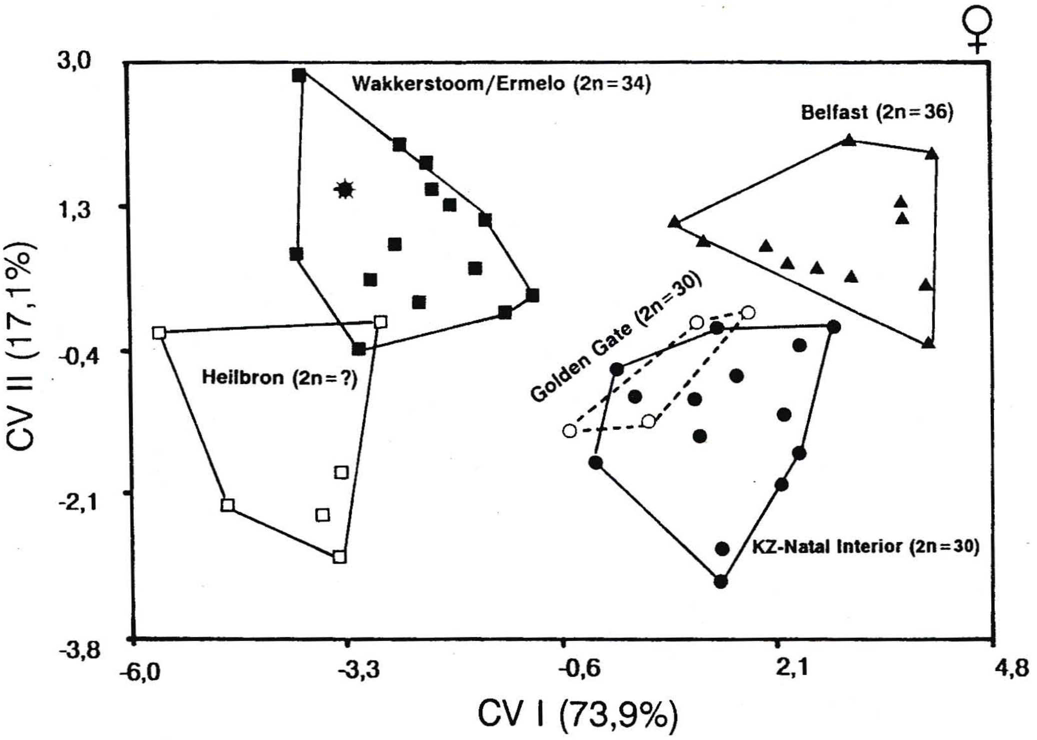

♀
4,0
2,0
0
-2,0
-4,0
CV II (21,6%)
-5,0
-2,5
0
2,5
5
CV I (61,1%)
E
B
A
D
C
Durban
Inland OTUs

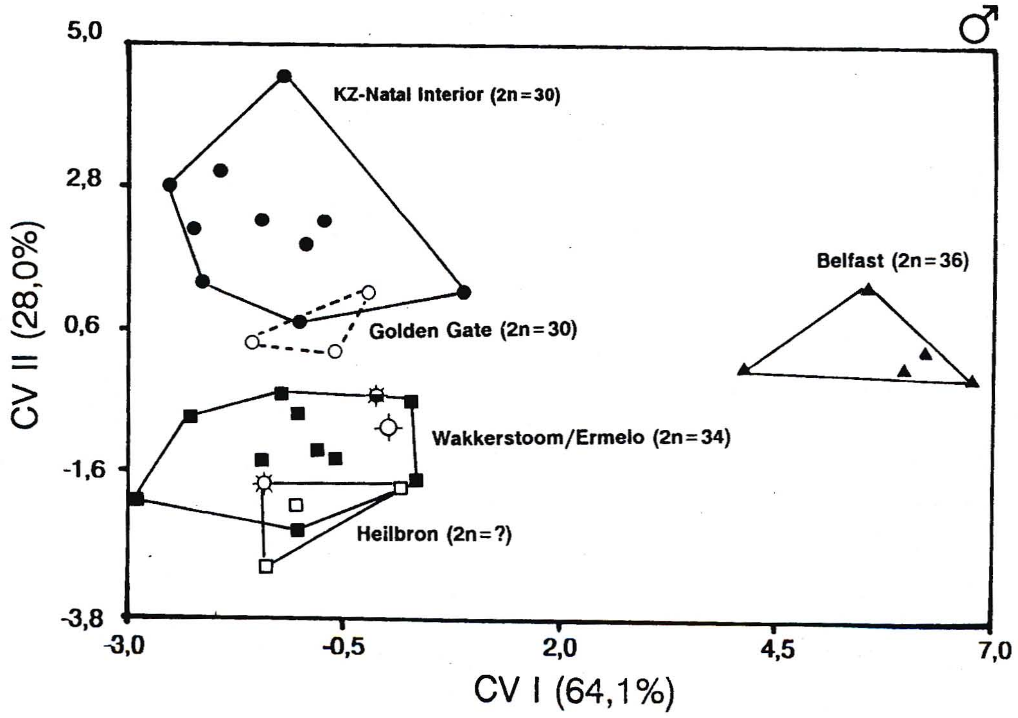

♂
5,0
2,5
0
-2,5
-5,0
CV II (15,0%)
-5,0
-2,3
0,4
3,1
5,8
CV I (75,3%)
Inland OTUs
E
C
Durban
A
D
B

functions analysis of four groups representing the three cytotypes (2n = 30: Pietermaritzburg/ Karkloof/ Estcourt [13-15]; 2n=?: Heilbron [19]; 2n = 34: Wakkerstroom/Ermelo [20-21]; and 2n = 36: Belfast [22]) revealed that multivariate differences between them were highly significant (♀: $F_{(48,87)} = 4{,}54$; $p < 0{,}001$; ♂: $F_{(48,39)} = 2{,}46$; $p = 0{,}002$). Individuals were assigned to their correct *a priori* groups with high accuracy (♀: 98%; ♂: 92%), and pairwise comparison of the first two canonical axes (Fig. 5.13) showed that specimens representing the 2n = 30 OTUs from inland KwaZulu-Natal clustered apart from the other cytotypes. Similarly, the 2n = 34 and 2n = 36 OTUs separated widely along the first axis, and specimens of unknown karyotype from Heilbron grouped with the 2n = 34 specimens from Wakkerstroom and Ermelo. The 2n = 30 specimens from Golden Gate (plotted *a posteriori* following the method of Dippenaar and Rautenbach 1986, owing to small sample sizes) showed closer phenetic affinity to the 2n = 30 cytotype from inland KwaZulu-Natal than to OTUs elsewhere in the Free State, or the 2n = 34/36 cytotypes in Mpumalanga.

While craniometric variation in *A. hottentotus* is dominated by overall size, subtle shape differences distinguish ten geographic subgroups within the three major size-delimited phena: 1) Ubombo [17] - markedly smaller in size, with relatively broader posterior palates but comparatively narrow rostra; 2) a Western Cape group [1-2] and 3) a Mpumalanga group [23] - both with relatively long mandibular rami; 4) an Eastern Cape group [3-5] - with relatively narrow posterior palates and rostra; 5) a coastal Transkei/KwaZulu-Natal group [6-12] - with mandibular rami intermediate in length, but comparatively broad rostra and palates; 6) a Zululand group [17] - characterized by smaller size, comparatively long mandibular rami, broad posterior palates and relatively narrow rostra; 7) an inland KwaZulu-Natal group [13-15], ranging marginally into the Free State [18] - with relatively broader rostra; 8) a Mpumalanga highveld group [20,21] - with comparatively narrow rostra; 9) a northwestern Free State group [19], which although similar in size to the preceding group (8), was well discriminated in ordination analyses (Figs. 5.9c and 5.12), and may be geographically isolated; and 10) a group [22] from the Steenkampsberge near Belfast - distinguished mainly by its markedly larger size.

Fig. 5.13. Pairwise comparisons of the first two canonical variate axes based on discriminant functions analyses of individuals representing four inland OTUs in *A. hottentotus*. Specimens from Golden Gate were plotted *a posteriori* using the method of Dippenaar and Rautenbach (1986), having been excluded from analyses owing to small sample sizes. Symbols are: (●/○) - 2n=30; (■) - 2n=34; (▲) - 2n=36; (□) - 2n=?; (✸) - holotype of *A. i. septentrionalis*; (☼) - holotype of *A. h. orangensis*; (✹) - holotype of *A. h. drakensbergensis*; (⌖) - holotype of *A. h. garneri*.


♀
3,0
1,3
-0,4
-2,1
-3,8
CV II (17,1%)
Wakkerstoom/Ermelo (2n=34)
Belfast (2n=36)
Golden Gate (2n=30)
Heilbron (2n=?)
KZ-Natal Interior (2n=30)
-6,0
-3,3
-0,6
2,1
4,8
CV I (73,9%)


♂
5,0
2,8
0,6
-1,6
-3,8
CV II (28,0%)
KZ-Natal Interior (2n=30)
Belfast (2n=36)
Golden Gate (2n=30)
Wakkerstoom/Ermelo (2n=34)
Heilbron (2n=?)
-3,0
-0,5
2,0
4,5
7,0
CV I (64,1%)

5.3.2.4 Transition zones and biogeographic barriers.

The geographical limits and extent of phenotypic differentiation between the geographic groups defined above are illustrated in Figure 5.14, where the position and intensity of transition zones are shown by symbols representing increasing ATD values. Within the major coastal phenon, the southern transition between nominotypical *A. hottentotus* [3-5] and the OTUs in the Western Cape [1-2] is steeper than the northern transition to the KwaZulu-Natal/Transkei [6-12] populations. The southern transition corresponds with biogeographic barriers, such as the dry Gouritz River valley which may act as an obstacle limiting genetic introgression between two subspecies of *Myosorex longicaudatus* (Dippenaar *pers. comm.*[1]), and the intrusion of karroid scrub to the coast in the vicinity of Mossel Bay. This transition zone also coincides with climatic changes from a summer to a winter rainfall pattern, and a major vegetational alteration from coastal savanna and woodland to false fynbos and fynbos (South-West Cape biotic zone). Similarly, the transition between nominotypical *A. hottentotus* [3-5] and those in coastal Transkei/KwaZulu-Natal [6-12] corresponds with the dry Great Fish River valley, the Amatola mountains, and a change from semi-karooid Valley Bushveld (Acocks' 1988 veld type 23) to coastal tropical forest vegetation (veld types 1, 3 and 7).

The more gradual northern cline, between southern KwaZulu-Natal and Zululand, does not correspond with major physiographic or climatic changes, but coincides with a region where there are many perennial rivers which reach the sea, often via estuaries that stretch several kilometres inland. These may act as barriers to inter-population gene flow. Large waterways are known to serve as biogeographic obstacles to several fossorial mammals, and although *A. hottentotus* is a competent swimmer in laboratory aquaria (Hickman 1986), there is no evidence to suggest that individuals will readily take to water. Even if forced to swim, for example during times of flooding, it seems unlikely that individuals will have sufficient stamina and navigation skills to successfully cross waterways where they will be exposed to swirling currents, predators and floating or static obstacles such as driftwood and rocks. Whatever gene flow takes

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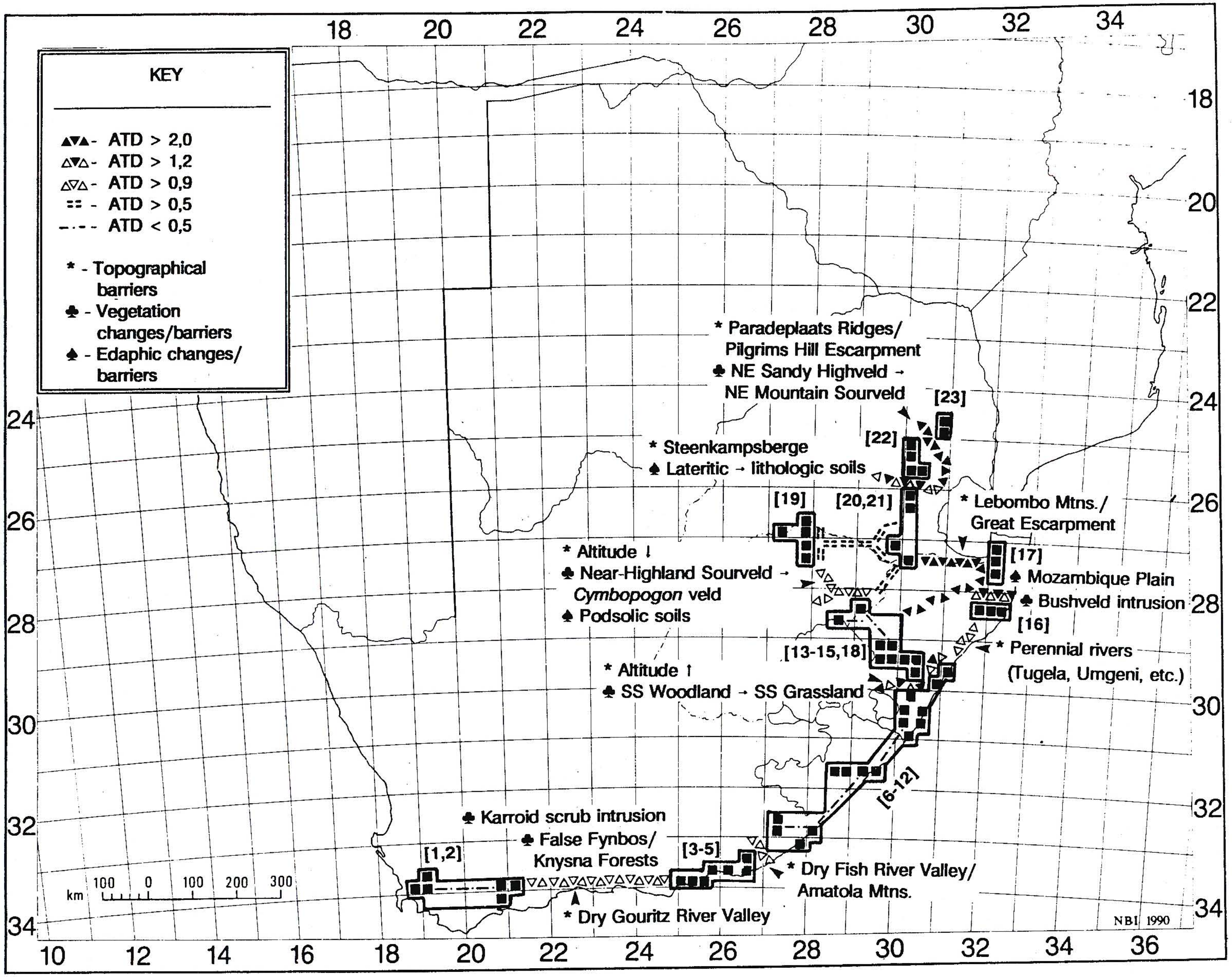
Fig. 5.14. Map showing the geographical pattern of phenetic differentiation in *A. hottentotus*, and the position and intensity of transition zones (indicated by mean ATD values between OTUs from single standardized data for males and females) in relation to topographical, vegetational and edaphic barriers that may limit gene flow. OTU numbers (see Table 5.1) within each group are given in square brackets.


KEY
▲▼▲- ATD > 2,0
△▼△- ATD > 1,2
△▽△- ATD > 0,9
== - ATD > 0,5
-·-- ATD < 0,5
* - Topographical barriers
♣ - Vegetation changes/barriers
♠ - Edaphic changes/barriers
* Paradeplaats Ridges/ Pilgrims Hill Escarpment
♣ NE Sandy Highveld → NE Mountain Sourveld
[23]
[22]
* Steenkampsberge
♠ Lateritic → lithologic soils
[19]
[20,21]
* Lebombo Mtns./ Great Escarpment
[17]
♠ Mozambique Plain
♣ Bushveld intrusion
[16]
* Altitude ↓
♣ Near-Highland Sourveld → Cymbopogon veld
♠ Podsolic soils
[13-15,18]
* Perennial rivers (Tugela, Umgeni, etc.)
* Altitude ↑
♣ SS Woodland → SS Grassland
[6-12]
♣ Karroid scrub intrusion
♣ False Fynbos/ Knysna Forests
[1,2]
[3-5]
* Dry Fish River Valley/ Amatola Mtns.
* Dry Gouritz River Valley
km 100 0 100 200 300
NBI 1990
18 20 22 24 26 28 30 32 34
18 20 22 24 26 28 30 32 34
24 26 28 30 32 34
10 12 14 16 18 20 22 24 26 28 30 32 34 36

place across these water barriers probably occurs during periods of drought when the rivers are greatly reduced in volume, or may even cease to flow with the result that temporary land connections for dispersal are available. Golden moles are known to use river systems for dispersal (Meester *et al.* 1986:21), and I have often observed their subsurface burrows in dry stream or river beds, implying that they are well-adapted for dispersal across such transient land bridges.

The steep transition zone between the St. Lucia [16] and Ubombo [17] OTUs in northern Zululand coincides with major physiographic and less marked vegetation changes. The Ubombo populations inhabit the eastern slopes of the Lebombo mountains where the most eastward extension of the plateau meets the Mozambique plain (Wellington 1955). Rainfall in this area is 500-900 mm p.a., and the vegetation is Zululand thornveld (Acocks' veld type 6) or lowveld (Acocks' veld type 10). The Mozambique plain, which consists of porous sand deficient in organic matter, supports lowveld and Zululand Palm Veld (Acocks' veld type 1b), and extends to just north of St. Lucia, where it gives way to the south-eastern coastal belt characterized by higher precipitation (about 1200 p.a.) and coastal dune forest (Acocks' 1988). There are no records of *Amblysomus* from the Mozambique plain, where the species *Calcochloris obtusirostris* instead predominates. The Maputaland coast was located at the foot of the Lebombo range until the Pliocene, when the Mozambique coastal plain was formed by gradual uplift of the subcontinent, and the deposition of shallow-water marine sediments (Maud 1980). This suggests that *A. hottentotus* may have ranged up the coast to Ubombo and Ingwavuma until geological events in the Pliocene resulted in the isolation of the northern populations on the eastern slopes of the Lebombo mountains, where these populations first appear in Pleistocene deposits (Avery 1991). The craniometric uniqueness of the Ubombo OTUs may thus be the result of differentiation following a vicariance event induced by physical, climatic and vegetation changes associated with the formation of the Mozambique plain. These factors probably serve to prevent geographic contact and gene exchange with the St. Lucia populations further south to the present day.

The transition zone between the Ubombo populations and those in Mpumalanga [20-21] corresponds with barriers such as Lebombo mountains and northern Drakensberg escarpment, and vegetational changes from savanna woodland to grassland. These physiographic and vegetational changes may underlie the absence of known intermediate demes, and thus effectively prevent gene flow between populations in these areas.

Between Durban [12] and Pietermaritzburg/Karkloof [13-14] in KwaZulu-Natal, the transition zone is as steep as that between the Western and Eastern Cape, and corresponds with major altitudinal, climatic and vegetational changes (as already discussed). Beyond this transition zone, clines within the inland phenon are more gradual. Although these localities span different physiographic regions divided by the Great Escarpment, all exist in Near-Highland Sourveld (Acocks' veld type 57b), supported by lateritic soils with a high humus content and good water-retaining properties (Wellington 1955). It is thus unlikely that edaphic and vegetation factors pose any obstacles to gene flow between the OTUs in this region. Instead, physiological adaptation to colder climates with gradually increasing altitudes as one ascends the Low Berg, is probably the main factor underlying the gradient in body size, whereas phenotypic variation may be the result of local area-effects, or negative heterotic effects associated with karyotypic incompatibility.

The steeper phenetic transition between Golden Gate [18] and Heilbron [19] coincides with a decrease in altitude, change from Near-Highland Sourveld to drier *Cymbopogon - Themeda* veld (Acocks' veld type 48), and with a transformation to podsolic soils with a high clay content and tendency to form impervious crusts during the dry winter months (Wellington 1955). These altitudinal, edaphic and vegetational changes may collectively act as a barrier to gene flow between the Golden Gate and Heilbron demes, the latter probably representing a relict and geographically-isolated population of the 2n = 34 cytotype.

Between the 2n = 34 population at Ermelo [21], and the 2n = 36 populations near Belfast [22], the steep phenotypic transition corresponds not only with an increase in altitude associated with the Steenkampsberge, but also with edaphic variation from lateritic to lithologic soils which are shallow and deficient in essential plant nutrients (Wellington 1955). Physiographic and geological factors associated with the incidence of the Steenkampsberge may thus reinforce possible chromosomal barriers to gene flow between these cytotypes.

The steepest morphometric transition of all is between the populations in the Belfast area [22], and those from Graskop about 80 km away [23]. Although these

OTUs both occur on the Great Escarpment, they represent different cytotypes separated by several mountain ranges (Wellington 1955), and deep valleys where sourish mixed bushveld intrudes from the north to separate Near-Highland sourveld in the vicinity of Belfast, from Mountain Sourveld (Acocks' veld type 8) in the Graskop-Sabie district.

The Graskop OTU(s) resembles the OTUs from coastal and inland KwaZulu-Natal karyotypically, but appear to be geographically disjunct from these taxa since no intermediate populations with 2n = 30 are known. Any geographic continuity that may occur between these groups is probably restricted to areas below the escarpment in Mpumalanga and northeastern KwaZulu-Natal, possibly on land supporting Piet Retief Sourveld (Acocks veld type 63) and Northern Tall Grassveld (Acocks' veld type 64) which connect these regions. However, the absence of known contact between these groups, together with the tendency for specimens from this region to plot apart from those in KwaZulu-Natal and Mpumalanga (Fig. 5.9), indicates that the Graskop OTUs should provisionally be considered a distinct geographic group.

5.4 TAXONOMIC CONCLUSIONS

5.4.1 Cryptic species

My analyses showed that *A. hottentotus*, as traditionally defined, comprises ten distinct geographic groups worthy of taxonomic recognition. Two populations in the Mpumalanga highveld - Wakkerstroom/Ermelo (2n = 34) and Belfast (2n = 36) - are phenotypically and karyotypically distinct. Based on indirect evidence from ordination analyses, they do not appear to interbreed with the 2n = 30 populations in KwaZulu-Natal, or at Graskop. These populations thus satisfy the criteria of the evolutionary species concept, and each should thus be afforded full specific status.

The 2n = 34 populations, including the Heilbron OTU(s) which group with the Mpumalanga populations in PCA scatterplots (Fig. 5.9d), include four type specimens (Fig. 5.13): *A. corriae septentrionalis* Roberts, 1913 (≡ *A. iris septentrionalis sensu* Meester 1974; type locality = Wakkerstroom); *A. h. garneri* Roberts, 1917 (type locality = Piggs Peak, Swaziland); *A. h. drakensbergensis* Roberts, 1946 (type locality = Wakkerstroom); and *A. h. orangensis* Roberts, 1946 (type locality = Heilbron). Since specimens from this region share a common karyotype, and group closely together in cluster and ordination analyses, there are not two species in Mpumalanga, but only one - for which *A. c. septentrionalis* is the prior name. Roberts (1913, 1946) was, therefore, apparently mistaken in referring *Amblysomus* from Wakkerstroom to two different species.

As *A. c. septentrionalis* differs craniometrically and karyotypically from all coastal *Amblysomus*, it cannot be assigned to either *A. corriae* or *A. hottentotus*. This taxon must, therefore, be referred to the distinct species *A. septentrionalis*, with *A. s. garneri*, *A. s. drakensbergensis* and *A. s. orangensis* as junior synonyms.

No name is available for the 2n = 36 OTU from the Belfast district of the Mpumalanga highveld. This species is hereafter referred to as *Amblysomus Species A*, pending the publication of a formal description elsewhere.

The Ubombo/Ingwavuma population(s) traditionally referred to *A. h. marleyi* are craniometrically well-differentiated from other *Amblysomus* in KwaZulu-Natal, not only by their markedly smaller size, but also by subtle differences in cranial shape. Given that these demes differ from others also in fur colour (Roberts 1951), and appear to be geographically isolated, they are here referred to the distinct species *A. marleyi*.

5.4.2 Subspecies in *Amblysomus hottentotus*

The populations of *A. hottentotus* in inland KwaZulu-Natal were distinguished by larger size and subtle differences in cranial shape. Indirect evidence from ordination analyses suggested that they do not interbreed with parapatric coastal OTUS. Their allocation to a distinct species thus seems warranted. However, the phenetic distinctness of these populations may be largely the result of clinal variation in size, with associated allometric differences in cranial shape. Furthermore, the extent of genetic differentiation between the Pietermaritzburg (inland) and Umdoni (coastal) populations is minimal (Filipucci *et al.* 1991), and well within the range characterizing conspecific populations of mammals (Ferguson 1980). This, together with the apparent chromosomal uniformity of all OTUs from KwaZulu-Natal (Section 4.3.1), indicated that the coastal and inland populations should be treated as only subspecifically distinct. The inland OTUs are, therefore, referred to the taxon *A. h. longiceps* (Broom, 1907a), the type locality of which is Pietermaritzburg.

The phenetic gaps separating the populations in KwaZulu-Natal, Transkei and the Eastern Cape are relatively small, and ordination analyses suggest that these geographic sub-groups intergrade in zones of parapatry. Only subspecific distinction between them seems warranted. The populations in the Eastern Cape (Albany, Port Elizabeth, Alexandria) represent the nominotypical subspecies *A. h. hottentotus*, whereas those from Transkei and southern KwaZulu-Natal are referred to *A. h. pondoliae* Thomas and Schwann, 1905, which has priority over *A. h. natalensis* Roberts, 1946.

5.4.3. Status and affinity of St. Lucia *Amblysomus*

The St. Lucia OTU of *A. hottentotus* is phenetically well-differentiated from *A. h. pondoliae* and *A. marleyi*, and would seem to represent a distinct subspecies of *A. hottentotus*. However, *Amblysomus* specimens from this area have traditionally been referred also to *A. i. iris* (type locality = Umfolozi Station), which is geographically isolated from *A. i. corriae* in the Cape. *A. i. iris* is cranially almost identical to *A. hottentotus*, although it tends to be somewhat smaller with more feeble claws (Ellerman *et al.* 1953). The main criterion used to distinguish between these forms is fur colour, which is smoky blackish in *A. i. iris*, without the rufous tinge characteristic of *A. hottentotus* (Thomas and Schwann, 1905b:259).

Broom (1907a:294) noted that fur colour varies markedly (from reddish brown to darkish black) in nominotypical *A. hottentotus*. He argued that since one of the *A. i. iris* paratypes designated by Thomas and Schwann (1905b) has fur with a rufous tinge, and size varies considerably within *A. hottentotus*, nominotypical *A. iris* should be afforded only subspecific status within *A. hottentotus*. This treatment was subsequently endorsed by Allen (1939) and Ellerman *et al.* (1953), leading to two null hypotheses:

H_{Φ}^{1}: all specimens of *Amblysomus* from St. Lucia represent a single, panmictic population; and

H_{Φ}^{2}: this population represents *A. hottentotus*, rather than the distinct species *A. iris*

In a series ($n = 35$) of *Amblysomus* from St. Lucia in the Transvaal Museum, dorsal fur colour shows almost complete intergradation, from reddish-black (10R 2/1) through very dark reddish brown (7,5R 2/2) to brownish-black (5YR 3/1). Fourteen specimens have a pronounced rufous tinge (reddish-brown 5YR 4-5/8) extensively on the flanks and rump, while another four show small rufous patches restricted to only certain parts of these regions. Specimens lacking any rufous tinge range in ventral colour from brownish-black (10YR 2/3) to dark-brown (7,5YR 3/3). But, those with a rufous tinge vary in ventral colour, from dark-brown (10YR 3/4) through brown (10YR 4/6) and dull yellow-orange (10YR 6/4) to orange (7,5YR 6/6). This is the result of a progressive increase in the area covered by reddish-brown fur, from the flanks inwards to the middle of the ventrum.

Multivariate analysis of variance indicated that those specimens lacking rufous fur (Dark group) differed significantly ($F_{(6,28)} = 3{,}21$; $p = 0{,}01$) in Munsell colour attributes (hue, value and chroma) from those with a rufous tinge (Red group). However, the population dispersions of these groups differed significantly ($F_{(21,1000)} = 2{,}338$; $p < 0{,}001$), indicating that a fundamental assumption of MANOVA was violated.

Principal components analysis, which does not suffer the rigid assumption of homoscedasticity, confirmed that there is considerable intergradation of colour between the Dark and Red groups. Although most of the specimens with a rufous tinge tended to plot above those lacking reddish-brown fur along PCII, there was overlap of component scores for the Red and Dark groups along both axes (Fig. 5.15). PCI was influenced most strongly by dorsal hue (-0,960), which declined from left to right, in contrast to dorsal value and chroma which did not load highly (-0,044 and -0,134 respectively), or vary conspicuously. Separation along this axis reflected mainly an increase in dominant spectral wavelength, with a change in dorsal colour from reddish-brown to reddish-black. The three ventral colour attributes loaded highest (-0,488 to -0,633) along PCII, with hue decreasing from bottom to top, while value and chroma increased. Separation along this axis thus reflected a progressive change in ventral colour from brownish-black to orange, caused by an increase in dominant spectral wavelength, and a tendency for fur colour to become lighter and richer.

Broom (1907a) suggested that colour variation in *A. hottentotus* might be related to age, with younger animals being more reddish-brown than older, blacker animals. Single classification analyses of dorsal and ventral colour attributes (hue, value and chroma) showed that there were no significant differences between the toothwear

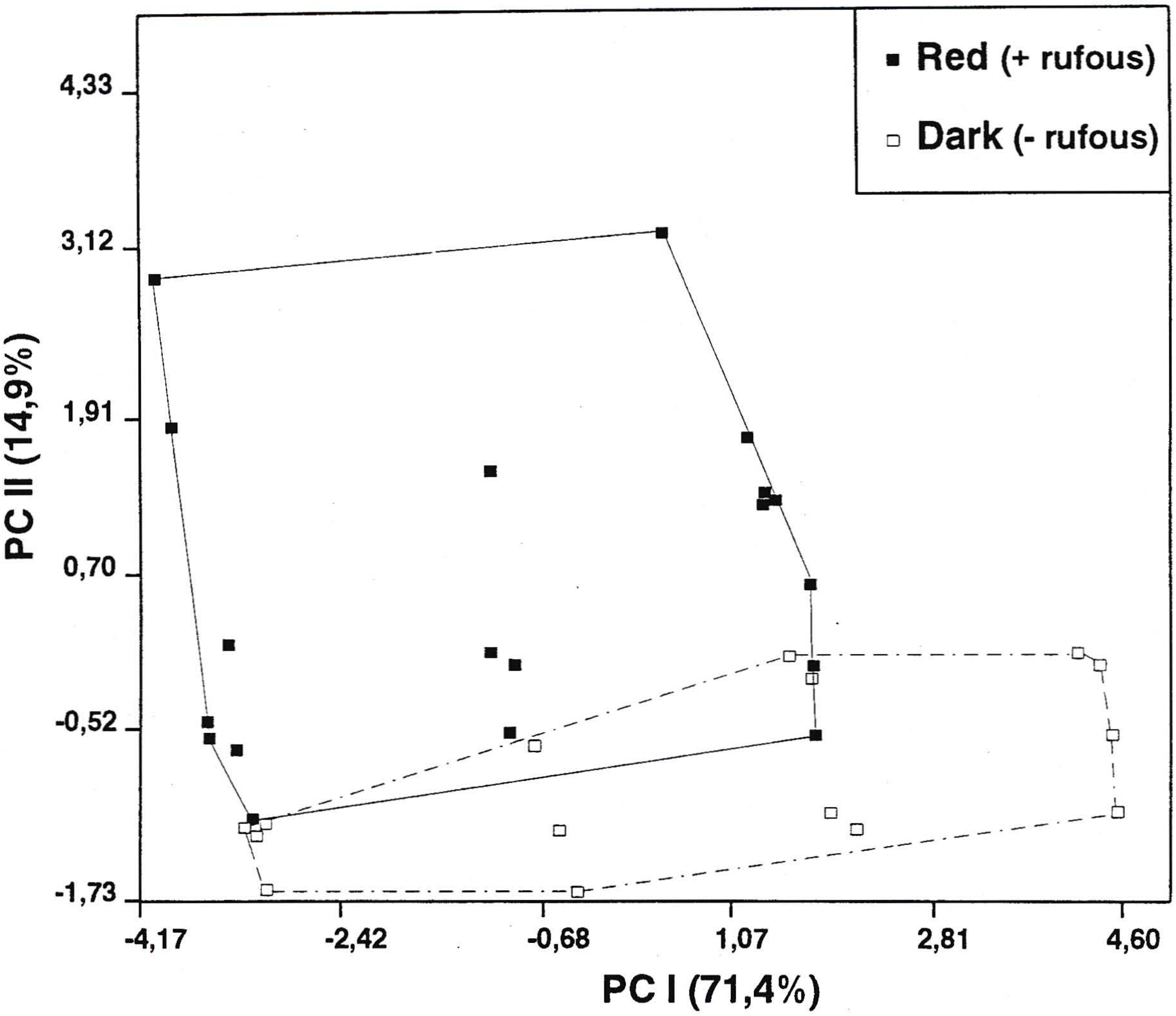


Fig. 5.15. Pairwise comparison of the first two principal component axes, computed from colourimetric data for specimens of *Amblysomus* from St. Lucia that have a rufous tinge (**Red**) to the fur, and also for those lacking any rufous tinge (**Dark**). The cophenetic correlation is 0,985

Table 5.12

Summary statistics and results of single classification analyses of variance to test for (a) age and (b) seasonal variation in dorsal and ventral colour attributes of *Amblysomus* specimens from St. Lucia, KwaZulu-Natal. H = hue; V = value; C = chroma; $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size. Although some samples showed slight skewness and/or kurtosis, Kolmogorov-Smirnoff tests indicated that normality could be assumed for all samples and variables.

a) Age\Toothwear Class variation

		DORSUM			VENTRUM		
OTU	STAT	H	V	C	H	V	C
TW2	$\bar{x}$	11,25	2,10	2,28	19,64	3,00	3,50
	sd	2,90	0,40	0,91	0,91	0,78	0,65
	n	14	8	4	14	8	4
TW3	$\bar{x}$	11,88	2,13	2,38	19,69	3,63	4,13
	sd	3,20	0,35	0,52	0,88	1,19	1,25
	n	14	8	4	14	8	4
TW4	$\bar{x}$	13,13	2,25	2,25	19,38	3,75	3,75
	sd	2,39	0,50	0,50	1,25	0,96	0,50
	n	14	8	4	14	8	4
	F	0,647	0,221	0,048	0,156	1,625	1,337
	p	0,537	0,806	0,953	0,857	0,218	0,282

b) Seasonal variation

		DORSUM			VENTRUM		
OTU	STAT	H	V	C	H	V	C
WINTER	$\bar{x}$	13,50	2,40	2,60	20,00	4,40	3,80
	sd	2,24	0,55	0,89	0,00	1,14	0,45
	n	5	5	5	5	5	5
SPRING	$\bar{x}$	12,27	2,06	2,18	19,32	3,27	3,73
	sd	2,61	0,32	0,75	1,17	0,79	1,01
	n	11	11	11	11	11	11
SUMMER	$\bar{x}$	10,00	2,17	2,33	20,00	2,50	3,33
	sd	3,16	0,41	0,52	0,00	0,55	0,52
	n	6	6	6	6	6	6
	F	2,473	1,200	0,563	1,781	7,294	0,598
	p	0,109	0,324	0,583	0,194	0,005	0,564

classes at St. Lucia (Table 5.12a). Colour variation in this sample cannot, therefore, be attributed to differences in the relative ages of adult specimens.

Colour is known to vary seasonally in some mammals, such as the yellow mongoose, which tends to be redder and darker in summer than winter (Taylor *et al.* 1990). Single classification analyses of variance of dorsal and ventral colour in winter (June, July), spring (September, October) and summer (December - February) samples revealed an analogous trend in St. Lucia *Amblysomus* (Table 5.12b). Ventral hue declined significantly from winter to summer, indicating a progressive and considerable darkening of the ventrum. Similarly, dorsal hue and ventral chroma declined (albeit non-significantly) from winter to summer samples, indicating a tendency for dorsal colour to become more reddish, and for ventral fur to become paler. Although samples sizes were small, these results suggest that colour variation observed in St. Lucia *Amblysomus* may be at least partly the result of seasonal differences in coat colour.

Another factor which may account for colour variation in the St. Lucia sample is moult stage, since in *A. hottentotus* new hairs tend to be dark in colour, and become more brownish with time between moults (Broom 1907a). Although none of the specimens studied were in the process of moulting, it is possible that some underwent their annual moult shortly before capture, and are thus darker than others. This could not be tested, however, since it is impossible to establish moult stage from study skins.

Analysis of colour attributes thus suggested that the observed intergradation in colour of St. Lucia *Amblysomus* may result from seasonal effects or the time between moults, and that interbreeding occurs between the Red and Dark specimens. However, similar colour variation exists also in large samples of nominotypical *A. h. hottentotus*, and in *A. h. pondoliae* from Port St. Johns (Broom 1907a). The existence of St. Lucia specimens with intermediate fur colour may, therefore, be simply the result of intra-populational variation in *A. hottentotus*, and not of interbreeding between the Red and Dark specimen groups. Colourimetric evidence is, therefore, too equivocal to allow acceptance of the null hypothesis that all *Amblysomus* from St. Lucia originate from the same panmictic population.

To test for possible cranial divergence among *Amblysomus* from St. Lucia, skull measurements of the Dark and Red groups were compared statistically. Univariate differences between these groups were not statistically significant (Table 5.13), except

Table 5.13

Summary statistics and results of two-way analyses of variance to test for sexual and taxonomic dimorphism in adult (TW 2-4) *Amblysomus* specimens with redder (**Red**) and darker (**Dark**) colouration, from St. Lucia, KwaZulu-Natal. $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size; * and $^\#$ denote significant *F* values at $p \leq 0{,}05$ and $p \leq 0{,}01$ respectively.

OTU	STAT	BCW	ARB	MIO	ZMB	IOW	GSL	GSH	P@P	PBM	PAL	MTL	IPG	PPL	BBW	FML	CPL	APW	MDL
Red ♀	$\bar{x}$	4,43	4,62	8,07	15,57	7,23	24,83	11,81	7,30	4,69	12,45	6,39	2,17	7,94	10,97	4,40	6,23	3,60	15,29
	sd	0,13	0,16	0,20	0,23	0,24	0,45	0,30	0,09	0,14	0,40	0,30	0,08	0,18	0,41	0,18	0,30	0,31	0,53
	n	5	5	5	5	5	5	5	5	4	5	5	5	5	5	5	5	5	5
Red ♂	$\bar{x}$	5,20	4,77	8,34	16,33	7,19	26,03	12,39	7,30	4,64	12,85	6,44	2,18	8,52	11,46	4,42	6,69	4,26	16,21
	sd	0,47	0,12	0,62	0,83	0,33	0,94	0,54	0,28	0,30	0,75	0,21	0,11	0,19	0,70	0,30	0,21	0,35	0,72
	n	4	6	6	6	6	6	6	6	6	6	6	6	4	6	6	5	6	6
Dark ♀	$\bar{x}$	4,34	4,58	7,98	15,46	6,94	24,98	11,72	7,27	4,54	12,49	6,49	2,03	8,18	11,02	4,29	6,28	3,74	15,47
	sd	0,21	0,16	0,17	0,48	0,21	0,56	0,32	0,27	0,28	0,29	0,20	0,09	0,09	0,33	0,10	0,32	0,19	0,42
	n	6	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7
Dark ♂	$\bar{x}$	4,64	4,79	8,11	15,83	7,39	25,35	12,26	7,27	4,72	12,80	6,39	2,21	8,15	11,00	4,27	6,40	3,89	15,87
	sd	0,30	0,43	0,45	0,78	0,47	1,26	0,45	0,49	0,34	0,95	0,43	0,10	0,45	0,86	0,30	0,52	0,40	0,84
	n	5	6	6	6	6	6	6	6	6	6	6	5	6	6	6	6	6	6
OTU	*F*	5,36*	0,06	1,15	1,81	0,23	0,90	0,91	0,05	0,09	0,02	0,05	3,36	0,10	0,78	1,84	0,69	1,46	0,26
SEX	*F*	15,46$^\#$	3,27	1,59	4,81*	2,95	4,77*	11,38$^\#$	0,01	0,49	1,72	0,08	6,62*	3,57	0,84	0,01	3,29	8,74	6,01*
INT	*F*	3,08	0,08	0,19	0,61	3,39	1,37	0,10	0,01	0,86	0,04	0,41	4,84*	6,77*	1,03	0,04	1,27	4,11	1,07

for basal claw width, which was slightly smaller in darker specimens. Sexual differences within each group were more pronounced, however, with males being significantly larger (particularly in ZMB, GSL, GSH and IPG).

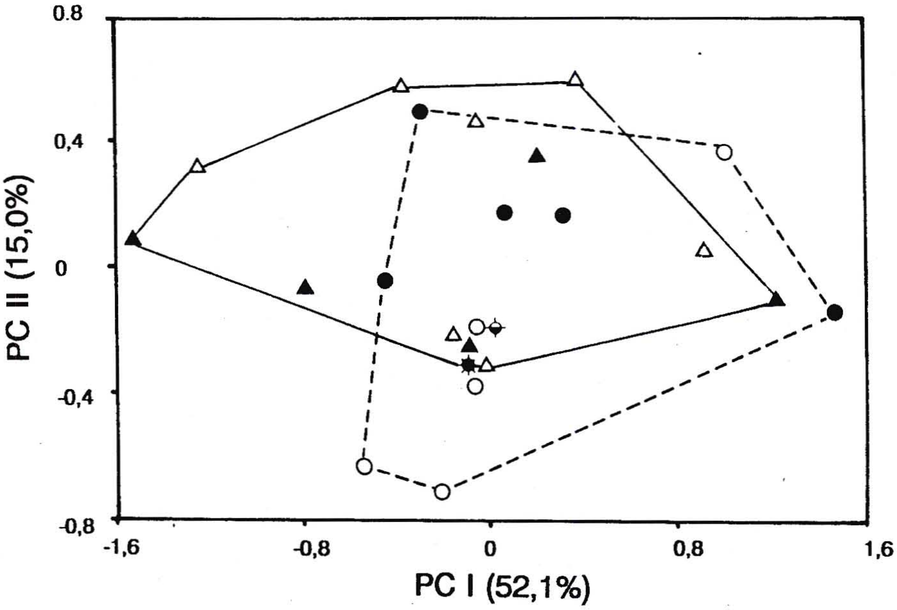
Multivariate analysis of variance showed that craniometric differences between the darker and redder forms are not significant ($F_{(18,5)} = 1{,}28$; $p = 0{,}423$). In principal components analysis scatterplots (Fig. 5.16), and in pairwise comparisons of the first two canonical variate axes (not illustrated), the two groups overlapped broadly with the holotypes of *A. h. pondoliae*, *A. h. natalensis* and *A. i. iris* plotting closely together. Similarly, the groups were not well-differentiated in phenograms based on average taxonomic distance coefficients (Fig. 5.16) or correlation coefficients (not illustrated).

The Red and Dark specimen groups from St. Lucia did not, therefore, differ significantly in cranial size and shape. This is consistent with the lack of apparent karyotypic differences between *A. hottentotus* and *A. i. iris* (Section 4.3.1), and the observed intergradation in fur colour. Craniometric, colourimetric and karyotypic evidence thus sanctioned acceptance of the null hypothesis (H_{Φ}^{1}) that all *Amblysomus* specimens from St. Lucia represent a single, panmictic population.

To test the null hypothesis (H_{Φ}^{2}) that the St. Lucia specimens represent *A. hottentotus* and not *A. iris*, colourimetric data for the Dark and Red groups from St. Lucia were compared with those of *A. i. corriae* from the Western Cape. Single classification analyses of variance indicated that significant differences exist between the three groups in all attributes except dorsal hue (Table 5.14). Similarly, MANOVA indicated that the three groups differed significantly when all attributes are analysed simultaneously ($F_{(18,130)} = 10{,}74$, $p < 0{,}001$).

In a scatterplot comparing the first two principal component axes (Fig. 5.17), the St. Lucia specimens plotted well to the left of *A. i. corriae* along PCI. Although the Red and Dark specimens from St. Lucia tended to plot apart along PCII, there was considerable overlap of their scores along both axes. PCI was influenced most strongly by dorsal and ventral chroma (-0,493 and -0,522 respectively), dorsal value (-0,412) and ventral hue (-0,522), all of which decreased from left to right. Increasing scores along axis reflected an increase in the dominant spectral wavelength of ventral fur, a

Fig. 5.16. Phenetic relationships among St. Lucia *Amblysomus* specimens which possess a rufous tinge (**H**) as in *A. hottentotus*, and those lacking any rufous tinge (**I**), as in *A. i. iris*. Data for the sexes were standardized individually and then pooled for principal components analysis (co-phenetic correlation = 0,987) and cluster analysis of average taxonomic distances (co-phenetic correlation = 0,865). Symbols indicate: (●) - male specimens with a rufous tinge; (○) - female specimens with a rufous tinge; (▲) - male specimens lacking a rufous tinge; (△) - female specimens lacking a rufous tinge; (◒) - holotype of *A. h. natalensis*; (✸) - holotype of *A. i. iris*.


0.8
0,4
0
-0,4
-0,8
PC II (15,0%)
-1,6
-0,8
0
0,8
1,6
PC I (52,1%)

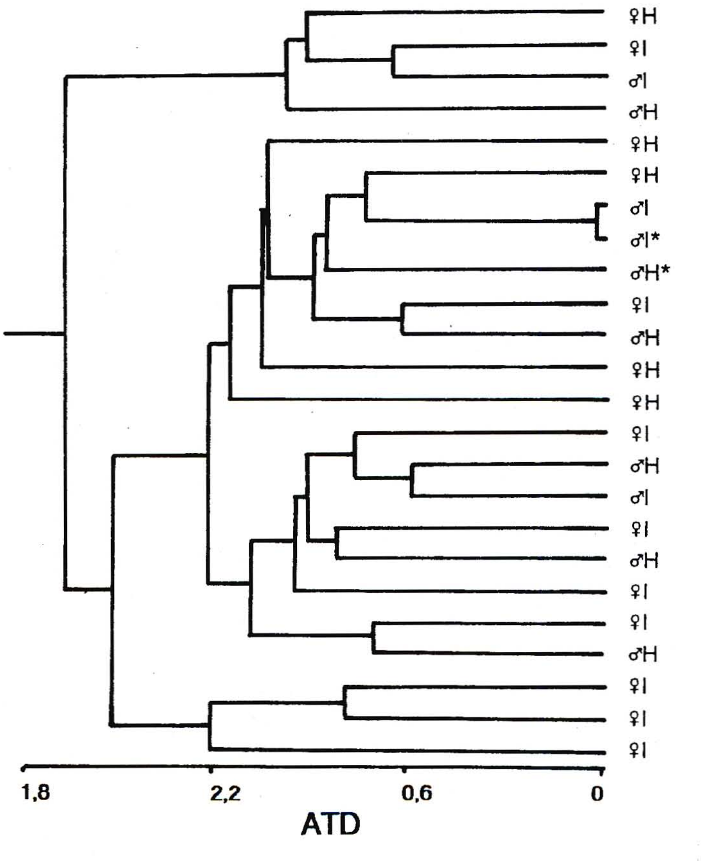

♀H
♀I
♂I
♂H
♀H
♀H
♂I
♂I*
♂H*
♀I
♂H
♀H
♀H
♀I
♂H
♂I
♀I
♂H
♀I
♀I
♂H
♀I
♀I
♀I
1,8
2,2
0,6
0
ATD

Table 5.14

Summary statistics and results of single classification analyses of variance of coat colour attributes in St. Lucia *Amblysomus* specimens lacking a rufous tinge (**Dark**), or which have a rufous tinge (**Red**), and in *A. i. corriae* (**AIC**) from the Western Cape. H = hue; V = value; C = chroma; $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size. Dorsal value and ventral hue attributes for the TW2 and TW3 samples showed slight skewness and/or kurtosis, but Kolmogorov-Smirnoff tests indicated that normality could be assumed for all variables.

		DORSUM			**VENTRUM**		
OTU	**STAT**	**H**	**V**	**C**	**H**	**V**	**C**
Dark	$\bar{x}$	10,74	2,28	1,94	20,00	2,65	3,29
	sd	3,03	0,49	0,66	0,00	0,49	0,58
	n	17	17	17	17	17	17
Red	$\bar{x}$	12,50	2,21	2,44	19,17	4,11	4,22
	sd	2,27	0,44	0,78	1,21	1,03	1,06
	n	18	18	18	18	18	18
AIC	$\bar{x}$	10,66	1,72	1,00	15,79	3,32	1,05
	sd	1,83	0,07	0,00	1,46	0,67	0,23
	n	19	19	19	19	19	19
	F	3,390	12,130	29,250	73,560	16,130	98,220
	p	0,054	0,0002	0,0001	0,0001	0,0001	0,0001

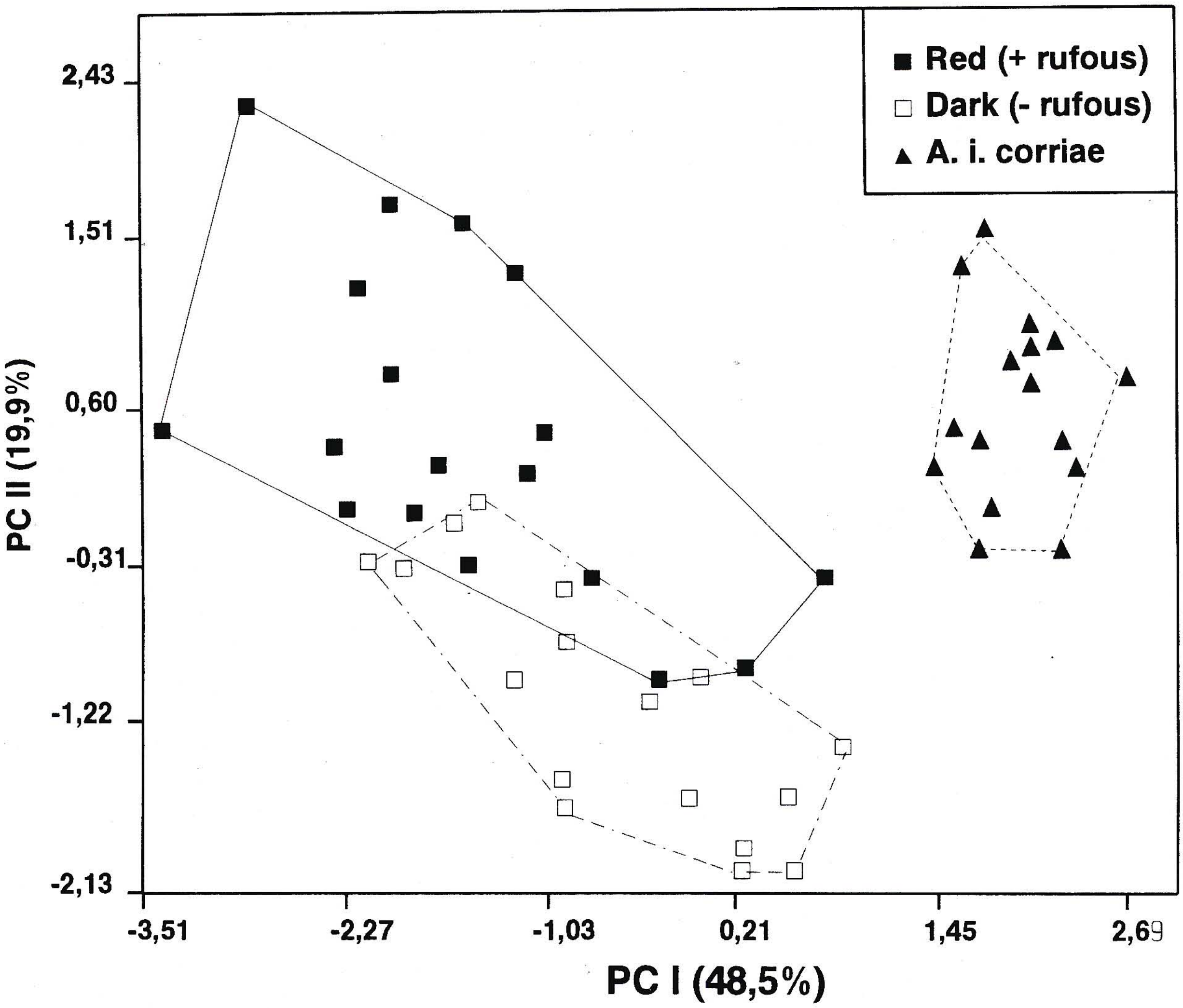


Fig. 5.17. Pairwise comparison of the first two principal component axes, computed from colourimetric data for *A. i. corriae*, and for St. Lucia *Amblysomus* having a rufous tinge (**Red**), or lacking rufous colouration (**Dark**). The cophenetic correlation is 0,794.

darkening of dorsal fur, and a tendency for both the dorsum and ventrum to become more drab.

Amblysomus specimens from St. Lucia which lack any rufous tinge (*cf. A. i. iris*) thus show closer colourimetric affinity to sympatric specimens having a rufous tinge (*cf. A. hottentotus*), and these specimens differ fundamentally in most colour attributes from *A. i. corriae*. Colourimetric data thus supported the null hypotheses that all specimens from St. Lucia represent the same species, namely *A. hottentotus*.

Craniometric data also supported this hypothesis. Comparison of the Red and Dark St. Lucia groups with samples of *A. i. corriae* (from Humansdorp, Knysna and George), *A. h. hottentotus* (Port Elizabeth and Albany), *A. h. pondoliae* (Durban) and *A. hottentotus* from Western Cape (Stellenbosch and Grootvadersbosch) indicated that significant differences exist among these OTUs in both males (Table 5.15) and females (Table 5.16). Most measurements showed broadly overlapping maximally non-significant subsets that did not correlate with *a priori* taxonomic divisions, this being largely due to size variation within *A. hottentotus*. The Western Cape and *A. i. corriae* OTUs were generally larger in measurements reflecting skull length (GSL, PPL, CPL, APW), but smaller in measurements summarizing skull height (GSH) and width (P@P, IOW). The Humansdorp population of *A. i. corriae* was larger than those from Knysna and/or George in most measurements (especially GSL and PAL of males), suggesting that size may vary geographically within *A. i. corriae*.

Discriminant functions analyses resulted in overall *a posteriori* classifications of 97% for females and 98% for males. Mis-identifications involved mainly specimens from different localities within the same *a priori* groups (*ie. A. h. hottentotus* from Port Elizabeth and Albany, and *A. i. corriae* from Knysna and George). The only mis-identifications between groups involved specimens of *A. h. pondoliae* from Durban, and the darker or redder specimens from St. Lucia.

MANOVA indicated that differences between the OTUs within each sex were highly significant when all variables were considered simultaneously (♂: $F_{(144,278)} = 3{,}37$; $p < 0{,}001$; ♀: $F_{(126,272)} = 3{,}70$; $p < 0{,}001$). Cluster analysis based on inter-OTU Mahalanobis' distances showed that the two St. Lucia samples were phenotypically most similar to *A. h. pondoliae* and *A. h. hottentotus*, since these OTUs formed a cluster distinct from the *A. i. corriae* populations (Fig. 5.18). The Western

Table 5.15

Summary statistics and *F* values from single-classification analyses of variance for one external (BCW) and various cranial measurements in males from various locality samples representing: **Dark**(St. Lucia) - *Amblysomus* specimens from St. Lucia, lacking any rufous tinge; **Red**(St. Lucia) - *Amblysomus* specimens from St. Lucia, with a rufous tinge; **AIC** - *A. i. corriae* from George, Humansdorp and Knysna; **AHD** - *A. hottentotus* from Western Cape; **AH** - *A. h. hottentotus* from Port Elizabeth and Albany; **AHP** - *A. h. pondoliae* from Durban. $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample sizes; *p* = significance of *F* values. Vertical lines denote maximally non-significant subsets indicated by SNK multiple comparisons tests. Only variables for which significant *F* values were found are shown.

BCW ($F=4{,}69$, $p<0{,}001$)

OTU	$\bar{x} \pm sd(n)$
Dark(St. Lucia)	4,64 ± 0,30(5)
AIC(George)	4,70 ± 0,15(4)
AIC(Knysna)	4,86 ± 0,08(5)
AIC(Humansdorp)	5,16 ± 0,36(4)
AHD	5,18 ± 0,11(8)
Red(St. Lucia)	5,19 ± 0,47(4)
AH(Port Elizabeth)	5,21 ± 0,34(5)
AHP	5,30 ± 0,37(25)
AH(Albany)	5,48 ± 0,17(5)

ARB ($F=2{,}31$, $p=0{,}04$)

OTU	$\bar{x} \pm sd(n)$
AIC(George)	4,59 ± 0,04(4)
AIC(Knysna)	4,66 ± 0,12(5)
Dark(St. Lucia)	4,80 ± 0,48(5)
Red(St. Lucia)	4,81 ± 0,18(4)
AH(Port Elizabeth)	4,82 ± 0,28(5)
AHD	4,91 ± 0,12(9)
AH(Albany)	4,94 ± 0,21(5)
AIC(Humansdorp)	4,97 ± 0,28(4)
AHP	5,01 ± 0,26(25)

ZMB ($F=3{,}94$, $p=0{,}002$)

OTU	$\bar{x} \pm sd(n)$
Dark(St. Lucia)	15,9 ± 0,8(5)
AIC(Knysna)	16,0 ± 0,5(5)
AIC(Humansdorp)	16,0 ± 0,6(4)
AIC(George)	16,1 ± 0,1(4)
AHD	16,1 ± 0,1(9)
AH(Port Elizabeth)	16,3 ± 0,4(5)
AH(Albany)	16,4 ± 0,5(5)
Red(St. Lucia)	16,6 ± 0,9(4)
AHP	17,0 ± 0,6(25)

GSL ($F=4{,}67$, $p<0{,}001$)

OTU	$\bar{x} \pm sd(n)$
Dark(St. Lucia)	25,5 ± 1,3(5)
AH(Port Elizabeth)	25,9 ± 0,7(5)
Red(St. Lucia)	26,4 ± 1,0(4)
AH(Albany)	26,7 ± 0,5(5)
AHP	27,0 ± 0,8(25)
AIC(Knysna)	27,1 ± 0,5(5)
AIC(George)	27,2 ± 0,8(4)
AHD	27,5 ± 0,4(8)
AIC(Humansdorp)	28,1 ± 1,1(4)

GSH ($F=3{,}78$, $p=0{,}002$)

OTU	$\bar{x} \pm sd(n)$
Dark(St. Lucia)	12,3 ± 0,5(5)
Red(St. Lucia)	12,4 ± 0,7(4)
AIC(Knysna)	12,5 ± 0,1(5)
AIC(George)	12,7 ± 0,3(4)
AH(Port Elizabeth)	12,8 ± 0,4(5)
AHD	12,9 ± 0,1(9)
AHP	13,0 ± 0,4(25)
AIC(Humansdorp)	13,0 ± 0,5(4)
AH(Albany)	13,1 ± 0,3(5)

P@P ($F=6{,}51$, $p<0{,}001$)

OTU	$\bar{x} \pm sd(n)$
AIC(George)	6,82 ± 0,31(4)
AIC(Knysna)	7,07 ± 0,20(5)
AHD	7,11 ± 0,26(8)
AIC(Humansdorp)	7,14 ± 0,19(4)
Dark(St. Lucia)	7,29 ± 0,54(4)
Red(St. Lucia)	7,34 ± 0,24(4)
AH(Albany)	7,48 ± 0,33(5)
AH(Port Elizabeth)	7,64 ± 0,39(5)
AHP	7,67 ± 0,27(25)

MTL ($F=4{,}56$, $p<0{,}001$)

OTU	$\bar{x} \pm sd(n)$
AIC(Knysna)	6,04 ± 0,27(5)
AHD	6,30 ± 0,41(9)
Dark(St. Lucia)	6,41 ± 0,48(5)
AIC(Humansdorp)	6,41 ± 0,20(4)
AIC(George)	6,42 ± 0,25(4)
Red(St. Lucia)	6,51 ± 0,22(4)
AH(Port Elizabeth)	6,52 ± 0,26(5)
AHP	6,71 ± 0,24(25)
AH(Albany)	6,73 ± 0,28(5)

PPL ($F=5{,}68$, $p<0{,}001$)

OTU	$\bar{x} \pm sd(n)$
Dark(St. Lucia)	8,25 ± 0,41(5)
AH(Port Elizabeth)	8,28 ± 0,18(5)
AH(Albany)	8,65 ± 0,45(5)
Red(St. Lucia)	8,75 ± 0,37(4)
AHD	8,82 ± 0,24(9)
AIC(Humansdorp)	8,83 ± 0,56(4)
AIC(Knysna)	8,91 ± 0,13(5)
AIC(George)	8,99 ± 0,14(4)
AHP	9,05 ± 0,33(25)

CPL ($F=5{,}11$, $p<0{,}001$)

OTU	$\bar{x} \pm sd(n)$
Dark(ST. Lucia)	6,49 ± 0,53(5)
AH(Port Elizabeth)	6,87 ± 0,27(5)
Red(St. Lucia)	6,97 ± 0,37(4)
AH(Albany)	7,06 ± 0,31(5)
AIC(George)	7,15 ± 0,19(4)
AHP	7,32 ± 0,35(25)
AIC(Knysna)	7,46 ± 0,18(5)
AIC(Humansdorp)	7,48 ± 0,48(4)
AHD	7,72 ± 0,31(8)

APW ($F=3{,}96$, $p=0{,}002$)

OTU	$\bar{x} \pm sd(n)$
Dark(St. Lucia)	3,96 ± 0,38(5)
AH(Port Elizabeth)	4,31 ± 0,36(5)
Red(St. Lucia)	4,43 ± 0,23(4)
AIC(George)	4,50 ± 0,11(4)
AHP	4,55 ± 0,24(25)
AH(Albany)	4,56 ± 0,15(5)
AIC(Humansdorp)	4,57 ± 0,34(4)
AIC(Knysna)	4,67 ± 0,23(5)
AHD	5,03 ± 0,23(9)

MDL ($F=2{,}84$, $p<0{,}05$)

OTU	$\bar{x} \pm sd(n)$
Dark(St. Lucia)	16,0 ± 0,9(5)
AH(Port Elizabeth)	16,4 ± 0,6(5)
Red(St. Lucia)	16,5 ± 0,7(4)
AIC(George)	16,6 ± 0,8(4)
AIC(Knysna)	16,7 ± 0,3(5)
AIC(Humansdorp)	17,0 ± 0,9(4)
AH(Albany)	17,0 ± 0,4(5)
AHP	17,1 ± 0,7(25)
AHD	17,4 ± 0,4(8)

Table 5.16

Summary statistics and *F* values from single-classification analyses of variance for one external (BCW) and various cranial measurements in females from various locality samples representing: **Dark**(St. Lucia) - *Amblysomus* from St. Lucia, lacking any rufous tinge; **Red**(St. Lucia) - *Amblysomus* from St. Lucia, with a rufous tinge; **AIC** - *A. i. corriae* from Humansdorp and Knysna; **AHD** - *A. hottentotus* from the Western Cape; **AH** - *A. hottentotus* from Port Elizabeth and Albany; **AHP** - *A. h. pondoliae* from Durban. $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample sizes; *p* = significance of *F* values. Vertical lines denote maximally non-significant subsets indicated by SNK multiple comparisons tests. Only variables for which significant *F* values were found are shown.

BCW ($F=8,28$, $p<0,001$)

OTU	$\bar{x} \pm sd(n)$
Dark(St. Lucia)	4,34±0,21(6)
AIC(Knysna)	4,43±0,15(6)
Red(St. Lucia)	4,44±0,15(4)
AHP	4,68±0,26(22)
AH(Albany)	4,99±0,27(6)
AHD	5,03±0,11(7)
AIC(Humansdorp)	5,12±0,47(10)
AH(Port Elizabeth)	5,13±0,41(6)

ARB ($F=6,55$, $p<0,001$)

OTU	$\bar{x} \pm sd(n)$
AIC(Knysna)	4,28±0,13(6)
Dark(St. Lucia)	4,55±0,14(6)
Red(St. Lucia)	4,61±0,19(4)
AH(Port Elizabeth)	4,68±0,24(6)
AHD	4,70±0,22(6)
AIC(Humansdorp)	4,74±0,24(10)
AH(Albany)	4,81±0,15(6)
AHP	4,81±0,21(22)

MIO ($F=6,15$, $p<0,001$)

OTU	$\bar{x} \pm sd(n)$
AIC(Knysna)	7,89±0,19(6)
AHD	7,89±0,26(7)
AH(Port Elizabeth)	7,93±0,26(6)
AH(Albany)	7,93±0,23(6)
Dark(St. Lucia)	7,96±0,18(6)
Red(St. Lucia)	8,04±0,22(4)
AHP	8,33±0,22(22)
AIC(Humansdorp)	8,37±0,39(10)

ZMB ($F=6,62$, $p<0,001$)

OTU	$\bar{x} \pm sd(n)$
AIC(Knysna)	15,1±0,2(6)
AHD	15,4±0,2(6)
Dark(St. Lucia)	15,4±0,5(6)
AH(Albany)	15,6±0,3(6)
AIC(Humansdorp)	15,7±0,5(10)
Red(St. Lucia)	15,7±0,1(4)
AH(Port Elizabeth)	16,1±0,8(6)
AHP	16,3±0,5(22)

IOW ($F=7,63$, $p<0,001$)

OTU	$\bar{x} \pm sd(n)$
AIC(Knysna)	6,78±0,18(6)
Dark(St. Lucia)	6,89±0,19(6)
AIC(Humansdorp)	6,89±0,23(10)
AHD	7,11±0,13(7)
AH(Albany)	7,22±0,17(6)
AHP	7,22±0,24(22)
Red(St. Lucia)	7,31±0,18(4)
AH(Port Elizabeth)	7,35±0,27(6)

GSL ($F=4,30$, $p<0,001$)

OTU	$\bar{x} \pm sd(n)$
Dark(St. Lucia)	24,7±0,5(4)
Red(St. Lucia)	24,9±0,5(6)
AH(Albany)	25,6±0,6(6)
AH(Port Elizabeth)	25,9±0,4(6)
AHP	26,0±0,5(22)
AIC(Knysna)	26,1±0,6(6)
AHD	26,4±0,2(7)
AIC(Humansdorp)	27,0±1,0(10)

GSH ($F=11,00$, $p<0,001$)

OTU	$\bar{x} \pm sd(n)$
Dark(St. Lucia)	11,6±0,3(6)
Red(St. Lucia)	11,8±0,3(4)
AIC(Knysna)	12,0±0,2(6)
AHD	12,4±0,2(7)
AH(Port Elizabeth)	12,5±0,2(6)
AH(Albany)	12,5±0,6(6)
AHP	12,6±0,3(22)
AIC(Humansdorp)	12,7±0,5(10)

P@P ($F=6,85$, $p<0,001$)

OTU	$\bar{x} \pm sd(n)$
AIC(Knysna)	6,61±0,24(6)
AIC(Humansdorp)	7,04±0,24(10)
AHD	7,16±0,01(6)
AH(Albany)	7,23±0,43(6)
Dark(St. Lucia)	7,26±0,29(6)
Red(St. Lucia)	7,32±0,09(4)
AH(Port Elizabeth)	7,36±0,60(6)
AHP	7,42±0,18(22)

PAL ($F=5,69$, $p<0,001$)

OTU	$\bar{x} \pm sd(n)$
Dark(St. Lucia)	12,5±0,3(6)
Red(St. Lucia)	12,5±0,5(4)
AH(Albany)	12,8±0,5(6)
AIC(Knysna)	12,9±0,4(6)
AH(Port Elizabeth)	12,9±0,3(6)
AHP	13,0±0,3(22)
AHD	13,1±0,2(7)
AIC(Humansdorp)	13,5±0,5(10)

MTL ($F=4,57$, $p<0,001$)

OTU	$\bar{x} \pm sd(n)$
AIC(Knysna)	5,95±0,23(6)
AHD	6,24±0,13(6)
AH(Albany)	6,30±0,22(6)
Red(St. Lucia)	6,37±0,34(4)
AIC(Humansdorp)	6,38±0,27(10)
Dark(St. Lucia)	6,47±0,21(6)
AH(Port Elizabeth)	6,50±0,27(6)
AHP	6,53±0,25(22)

IPG ($F=9,51$, $p<0,001$)

OTU	$\bar{x} \pm sd(n)$
Dark(St. Lucia)	2,00±0,08(6)
AH(Port Elizabeth)	2,01±0,18(6)
AHD	2,05±0,10(6)
AH(Albany)	2,06±0,11(6)
AIC(Humansdorp)	2,07±0,29(10)
AIC(Knysna)	2,09±0,10(6)
Red(St. Lucia)	2,19±0,08(4)
AHP	2,29±0,14(22)

PPL ($F=8,47$, $p<0,001$)

OTU	$\bar{x} \pm sd(n)$
Red(St. Lucia)	7,92±0,21(4)
Dark(St. Lucia)	8,16± ±0,08(6)
AH(Albany)	8,30±0,38(6)
AH(Port Elizabeth)	8,35±0,31(6)
AIC(Knysna)	8,66±0,29(6)
AIC(Humansdorp)	8,70±0,29(10)
AHD	8,70±0,11(7)
AHP	8,73±0,29(22)

FML ($F=3,65$, $p<0,005$)

OTU	$\bar{x} \pm sd(n)$
Dark(St. Lucia)	4,28±0,11(6)
Red(St. Lucia)	4,34±0,14(4)
AHP	4,50±0,19(22)
AIC(Knysna)	4,59±0,25(6)
AHD	4,61±0,12(6)
AH(Albany)	4,62±0,28(6)
AIC(Humansdorp)	4,64±0,14(10)
AH(Port Elizabeth)	4,67±0,27(6)

CPL ($F=10,65$, $p<0,001$)

OTU	$\bar{x} \pm sd(n)$
Red(St. Lucia)	6,24±0,24(4)
Dark(St. Lucia)	6,25±0,25(6)
AH(Albany)	6,81±0,26(6)
AIC(Knysna)	6,87±0,26(6)
AH(Port Elizabeth)	6,95±0,30(6)
AHP	6,97±0,28(22)
AHD	7,13±0,14(7)
AIC(Humansdorp)	7,24±0,31(10)

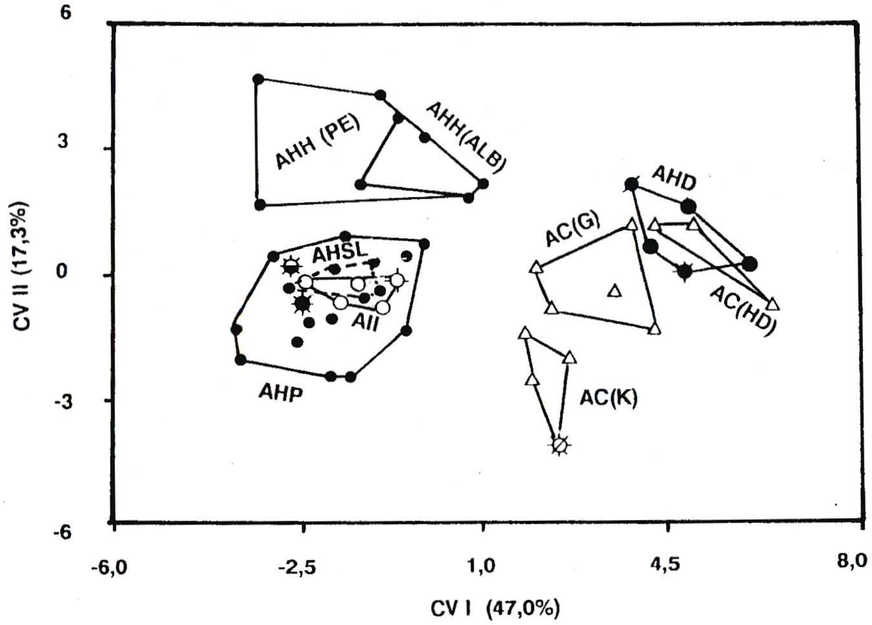
APW ($F=9,23$, $p<0,001$)

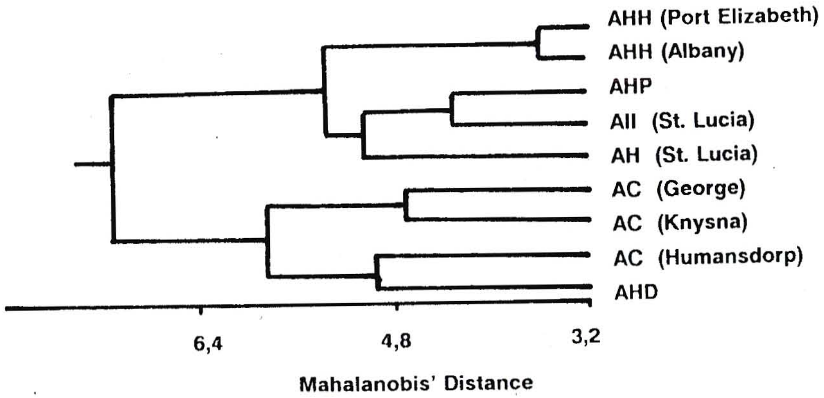
OTU	$\bar{x} \pm sd(n)$
Red(St. Lucia)	3,61±0,36(4)
Dark(St. Lucia)	3,70±0,15(6)
AIC(Knysna)	4,21±0,20(6)
AHP	4,23±0,24(22)
AH(Albany)	4,36±0,28(6)
AIC(Humansdorp)	4,36±0,23(10)
AH(Port Elizabeth)	4,36±0,32(6)
AHD	4,44±0,10(9)

MDL ($F=8,42$, $p<0,001$)

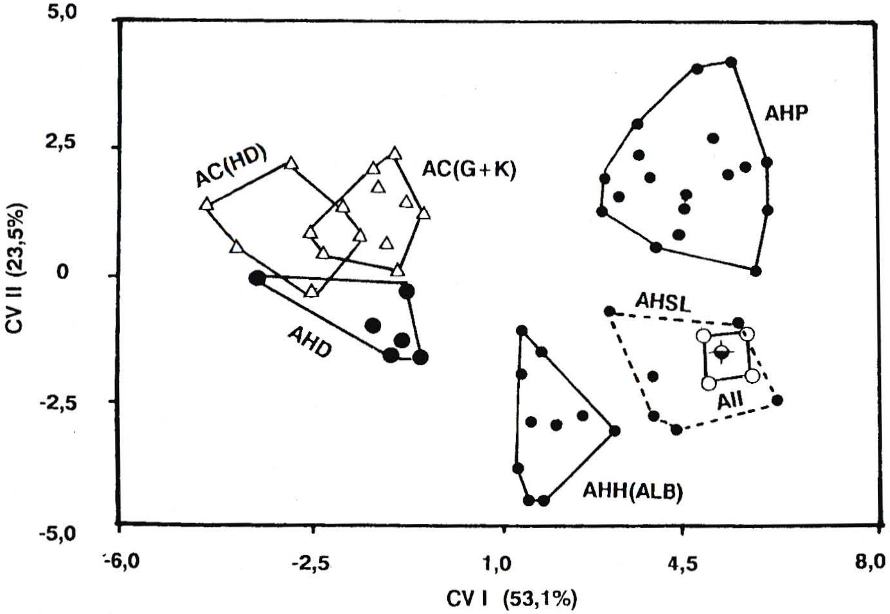
OTU	$\bar{x} \pm sd(n)$
Red(St. Lucia)	15,4±0,4(4)
Dark(St. Lucia)	15,4±0,4(6)
AIC(Knysna)	15,8±0,4(6)
AH(Albany)	16,3±0,5(6)
AH(Port Elizabeth)	16,4±0,3(6)
AHD	16,4±0,2(9)
AHP	16,6±0,5(22)
AIC(Humansdorp)	16,8±0,8(10)

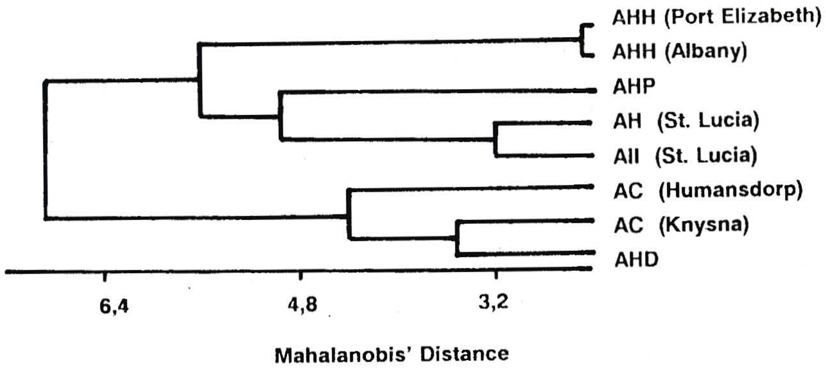
Fig. 5.18. Phenetic relationships among male and female specimens of *A. iris* and *A. hottentotus*, as indicated by cluster analyses of Mahalanobis' distances between group centroids; and pairwise comparison of the first two canonical variate axes. Taxa are: AHH - *A. h. hottentotus* (PE = Port Elizabeth; ALB = Albany); AHP - *A. h. pondoliae*; AHSL - *Amblysomus* from St. Lucia that have rufous fur; AII - *Amblysomus* from St. Lucia lacking rufous fur; AC - *A. i. corriae* (HD = Humandorp; G = George; K = Knysna); and AHD - *A. hottentotus* from Western Cape. Symbols indicate: (●) - *A. hottentotus*; (△) - *A. i. corriae*; (○) - *Amblysomus* from St. Lucia lacking a rufous tinge; (✸) - holotype of *A. h. pondoliae*; (✹) - holotype of *A. h. natalensis*; (✧) - holotype of *A. i. iris*; (✲) - holotype of *A. i. corriae*; (◆) - holotype of *A. c. littoralis*; (●) - holotype of *A. h. devilliersi*; (✦) - holotype of *A. h. swellendamensis*.


6
3
0
-3
-6
CV II (17,3%)
-6,0
-2,5
1,0
4,5
8,0
CV I (47,0%)
AHH (PE)
AHH(ALB)
AHSL
AII
AHP
AC(G)
AHD
AC(HD)
AC(K)


AHH (Port Elizabeth)
AHH (Albany)
AHP
AII (St. Lucia)
AH (St. Lucia)
AC (George)
AC (Knysna)
AC (Humansdorp)
AHD
6,4
4,8
3,2
Mahalanobis' Distance

♂


5,0
2,5
0
-2,5
-5,0
CV II (23,5%)
-6,0
-2,5
1,0
4,5
8,0
CV I (53,1%)
AC(HD)
AC(G+K)
AHP
AHD
AHSL
AII
AHH(ALB)


AHH (Port Elizabeth)
AHH (Albany)
AHP
AH (St. Lucia)
AII (St. Lucia)
AC (Humansdorp)
AC (Knysna)
AHD
6,4
4,8
3,2
Mahalanobis' Distance

♀

Cape OTUs grouped with *A. i. corriae*, rather than with the two St. Lucia samples, or with *A. h. pondoliae*. In pairwise comparisons of the first two canonical variate axes for males (Fig. 5.18), specimens of *A. i. corriae* (including the holotype) and the Western Cape OTUs plotted to the extreme right along the first axis (which was influenced mainly by P@P, FML, GSL and PPL), but the St. Lucia specimens formed a distinct cluster overlapping with the *A. h. pondoliae* specimens. These were in turn separated from *A. h. hottentotus* along the second axis (reflecting mainly differences in IPG, PPL, MTL and APW). The holotype of *A. i. iris* plotted within the St. Lucia sub-cluster, whereas the holotypes of *A. h. pondoliae* and *A. h. natalensis* did not.

A similar pattern of separation was evident for females. Individuals from the Western Cape OTUs grouped with *A. i. corriae*, while the dark and red specimens from St. Lucia plotted together between *A. h. pondoliae* and *A. h. hottentotus* along CV II.

The St. Lucia specimens thus have greater craniometric and colourimetric affinity to *A. hottentotus* than to *A. i. corriae*. The null hypothesis (H_{Φ}^{2}) that all of the St. Lucia specimens represent *A. hottentotus*, rather than a distinct species previously referred to as *A. iris*, could thus be accepted.

Although craniometrically very similar to *A. h. pondoliae*, specimens from St. Lucia are smaller in most measurements (Tables 5.15 and 5.16), and form a distinct cluster in ordination scatterplots and phenograms for females (Fig. 5.18). Furthermore, the transition zone separating the St. Lucia OTU from *A. h. pondoliae* in Durban was similar in magnitude to that between *A. h. pondoliae* and *A. h. hottentotus* in the Eastern Cape (Fig. 5.14). This implied that the St. Lucia specimens must be referred to the distinct subspecies *A. h. iris*, as recognized by Broom (1907a), with *A. corriae littoralis* as a junior synonym.

5.4.4 Status of populations in Western Cape

The Western Cape populations previously assigned to the subspecies *A. i. corriae* are characterized by longer, but generally narrower, skulls than *A. hottentotus*. The wide separation of *A. i. corriae* and *A. hottentotus* specimens in ordination scatterplots and phenograms (Fig. 5.18), and the consistent differences in fur colour between these OTUs (Fig. 5.17), implied that these taxa do not represent merely subspecific varieties of the same species, as maintained by Broom (1907a). The populations from the Western Cape must, therefore, be referred to the distinct species *A. corriae*.

The tendency for the Stellenbosch [1] and Grootvadersbosch [2] OTUs to group with *A. corriae*, rather than with any of the *A. hottentotus* subspecies, was unexpected because these populations were traditionally relegated to the subspecies *A. h. devilliersi*. Examination of a small (n = 8) series of specimens from these populations revealed that the fur is reddish-black (10R 1,7/1) mid-dorsally, as in *A. corriae*. From the mid-dorsal line, the fur becomes progressively redder, lighter and richer in colour towards the flanks and abdomen, which are reddish brown (5YR 4-6/4-6), as in *A. hottentotus*. Even in this sample, there is considerable variability in the extent of reddish-brown fur on the dorsum and flanks. Some specimens (*e.g.* TM40564 and TM40556 from Stellenbosch) are almost completely reddish-black dorsally, whereas others from the same locality have distinctly reddish-brown flanks. In specimens from Grootvadersbosch, reddish-brown extends almost to the mid-dorsal region, so that the extent of reddish-black fur is reduced to a narrow band along the back.

Fur colour thus appears to vary significantly within and between populations previously referred to *A. h. devilliersi*, with attributes that are typical of both *A. hottentotus* and *A. corriae*. Colourimetric data are, therefore, too equivocal to offer any clues to the affinity of the Stellenbosch and Grootvadersbosch populations. Craniometric evidence must, therefore, be given preference. Populations previously assigned to *A. h. devilliersi* are thus provisionally relegated to *A. corriae*. This treatment is biogeographically consistent, in that all of these populations exist in the South-West Cape biotic zone, and the Stellenbosch/Grootvadersbosch populations appear to be geographically separated from *A. h. hottentotus* (Section 5.3.2.4). Colourimetric analysis of considerably larger samples are needed, however, to clarify the taxonomic status of these populations.

5.4.5 Status and affinity of Graskop *Amblysomus*

Ordination analyses (Fig. 5.9) showed that the Graskop OTU is craniometrically more similar to *A. h. pondoliae* from Transkei and KwaZulu-Natal than to

A. h. longiceps, *A. septentrionalis* in Mpumalanga, or *Amblysomus Species A* at Belfast. But, the Graskop population differs from these taxa in that some individuals lack well-developed molar talonids. In this respect, some of the Graskop specimens resemble *A. gunningi* (Section 6.3.4), as well as *A. h. garneri* - a taxon supposedly also lacking molar talonids (Roberts 1917), and which Roberts (1951) claimed to occur in the Graskop area. A six-group discriminant functions analysis showed, however, that the Graskop OTU cannot considered synonymous with any of these taxa. In scatterplots comparing the first two canonical variate axes (Fig. 5.19), specimens from Graskop plotted apart from *A. septentrionalis* (including *A. s. garneri*), and between *A. h. pondoliae* and *A. gunningi* along CV II. Multivariate differences between these groups were highly significant in males ($F_{(55,281)} = 8{,}28$; $p < 0{,}001$), and in females ($F_{(22,34)} = 3{,}85$; $p < 0{,}001$) which showed essentially the same pattern of separation (not illustrated).

Specimens of *Amblysomus* from Graskop resemble *A. hottentotus*, rather than *A. gunningi*, *A. septentrionalis* or *Amblysomus Species A*, in karyotypic properties (Section 4.3.1), hyoid morphology (Section 3.3.3), and malleus morphology (Section 9.2). Assignment of these specimens to *A. hottentotus* is thus justified. But, the few ($n = 11$) Graskop specimens available for study are unique in having reddish-black (10R 2/1) fur mid-dorsally, in contrast to the reddish-brown fur typical of most *A. hottentotus*. Since colour varies markedly in *A. hottentotus*, this difference alone does not seem sufficient for subspecific recognition. This divergence in fur colour is, however, correlated with subtle differences in cranial shape between the Graskop and *A. h. pondoliae* populations, and marked differences in size between the Graskop OTU and *A. h. longiceps* (Fig. 5.19). Given also the apparent geographic disjunction of these groups (Section 5.3.2.4), subspecific recognition of the Graskop OTU is warranted. No published name is yet available for this subspecies, which is hereafter referred to as *A. hottentotus subspecies A*.

5.4.6 Synopsis

The species *A. hottentotus*, as traditionally delimited, thus includes five subspecies (*A. h. hottentotus*, *A. h. pondoliae*, *A. h. longiceps*, *A. h. iris* and

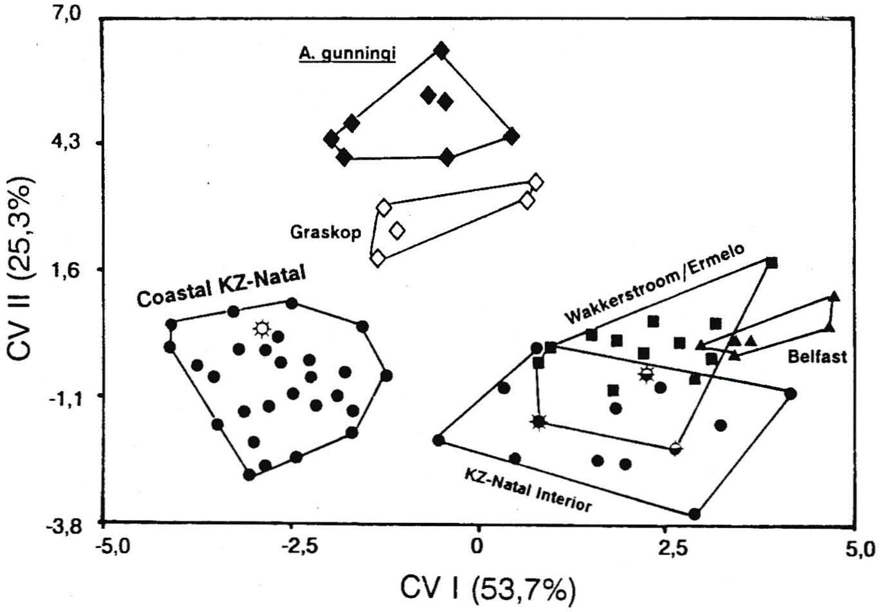


Fig. 5.19. Pairwise comparison of the first two canonical variate axes based on a six group discriminant functions analysis of males representing *A. gunningi* and five OTUs in *A. hottentotus*. Symbols indicate: (●) - 2n=30; (■) - 2n=34; (▲) - 2n=36; (♦) - *A. gunningi*; (◇) - *A. hottentotus* from Graskop (2n=30); (☼) - holotype of *A. h. pondoliae*; (✸) - holotype of *A. h. garneri*; (✧) - holotype of *A. h. drakensbergensis*; (✹) - holotype of *A. i. septentrionalis*.

A. hottentotus subspecies A), three cryptic species (*A. septentrionalis*, *A. marleyi* and *Amblysomus Species A*), and several populations of *A. corriae*. Accounts for the five subspecies within *A. hottentotus* are given in Chapter 10, whereas patterns of variation within the other species delimited above are discussed further in Chapter 6.

CHAPTER 6

INTRA-SPECIFIC MORPHOMETRIC AND DENTAL VARIATION IN OTHER *Amblysomus* SPECIES

6.1 INTRODUCTION

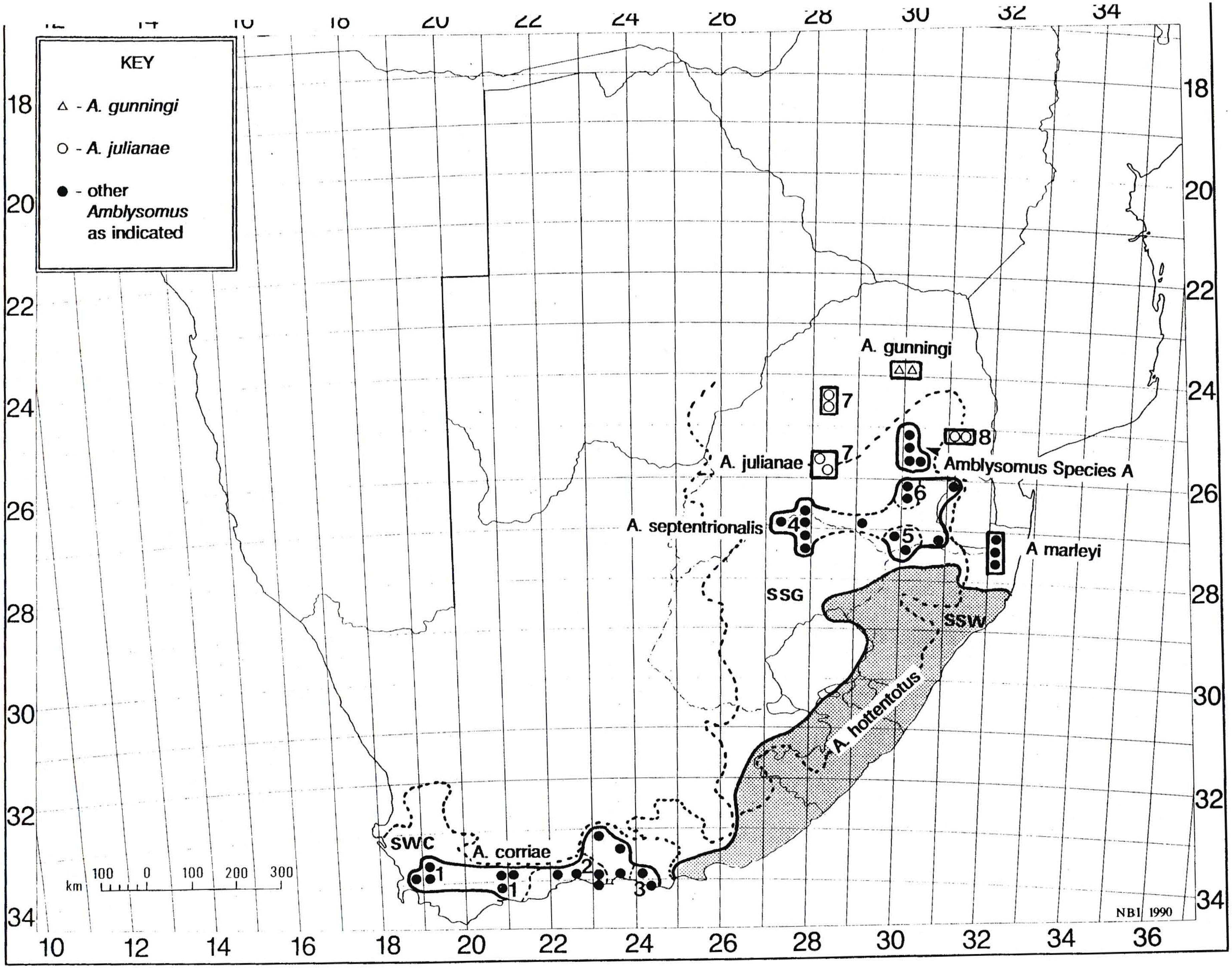
The genus *Amblysomus* has been subjected to successive lumping and splitting over the last century. Unlike Broom (1907a), most subsequent authors recognized *Amblysomus* as distinct from *Chrysochloris*, but differed in their treatment of the genera *Chlorotalpa* and *Calcochloris* (Table 1.1), which they either synonymized with *Amblysomus* (Ellerman *et al.* 1953; Petter 1981), or recognized with differing species allocations (Meester 1974; Simonetta 1968; Roberts 1951). As a result, the systematic affinities of the species included in these three genera remain obscure.

The limits of the genus *Amblysomus*, and the generic affinities of the various taxa included in this genus previously, are analysed in Chapter 9. In this chapter I assess variation within species of the genus only as recognized by Meester (1974) and Meester *et al.* (1986), but with the addition of several taxa (*A. septentrionalis*, *A. marleyi*, *Amblysomus Species A*) shown in Chapter 5 to be worthy of full specific rank. The genus *Amblysomus* accordingly includes seven species: *A. julianae* and *A. gunningi*, characterized by 2n=30 and with nucleolar organizer regions (NORs) on chromosomes 12 and 13; *A. corriae*, *A. hottentotus* and *A. marleyi*, also with 2n=30 but with NORs on chromosomes 8 and 11; *A. septentrionalis* with 2n=34 and NORs on chromosomes 8, 9 and 11; and *Amblysomus Species A* with 2n=36 (Section 4.3.1). Most of these species have limited distributions and tend to occur allopatrically or parapatrically, with localized ranges in forest-savanna mosaic and temperate grasslands of the Southern Savanna and South-West Cape biotic zones (Fig. 6.1). The notable exception is *A. hottentotus sensu stricto*, which is more widespread and has already been discussed in detail (Chapter 5).

6.2 MATERIALS AND METHODS

Two hundred and fifty-six specimens from various museums (Chapter 2) were examined and measured. Owing to small sample sizes, morphometric analyses were

Fig. 6.1. Distribution of *Amblysomus* species in the Southern Savanna Grassland (SSG), Southern Savanna Woodland (SSW) and South-West Cape (SWC) biotic zones of southern Africa, plotted by quarter degree squares. The shaded area is the range of *A. hottentotus*, which was examined in detail in Chapter 5. Species formerly included wholly or partly in *A. hottentotus* are indicated by solid circles. Numbers indicate localities pooled for intraspecific analyses, as follows:
1 - *A. corriae* (Western Cape); 2 - *A. corriae* (Knysna\George); 3 - *A. corriae* (Humansdorp);
4 - *A. septentrionalis* (Heilbron); 5 - *A. septentrionalis* (Wakkerstroom); 6 - *A. septentrionalis* (Ermelo); 7 - *A. julianae* (Pretoria and Nylsvley); 8 - *A. julianae* (Kruger National Park).


KEY
△ - A. gunningi
○ - A. julianae
● - other Amblysomus as indicated
A. gunningi
7
8
A. julianae
7
Amblysomus Species A
6
A. septentrionalis
4
5
A marleyi
SSG
SSW
A. hottentotus
SWC
A. corriae
1
1
2
3
km 100 0 100 200 300
NB1 1990
10
12
14
16
18
20
22
24
26
28
30
32
34
36
18
20
22
24
26
28
30
32
34

restricted to statistical comparisons of the sexes (TW2-4 specimens combined) in single or pooled locality samples, and of pooled locality samples from different geographic areas in species that are more widespread (*A. corriae* and *A. septentrionalis*).

6.3 RESULTS AND DISCUSSION

6.3.1 *Amblysomus marleyi*

This species, which was traditionally included as a subspecies in *A. hottentotus*, has a limited distribution, and occurs on only the eastern slopes of the Lebombo Mountains in northern KwaZulu-Natal. Although two populations (Ubombo and Ingwavuma), situated about 50 km apart, are represented in museum collections, sample sizes of both were too small for detailed examination of intra-specific variation.

Statistical comparison of male and female samples from these localities (Table 6.1) suggests that sexual size dimorphism is negligible, with males being slightly larger than females in most measurements, but significantly larger in only basal claw width (BCW).

Dental variability within this species appears to be minimal, and involves only the absence of protocones on P^{2-3} in three of the 15 specimens available for study (Section 5.3.2.1).

6.3.2 *Amblysomus julianae*

This is the only species inhabiting bushveld, and is known from only three widely-separated populations (Pretoria, Nylsvley and the Pretoriuskop district of the Kruger National Park), but may be more widespread (Bronner 1990; Meester 1972). The three known populations differ in colour and dental characters. Specimens from the Kruger National Park, which possess M_3, are dark reddish brown (2,5YR 3/4) dorsally, and dull reddish brown (5YR 5-6/4) ventrally. Specimens from the Pretoria (type locality) and Nylsvley populations lack M_3, and are reddish brown (5YR 3-4/4-6) or brown (7,5YR 4/6) dorsally, while the ventral fur varies from orange (7,5YR 6/6-8) through yellow orange (7,5YR 7/8) to bright yellowish-brown (10YR 7/6). However, specimens from all of these areas are similar in possessing sectorial canines and semi-molariform first premolars. All but one (TM39769) of the 17 specimens examined lack protocones on P^1, and all lack molar talonids, which are absent also on P_3 in four specimens (TM40126, TM39932, TM39970 and TM39769).

Table 6.1

Summary statistics and results of single-classification analysis of variance to test for sexual dimorphism in adult (TW 2-4) *A. marleyi* from Ubombo and Ingwavuma, northern KwaZulu-Natal. $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size; * - $p < 0,05$.

OTU	STAT	BCW	ARB	MIO	ZMB	IOW	GSL	GSH	P@P	PBM	PAL	MTL	IPG	PPL	BBW	CPL	APW	MDL
♂	$\bar{x}$	4,25	4,56	7,11	15,32	6,92	23,94	11,63	6,67	4,47	11,81	5,81	2,09	7,81	10,84	6,85	4,27	15,20
	sd	0,13	0,11	0,07	0,59	0,15	0,69	0,43	0,27	0,32	0,60	0,37	0,08	0,30	0,57	0,34	0,24	0,64
	Min	4,12	4,47	6,88	14,75	6,77	23,06	11,25	6,34	4,19	11,07	5,38	2,00	7,48	10,23	6,45	4,09	14,39
	Max	4,37	4,71	7,48	16,00	7,12	24,58	12,09	6,93	4,79	12,41	6,23	2,19	8,16	11,56	7,27	4,59	15,72
	n	3	4	4	4	3	4	4	4	4	4	4	4	4	4	4	4	4
♀	$\bar{x}$	3,91	4,29	6,84	14,62	6,73	23,50	11,32	6,53	4,49	11,59	5,65	2,03	7,84	10,65	6,50	4,07	14,75
	sd	0,17	0,27	0,29	0,75	0,36	0,80	0,48	0,38	0,24	0,51	0,26	0,08	0,31	0,55	0,41	0,33	0,63
	Min	3,70	3,87	6,51	13,91	6,23	22,40	10,67	6,10	4,10	10,78	5,32	1,91	7,35	10,05	5,87	3,68	13,88
	Max	4,20	4,71	7,19	16,00	7,22	24,76	12,69	7,20	4,74	12,25	6,11	2,17	8,27	11,56	7,27	4,59	15,70
	n	7	8	8	8	8	8	8	8	8	8	8	7	8	8	8	8	8
SEX	*F*	9,39*	3,40	2,45	2,58	0,99	0,86	0,99	0,40	0,03	0,43	0,79	1,55	0,04	0,30	2,21	1,09	1,34

Statistical comparison (Table 6.2) of male and female samples from Pretoria showed that males were significantly larger than females in six measurements summarizing skull length (GSL, PAL, MDL), height (GSH), width (ARB and mandible size (APW). Sexual size dimorphism is thus quite pronounced in *A. julianae*, although not to the same extent as in *A. hottentotus*. Sample sizes were too small for multivariate analyses to test for shape differences between the sexes within the Pretoria population, or for interpopulational variation between this deme and the Nylsvley (n = 3) or Kruger National Park (n = 3) OTUs.

6.3.3 *Amblysomus Species A.*

This robust species favours montane vleis, and is known from only four sites in the Steenkampsberge, near Belfast and Dullstroom in Mpumalanga. These localities are close together, and occur in similar grassland habitats (Near-Highland Sourveld; Acocks' veld type 57b), so specimen data were pooled for sexual comparisons.

Analyses of variance showed that males were significantly larger than females in 15 (88%) of the 17 cranial measurements examined (Table 6.3a). Principal components analysis resulted in separation of the male and female specimens along PC I, with broad overlap along PC II (Fig. 6.2a). PC I was a size vector (as demonstrated by the high, positive loadings for all variables; Table 6.3b) that accounted for for than 69% of the sample variance, indicating that craniometric variation in *Amblysomus Species A* is dominated by overall size. However, interpterygoid width (IPG) and palate width (PBM) loaded relatively low along this axis. These variables were similar in magnitude in both sexes, despite the significantly larger size of males, indicating that males have narrower palates (PBM:GSL = 16,8±0,7%; IPG:GSL = 7,6±0,4%) than females (PBM:GSL = 17,5±1,0%; IPG:GSL = 8,0.±0,4). The separation according to sex along PC I thus reflects differences in both size and shape. This may underlie the tendency for male and female specimens to cluster apart in a correlation phenogram (Fig. 6.2b) reflecting mainly shape variation (Sneath and Sokal 1973).

Sexual dimorphism is therefore pronounced in *Amblysomus Species A*, and involves mainly differences in overall size, and subtle divergence in the configuration of the posterior palatal region. In this regard, *Amblysomus Species A* closely resembles its sister species, *A. hottentotus* (Section 5.3.1.3).

Table 6.2

Summary statistics and results of single-classification analysis of variance to test for sexual dimorphism in adult (TW 2-4) *A. julianae* from Pretoria, Gauteng. $\overline{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size; * - $p < 0,05$.

OTU	STAT	BCW	ARB	MIO	ZMB	IOW	GSL	GSH	P@P	PBM	PAL	MTL	IPG	PPL	BBW	CPL	APW	MDL
♂	$\overline{x}$	3,83	4,70	7,41	15,85	7,44	23,16	11,45	7,26	4,26	11,72	5,92	1,90	7,56	10,48	6,03	3,42	14,44
	sd	0,16	0,15	0,27	0,39	0,18	0,43	0,05	0,15	0,12	0,30	0,14	0,11	0,20	0,33	0,12	0,12	0,18
	Min	3,60	4,50	7,07	15,44	7,17	22,44	11,39	7,14	4,15	11,38	5,67	1,80	7,30	10,11	5,83	3,23	14,14
	Max	4,01	4,87	7,79	16,36	7,63	23,62	11,51	7,40	4,39	12,08	6,07	2,07	7,76	10,87	6,13	3,58	14,61
	n	6	5	6	6	5	6	6	6	6	4	6	6	6	6	6	6	6
♀	$\overline{x}$	3,68	4,45	7,32	15,71	7,21	22,44	11,11	7,21	4,26	11,13	5,74	1,92	7,50	10,36	5,87	3,25	13,92
	sd	0,13	0,14	0,26	0,34	0,18	0,41	0,27	0,14	0,12	0,34	0,16	0,04	0,22	0,22	0,10	0,08	0,25
	Min	3,51	4,24	6,99	15,40	7,05	21,83	10,76	7,01	4,11	10,64	5,52	1,87	7,19	10,10	5,79	3,15	13,60
	Max	3,83	4,55	7,58	16,19	7,47	22,68	11,39	7,31	4,40	11,44	5,88	1,95	7,59	10,63	6,01	3,35	14,14
	n	5	5	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
SEX	*F*	0,42	7,18*	0,25	0,34	3,50	6,96*	9,97*	0,32	0,01	6,94*	3,84	0,09	0,22	0,38	4,83	5,66*	14,40*

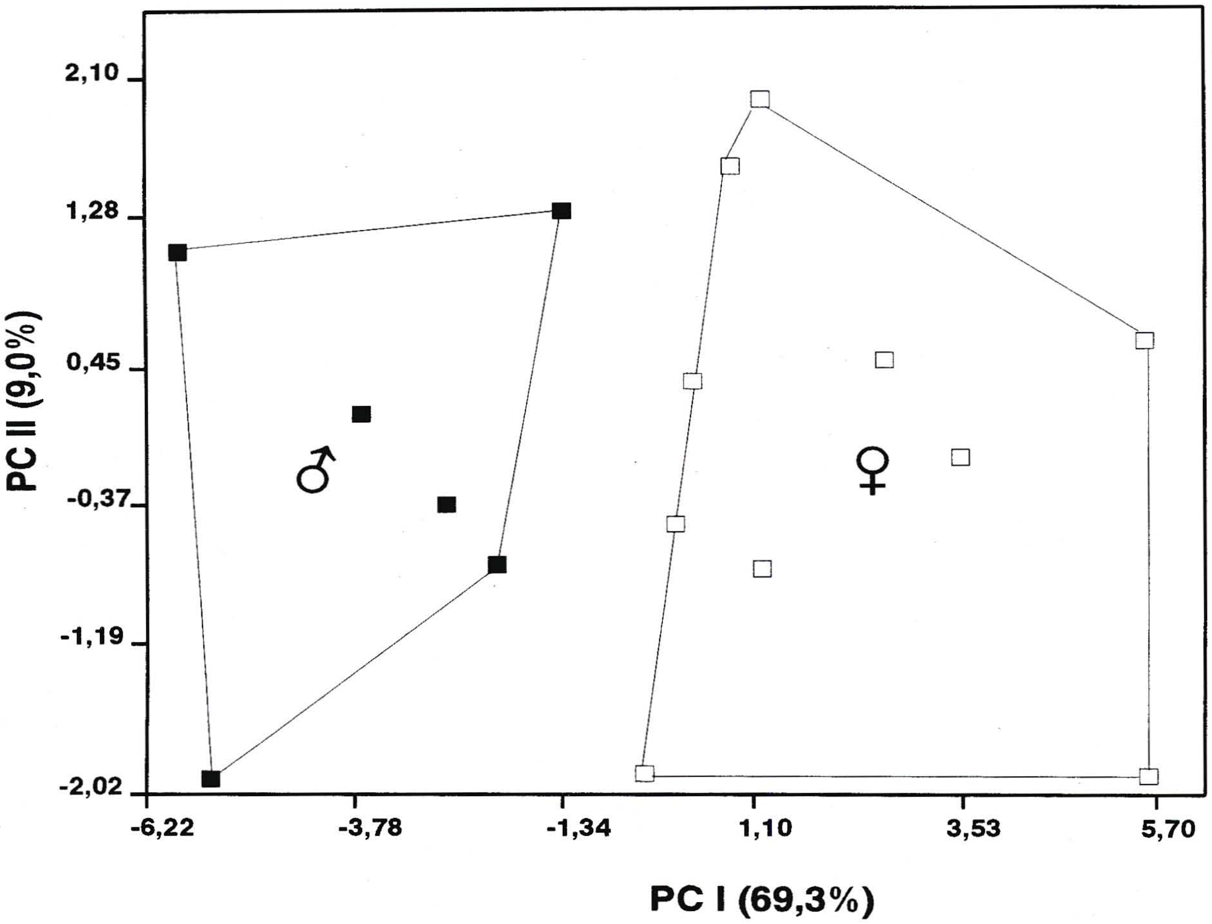
Table 6.3

Summary statistics and results of single-classification analysis of variance (a), and eigenvector coefficients from a principal components analysis (b), comparing male and female specimens (TW 2-4) of *Amblysomus Species A* from the Belfast\Dullstroom district of Mpumalanga. $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size; $^{\#}$ - $p < 0,01$.

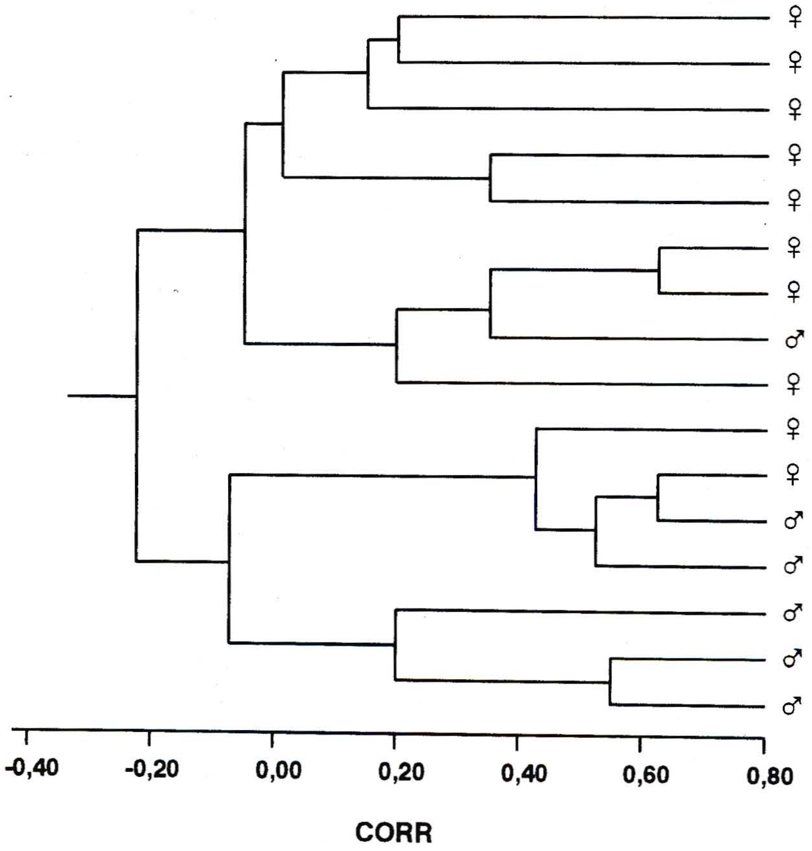
OTU	STAT	BCW	ARB	MIO	ZMB	IOW	GSL	GSH	P@P	PBM	PAL	MTL	IPG	PPL	BBW	CPL	APW	MDL
a) Summary statistics																		
♂	$\bar{x}$	6,81	5,66	9,80	19,24	8,28	30,87	14,69	8,22	5,18	15,65	7,41	2,34	9,83	13,25	8,31	5,44	19,32
	sd	0,28	0,16	0,35	0,62	0,28	0,64	0,41	0,24	0,26	0,42	0,18	0,12	0,28	0,49	0,18	0,28	0,40
	Min	6,49	5,43	9,57	18,60	7,95	29,92	14,26	7,80	4,79	15,06	7,14	2,22	9,33	12,81	8,04	5,12	18,96
	Max	7,19	5,89	10,56	20,43	8,67	31,96	15,26	8,52	5,47	16,16	7,58	2,59	10,10	14,07	8,51	5,79	19,95
	n	7	7	7	7	7	7	7	7	6	7	6	7	6	7	7	7	7
♀	$\bar{x}$	5,88	5,12	9,15	17,56	7,87	28,75	13,69	7,75	5,01	14,34	6,90	2,31	9,16	12,15	7,59	4,80	18,08
	sd	0,27	0,23	0,36	0,56	0,34	0,84	0,28	0,37	0,29	0,51	0,31	0,11	0,39	0,74	0,23	0,23	0,45
	Min	5,26	4,75	8,21	16,60	7,25	27,21	13,09	7,24	4,59	13,04	6,01	2,07	8,69	10,95	7,24	4,35	17,47
	Max	6,19	5,55	9,63	18,24	8,34	29,67	14,08	8,27	5,60	14,98	7,32	2,50	9,61	13,23	7,96	5,14	18,87
	n	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14
SEX	*F*	55,47$^{\#}$	30,51$^{\#}$	15,69$^{\#}$	38,78$^{\#}$	7,75$^{\#}$	34,72$^{\#}$	43,06$^{\#}$	9,28$^{\#}$	1,44	35,11$^{\#}$	13,53$^{\#}$	0,54	14,55$^{\#}$	12,09$^{\#}$	52,96$^{\#}$	30,59$^{\#}$	38,20$^{\#}$
b) Eigenvector coefficients																		
	PC I	0.868	0.965	0.733	0.959	0.826	0.975	0.907	0.785	0.418	0.934	0.830	0.209	0.892	0.902	0.965	0.936	0.980
	PC II	-0.022	-0.100	-0.104	0.045	-0.237	-0.065	0.104	0.040	0.594	-0.142	0.297	0.713	-0.108	0.144	0.010	-0.143	0.075

Fig. 6.2. Results of ordination and cluster analyses of single-standardized data for male (■) and female (□) *Amblysomus Species A* from Belfast/Dullstroom in Mpumalanga. a) pairwise comparison of the first two principal component axes (co-phenetic correlation = 0,967); b) correlation phenogram (co-phenetic correlation = 0,819).

a)


2,10
1,28
0,45
-0,37
-1,19
-2,02
PC II (9,0%)
♂
♀
-6,22
-3,78
-1,34
1,10
3,53
5,70
PC I (69,3%)

b)


♀
♀
♀
♀
♀
♀
♀
♂
♀
♀
♀
♂
♂
♂
♂
♂
-0,40
-0,20
0,00
0,20
0,40
0,60
0,80
CORR

The 21 specimens examined resemble *A. hottentotus* also in having sectorial canines and first premolars. M3 are absent in all individuals, while the lower molars always have well-developed talonids. Dental variability in this species is thus negligible.

6.3.4 *Amblysomus gunningi*

Hickman (1990) noted that this species and *A. hottentotus* coexist in the New Agatha Forest near Tzaneen. However, this conclusion must have been based on misidentified specimens, since all individuals from this district that were examined lack talonids on the lower molars, in contrast to *A. hottentotus* which has well-developed molar talonids. Also, these localities are separated from the range of *A. hottentotus* by a corridor of bushveld in which only *A. julianae* is known to exist (Section 5.3.2.4).

Single classification analysis of variance showed that sexual dimorphism is not very pronounced in this species, males being slightly larger in most measurements but significantly larger in only ARB, PAL, APW and MDL (Table 6.4a). Principal components analysis resulted in the separation of the sexes along PC I (Fig. 6.3a), which was a size vector (as indicated by the high, positive loadings for all variables; Table 6.4b), but broad overlap of the male and female groups along PC II. The male and female specimens tended to cluster apart in phenograms based on average taxonomic distances (not illustrated), confirming their divergence in overall size, but not in phenograms based on correlation coefficients (Fig. 6.3b), indicating that shape differences between the sexes are negligible. Principal components and cluster analyses were thus congruent in showing that intra-populational craniometric variation in *A. gunningi* is dominated by sexual differences in size.

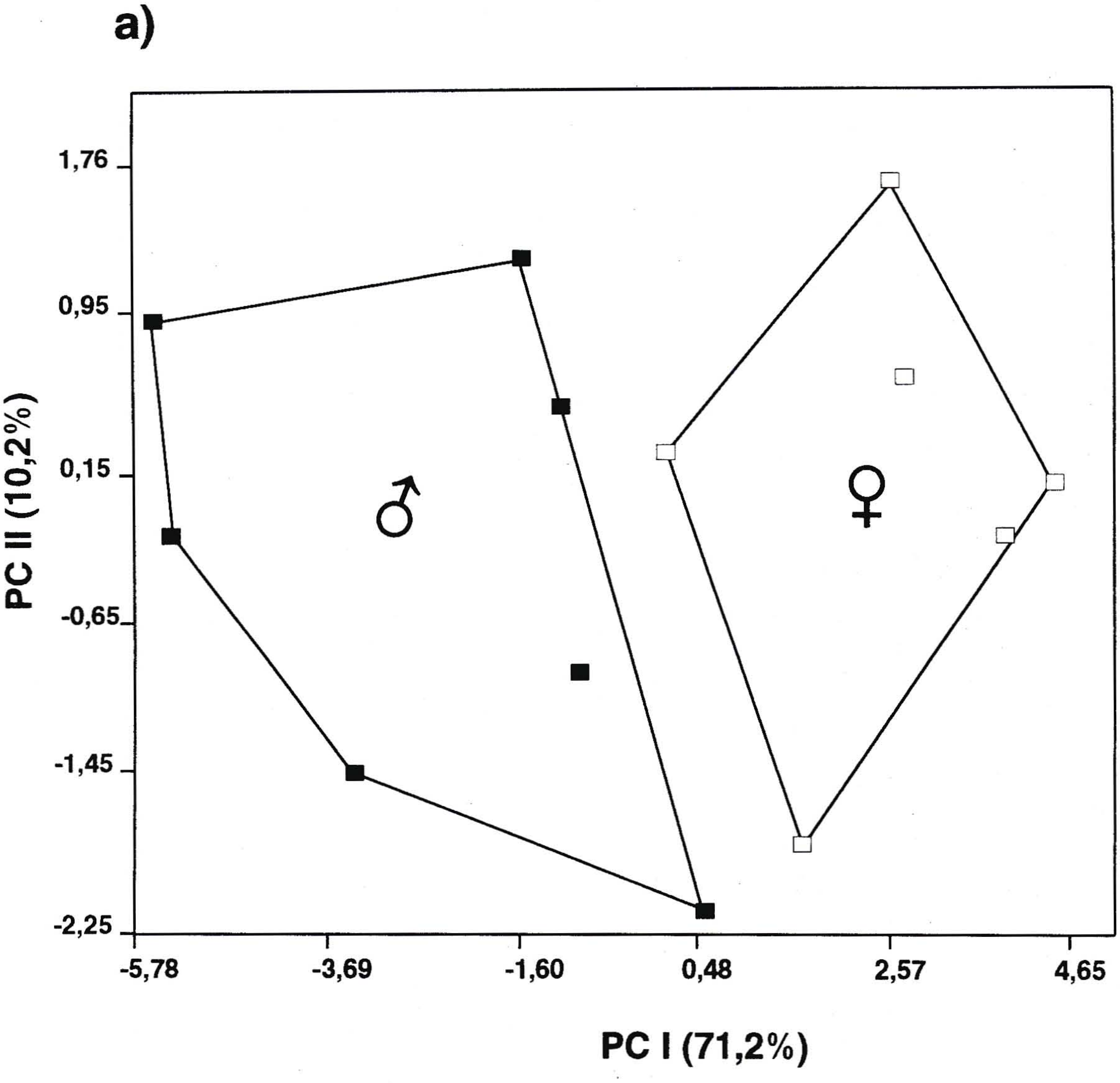
This species is unique in that all specimens lack well developed talonids on the lower molars, although traces of weak talonids are present in two specimens. Thirteen (75%) of the 17 specimens examined show M3, although variably between jaw quadrants. When present, these teeth are much smaller than the other molars, but do not necessarily have a peg-like appearance often claimed (Meester *et al.* 1985; Roberts 1951). As in *A. hottentotus*, M3 are distinctly triconid in younger (TW2) specimens, but are sometimes reduced to stumps by occlusal attrition in older (TW3-4) individuals. The morphology of these teeth is thus heavily dependent on toothwear, and this character thus has little taxonomic value.

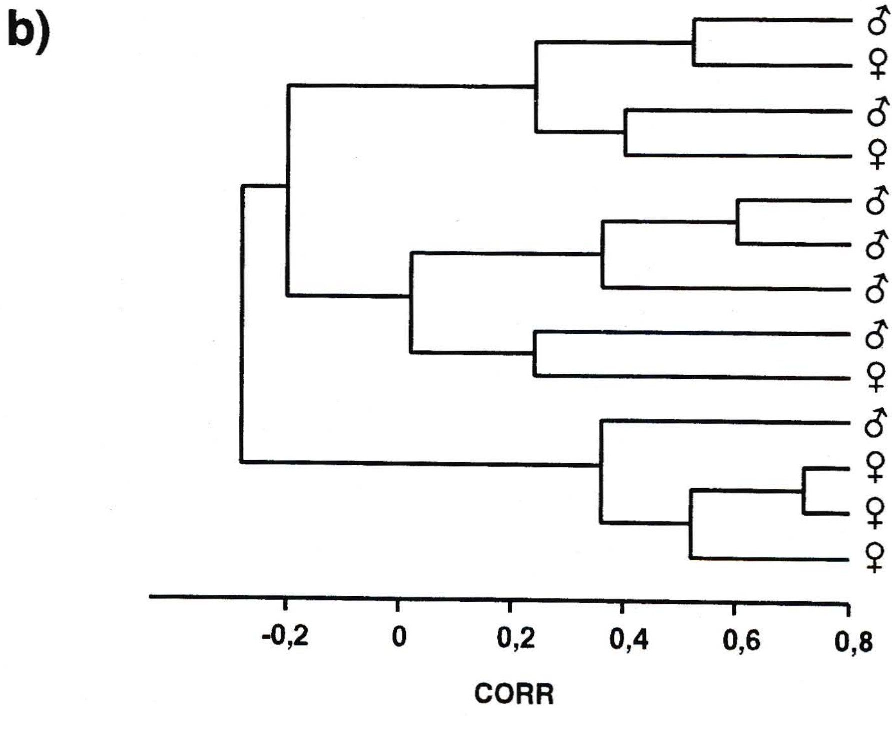
Table 6.4

Summary statistics and results of single-classification analysis of variance (a), and eigenvector coefficients from a principal components analysis (b), comparing male and female specimens (TW 2-4) of *A. gunningi* from Woodbush Forest, Northern Province. $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size; * - $p < 0,05$.

OTU	STAT	BCW	ARB	MIO	ZMB	IOW	GSL	GSH	P@P	PBM	PAL	MTL	IPG	PPL	BBW	CPL	APW	MDL
a) Summary statistics																		
♂	$\bar{x}$	4,72	4,99	8,13	17,33	7,91	28,41	13,23	8,26	4,81	14,98	7,05	2,12	8,89	12,24	7,41	4,51	17,67
	sd	0,10	0,19	0,39	0,68	0,29	0,73	0,35	0,32	0,22	0,50	0,22	0,16	0,34	0,53	0,37	0,23	0,58
	Min	4,51	4,70	7,61	16,12	7,56	27,13	12,76	7,75	4,49	14,02	6,75	1,74	8,39	11,44	6,85	4,16	16,66
	Max	4,94	5,30	8,74	18,20	8,34	29,33	13,83	8,73	5,11	15,60	7,31	2,35	9,34	13,19	8,13	4,83	18,57
	n	10	11	11	11	11	11	11	10	8	11	10	11	11	11	11	11	11
♀	$\bar{x}$	4,51	4,69	7,82	16,55	7,60	27,53	12,91	8,04	4,67	14,41	7,00	2,21	8,65	11,94	6,98	4,12	17,07
	sd	0,17	0,11	0,14	0,39	0,13	0,36	0,25	0,24	0,28	0,32	0,16	0,18	0,17	0,28	0,25	0,13	0,27
	Min	4,31	4,59	7,63	15,85	7,41	27,01	12,60	7,66	4,23	14,00	6,80	1,88	8,51	11,70	6,68	3,95	16,84
	Max	4,79	4,86	8,00	16,88	7,69	27,83	13,29	8,32	4,94	14,84	7,19	2,34	8,93	12,47	7,32	4,35	17,48
	n	6	6	6	6	6	6	6	5	5	6	6	6	6	6	6	6	6
SEX	*F*	2,12	8,98*	2,28	3,09	3,23	3,63	3,04	1,86	1,30	5,33*	0,56	0,65	1,26	0,58	3,80	6,65*	4,74*
b) Eigenvector coefficients																		
	PCI	0,607	0,961	0,822	0,945	0,920	0,961	0,955	0,863	0,771	0,893	0,501	0,364	0,907	0,907	0,913	0,861	0,946
	PCII	-0,712	-0,083	0,132	-0,097	-0,243	0,019	0,194	0,288	0,296	0,274	0,804	0,249	-0,177	-0,195	-0,175	-0,244	0,007

Fig. 6.3. Results of ordination and cluster analyses of single-standardized data for male (■) and female (□) *A. gunningi* from Woodbush Forest, Northern Province. a) scatterplot comparing the first axes from a principal components analysis (co-phenetic correlation = 0,991); b) phenogram based on UPGMA clustering of correlation coefficients (co-phenetic correlation = 0,783).


a)
1,76
0,95
0,15
-0,65
-1,45
-2,25
PC II (10,2%)
-5,78
-3,69
-1,60
0,48
2,57
4,65
PC I (71,2%)
♂
♀


b)
♂
♀
♂
♀
♂
♂
♂
♂
♀
♂
♀
♀
♀
-0,2
0
0,2
0,4
0,6
0,8
CORR

6.3.5 *Amblysomus corriae*

Contrary to previous taxonomic treatments, this species is here considered distinct from *A. h. iris*, and includes the taxon *devilliersi* (from the Western Cape) classically referred to *A. hottentotus* (Section 5.4.4). It is confined to forest and fynbos habitats of the South-West Cape biotic zone.

Dental variability is negligible in *A. corriae*. All of the specimens examined have sectorial first premolars and well-developed molar talonids while lacking M3. One specimen (TM8995) from Grootvadersbosch lacks erupted teeth altogether while having the cranial dimensions of an adult, and thus is teratological.

Two-way analyses of variance comparing sexual samples from three pooled population samples (Humansdorp, Knysna = George and Knysna, Western Cape = Stellenbosch and Grootvadersbosch) indicated that size dimorphism is negligible (Table 6.5). Only four variables - basal claw width (BCW), palate width across P^2 (P@P), coronoid process length (CPL) and ascending process width (APW) - differed significantly between males and females. But, the three populations differed significantly in 12 (80%) of the measurements analysed, indicating that size varies quite markedly on a geographic basis. Highly significant ($p < 0{,}01$) interaction between the sex and locality groups was indicated for two measurements summarizing coronoid process morphology (CPL, APW). Examination of subclass means revealed that this interaction was synergistic by nature. While both measurements increased through the geographic sequence Knysna→Humandorp→Western Cape in the male samples, the female samples showed the opposite trend for APW, while CPL remained almost constant. Divergent patterns of geographic variation were, therefore, manifest in the male and female samples.

Within each sex, the Humansdorp samples were largest in most measurements, but were characterized by significantly smaller inter-orbital widths (IOW) than either the Knysna or Western Cape OTUs. The Knysna samples were smallest in most measurements. The Western Cape (Stellenbosch/Grootvadersbosch) OTUs, although of intermediate size in most measurements, had significantly wider inter-orbital widths (IOW) and longer coronoid processes (APW) than the other groups. No obvious pattern of clinal size variation in any measurement was apparent on either a latitudinal or a longitudinal basis.

Table 6.5

Summary statistics and results of two-way analyses of variance to test for sexual dimorphism and geographic variation in adult (TW 2-4) *A. corriae* specimens representing three populations (Kny = Knysna and George; HD = Humansdorp; DEV = Western Cape). $\overline{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size; * and # denote significant *F* values at $p \leq 0{,}05$ and $p \leq 0{,}01$ respectively.

OTU	STAT	BCW	ARB	MIO	ZMB	IOW	GSL	GSH	P@P	PAL	MTL	PPL	BBW	CPL	APW	MDL
KNY♀	$\overline{x}$	4,74	4,58	8,13	15,80	7,06	26,87	12,50	6,89	13,55	6,03	8,83	11,31	7,34	4,58	16,62
	sd	0,13	0,11	0,36	0,56	0,19	0,53	0,20	0,25	0,57	0,21	0,13	0,46	0,21	0,22	0,43
	Min	4,57-	4,45-	7,51-	14,90-	6,77-	26,08-	12,27-	6,59-	12,61-	5,61-	8,68-	10,65-	7,05-	4,28-	16,11-
	Max	4,91	4,79	8,44	16,38	7,31	27,53	12,84	7,26	14,22	6,21	9,04	11,88	7,64	4,88	17,28
	n	7	7	7	7	7	7	7	7	7	7	7	6	7	7	7
KNY♂	$\overline{x}$	4,57	4,40	8,01	15,58	7,04	26,54	12,26	6,69	13,23	6,16	8,72	11,03	6,98	4,28	16,12
	sd	0,22	0,21	0,23	0,56	0,31	0,79	0,35	0,28	0,61	0,27	0,30	0,36	0,27	0,24	0,52
	Min	4,20-	4,10-	7,73-	14,90-	6,66-	25,34-	11,75-	6,38-	12,28-	5,89-	8,32-	10,56-	6,58-	3,94-	15,22-
	Max	4,97	4,77	8,51	16,45	7,54	27,79	12,76	7,17	14,24	6,75	9,16	11,68	7,50	4,69	16,87
	n	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
HD♀	$\overline{x}$	5,25	4,84	8,48	15,93	6,93	27,29	12,92	7,12	13,63	6,48	8,72	11,55	7,32	4,48	17,14
	sd	0,35	0,23	0,23	0,50	0,20	0,96	0,47	0,19	0,50	0,26	0,31	0,52	0,34	0,26	0,69
	Min	4,92-	4,42-	8,27-	15,26-	6,52-	26,04-	12,32-	6,91-	12,80-	6,14-	8,32-	10,86-	6,87-	4,00-	16,34-
	Max	5,94	5,13	8,83	16,90	7,22	28,59	13,76	7,47	14,34	6,95	9,12	12,45	7,80	4,79	18,08
	n	10	9	10	10	10	10	10	10	10	10	10	10	10	10	10
HD♂	$\overline{x}$	5,13	4,83	8,17	15,87	6,99	27,78	12,89	7,07	13,79	6,40	8,86	11,52	7,40	4,54	16,83
	sd	0,30	0,30	0,26	0,60	0,31	0,95	0,42	0,19	0,43	0,16	0,34	0,29	0,40	0,27	0,68
	Min	4,77-	4,49-	7,75-	15,28-	6,67-	26,50-	12,49-	6,87-	13,20-	6,23-	8,40-	11,20-	6,85-	4,11-	15,99-
	Max	5,55	5,25	8,50	16,85	7,38	28,88	13,42	7,39	14,22	6,59	9,34	11,98	7,90	4,90	18,01
	n	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
DEV♀	$\overline{x}$	5,05	4,75	7,95	15,47	7,19	26,66	12,55	7,22	13,45	6,27	8,63	11,22	7,35	4,44	16,68
	sd	0,27	0,27	0,24	0,28	0,29	0,66	0,30	0,17	0,72	0,23	0,32	0,37	0,41	0,35	0,58
	Min	4,72-	4,29-	7,52-	15,19-	6,61-	25,70-	12,02-	6,95-	12,15-	5,92-	8,39-	10,83-	7,03-	4,17-	16,21-
	Max	5,38	5,17	8,31	16,04	7,63	27,95	12,93	7,42	14,39	6,62	9,39	11,72	8,35	5,27	17,96
	n	9	11	11	10	11	10	10	10	10	9	10	10	11	11	10
DEV♂	$\overline{x}$	5,17	4,96	8,04	15,91	7,27	27,41	12,78	7,11	13,90	6,31	8,76	11,38	7,75	5,03	17,34
	sd	0,07	0,12	0,22	0,17	0,18	0,37	0,12	0,31	0,37	0,31	0,14	0,44	0,37	0,18	0,42
	Min	5,04-	4,89-	7,76-	15,64-	7,09-	26,92-	12,65-	6,68-	13,37-	5,88-	8,54-	10,83-	7,48-	4,83-	16,99-
	Max	5,23	5,18	8,31	16,03	7,52	27,95	12,91	7,42	14,39	6,62	8,91	11,77	8,35	5,27	17,96
	n	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
SEX	*F*	6,34*	2,10	2,75	0,00	0,03	0,35	1,60	10,20#	0,00	0,14	0,52	1,14	4,21*	5,88#	2,21
OTU	*F*	24,40#	14,01#	10,30#	1,69	4,46*	4,87*	11,09#	15,49#	1,57	8,51#	0,62	4,12*	0,03*	0,59	7,45#
INT	*F*	2,63	3,67*	2,31	1,84	0,23	2,32	2,21	1,55	1,89	1,18	1,04	1,20	8,76#	11,16#	4,65*

Multivariate analysis of variance revealed that differences between the six samples were highly significant ($F_{(75,114)} = 2,99$, $p < 0,001$). Multiple discriminant functions analysis resulted in an overall *a posteriori* classification of 95%. The only mis-identifications ($n = 2$) involved female specimens that were allocated to the male groups from the same localities (Knysna and Humansdorp). No specimens were classified to the incorrect locality, indicating that the three geographic groups were well differentiated from each other.

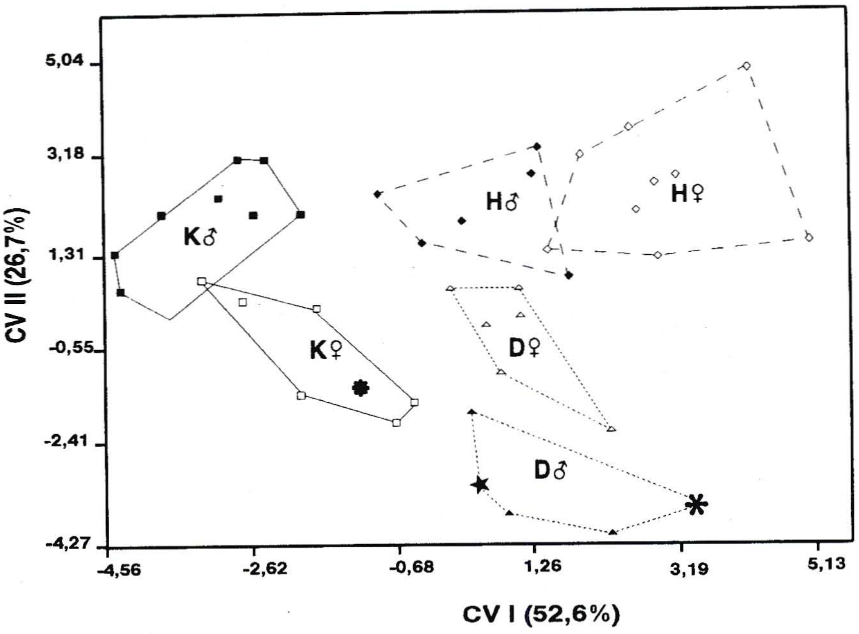
In scattergrams comparing the first two canonical variate axes the Knysna and Western Cape OTUs separated along CV I, while the samples of either sex plotted apart along CV II (Fig. 6.4a). In contrast, the Humansdorp and Western Cape OTUs separated along CV II, whereas the Humansdorp male and female samples tended to plot apart along CV I.

A similar result, albeit less pronounced, was evident also in a scatterplot (Fig. 6.4b) comparing the first two axes from a principal components analysis based on single-standardized data. Although no separation of the sex samples from Knysna was evident along either axis, the male and female samples from the Western Cape plotted apart along PC I, while the two Humansdorp samples tended to separate from each other, and the other OTUs, along primarily PC II. All 15 of the variables used in this analysis loaded high and positive along PC I (Table 6.6a), indicating that this axis reflected mainly differences in overall size (which decreased from left to right). PC II was influenced most strongly by mid inter-orbital breadth (MIO) and ascending process width (APW). Increasing scores along this axis reflected a relative broadening of the mid inter-orbital region (as indicated by MIO:ZMB in Table 6.6b), and a relative decrease in the length of the coronoid process of the mandible, the interactive effect between sex and locality being less pronounced when this variable is expressed in relative terms (APW:MDL). Separation along PC II thus reflected divergence in shape among the geographic groups, and also between the male and female samples from each locality.

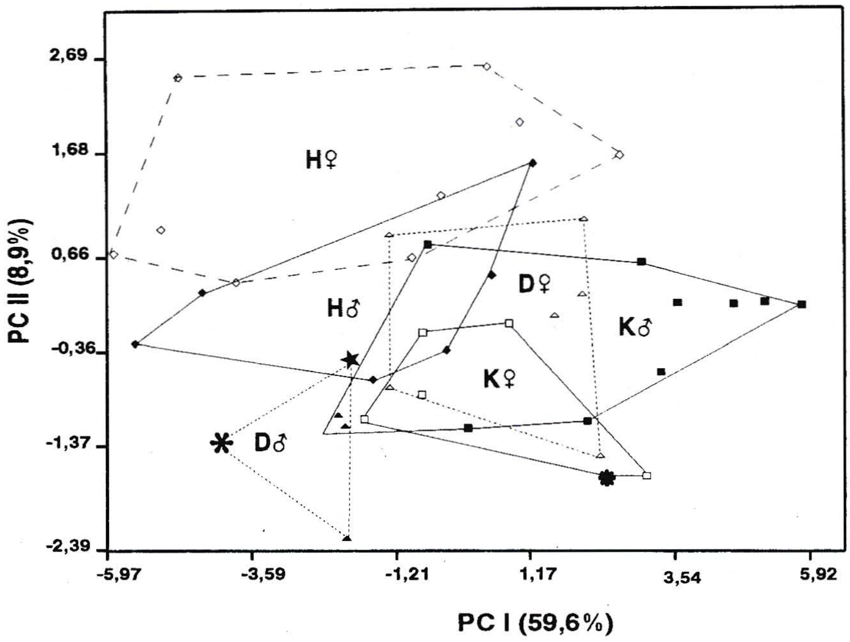
Cluster analyses confirmed the existence of pronounced divergence in both cranial size and shape between the sexes, and among the three geographic OTUs. In a phenogram based on average taxonomic distances (Fig. 6.5), three major phena (A-C) were evident. Most ($^{13}/_{15}$) of the Humansdorp specimens plotted together in distinct subphena (A and B1), but no separation according to sex was evident. Conversely, the

Fig. 6.4. Results of ordination analyses of male and female *A. corriae* from three localities. Population codes are: H - Humansdorp; K - Knysna and George; D - Western Cape. a) scatterplot of the first two canonical variate axes, from a six-group discriminant functions analysis; b) pairwise comparison of the first two axes from a principal components analysis based on single standardized data (co-phenetic correlation = 0,972); c) scatterplot of the first two principal component axes, computed from data standardized independently by sex to remove sexual dimorphism (co-phenetic correlation = 0,986). Symbols indicate: (▲) - Western Cape; (◇) - Humansdorp; (■) - Knysna and George; (✱) - holotype of *A. h. devilliersi*; (★) - holotype of *A. h. swellendamensis*; (✸) - holotype of *A. corriae*.

a)


5,04
3,18
1,31
-0,55
-2,41
-4,27
CV II (26,7%)
-4,56
-2,62
-0,68
1,26
3,19
5,13
CV I (52,6%)
K♂
K♀
H♂
H♀
D♀
D♂

b)


2,69
1,68
0,66
-0,36
-1,37
-2,39
PC II (8,9%)
-5,97
-3,59
-1,21
1,17
3,54
5,92
PC I (59,6%)
H♀
H♂
D♀
K♂
K♀
D♂

c)

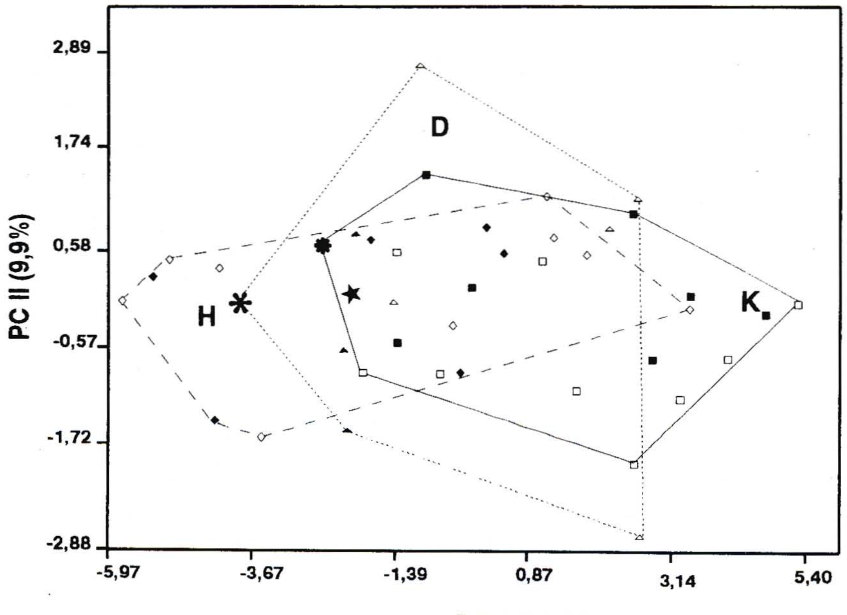

2,89
1,74
0,58
-0,57
-1,72
-2,88
PC II (9,9%)
-5,97
-3,67
-1,39
0,87
3,14
5,40
PC I (59,3%)
D
H
K

Table 6.6

Results of a principal components analysis of three populations of *A. corriae*: a) eigenvector coefficients for the first two principal components axes (see Fig. 6.4), with boldfaced loadings indicating variables that influence each axis strongly; and b) selected cranial ratios illustrating subtle differences in cranial shape between samples.

a) Eigenvector coefficients

Variable	PC I	PC II
BCW	**0,791**	-0,274
ARB	**0,818**	-0,018
MIO	**0,582**	**-0,554**
ZMB	**0,844**	0,007
IOW	**0,457**	0,271
GSL	**0,918**	0,063
GSH	**0,901**	-0,148
P@P	**0,654**	-0,242
PAL	**0,860**	0,050
MTL	**0,684**	-0,480
PPL	**0,568**	0,387
BBW	**0,846**	-0,046
CPL	**0,816**	0,362
APW	**0,743**	**0,519**
MDL	**0,910**	0,084

b) Cranial ratios (groups listed in descending order along PC II)

OTU	MIO:ZMB	APW:MDL
HUMANSDORP♀	53,42±1,66	25,61±1,10
HUMANSDORP♂	51,51±1,47	26,99±0,65
KNYSNA♂	51,46±1,75	26,52±0,86
W.CAPE♀	51,42±1,37	27,06±1,10
KNYSNA♀	51,70±0,75	27,80±0,85
W.CAPE♂	50,56±1,17	29,03±0,53

Fig. 6.5. Phenogram based on average taxonomic distance coefficients (ATD) computed from single-standardized data for *A. corriae* (co-phenetic correlation = 0,687). Population codes are: K - Knysna and George; H - Humansdorp; D - Western Cape (Stellenbosch and Grootvadersbosch).

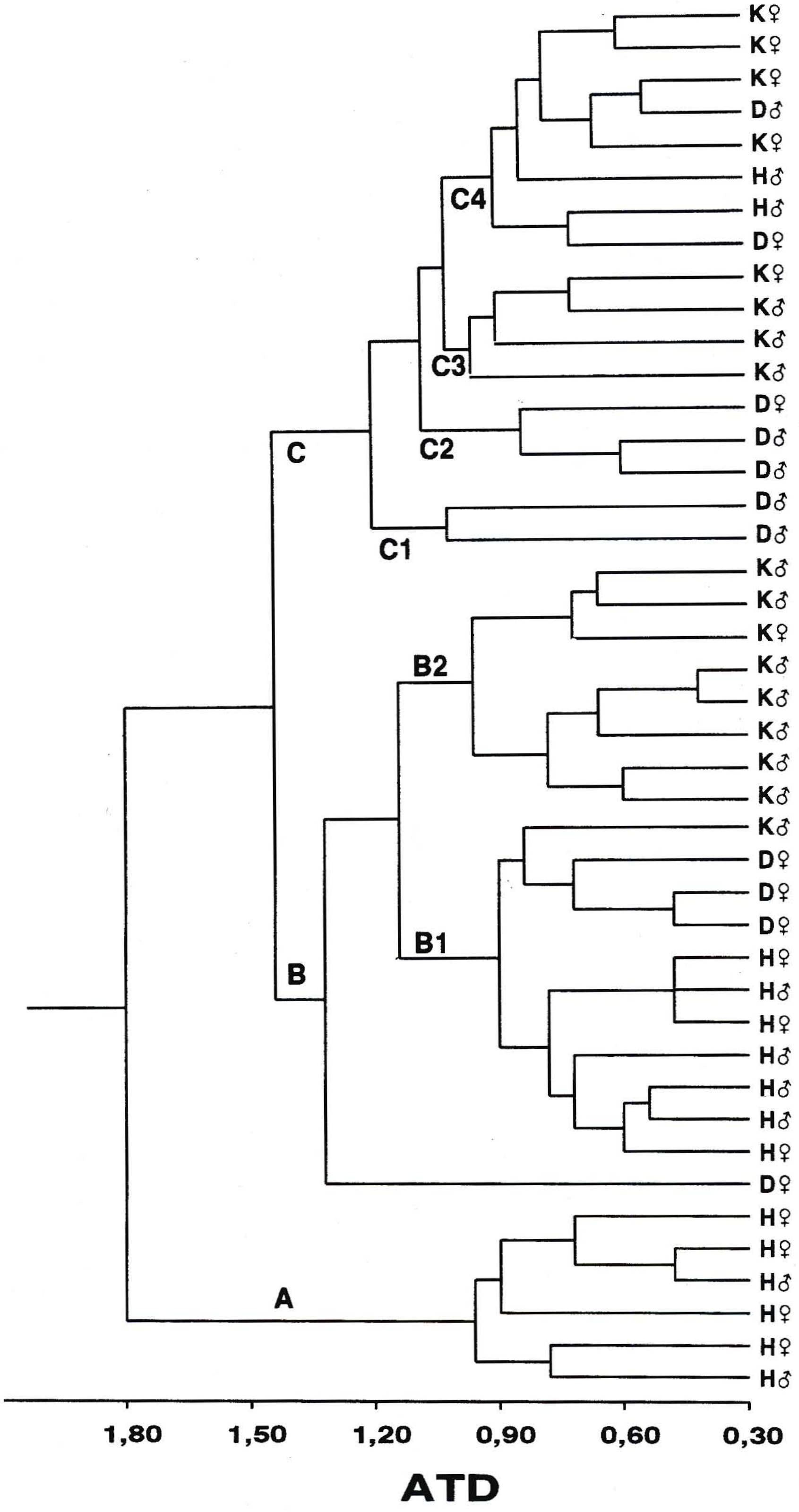

K♀
K♀
K♀
D♂
K♀
H♂
H♂
D♀
K♀
K♂
K♂
K♂
D♀
D♂
D♂
D♂
D♂
K♂
K♂
K♀
K♂
K♂
K♂
K♂
K♂
K♂
D♀
D♀
D♀
H♀
H♂
H♀
H♂
H♂
H♂
H♀
D♀
H♀
H♀
H♂
H♀
H♀
H♂
C4
C3
C2
C1
C
B2
B1
B
A
1,80
1,50
1,20
0,90
0,60
0,30
ATD

Fig. 6.6. Phenogram based on correlation coefficients (CORR) computed from single-standardized data for *A. corriae* (co-phenetic correlation = 0,592). Population codes are: K - Knysna and George; H - Humansdorp; D - Western Cape (Stellenbosch and Grootvadersbosch).

joint influence of sex and locality was evidenced by a tendency for male and female specimens from the Western Cape to separate into distinct subclusters (♂: C1 and C2; ♀: B2) within Phena B and C, and by the grouping of most of the male specimens from Knysna (subphenon B3) apart from most of the Knysna females (subphenon C4).

A comparable result was apparent also in a phenogram based on correlation coefficients (Fig. 6.6), which separated the specimens into two main groups (Phena A and B). Phenon A contained all of the females from Humansdorp, and most of the females from the Western Cape, which separated into two subphena (A1 and A2 respectively) according to locality. Similarly, most of male specimens from Knysna grouped in a distinct cluster (subphenon B1), and apart from Knysna females, which instead plotted in subphenon B2 together with an assortment of specimens from all three localities.

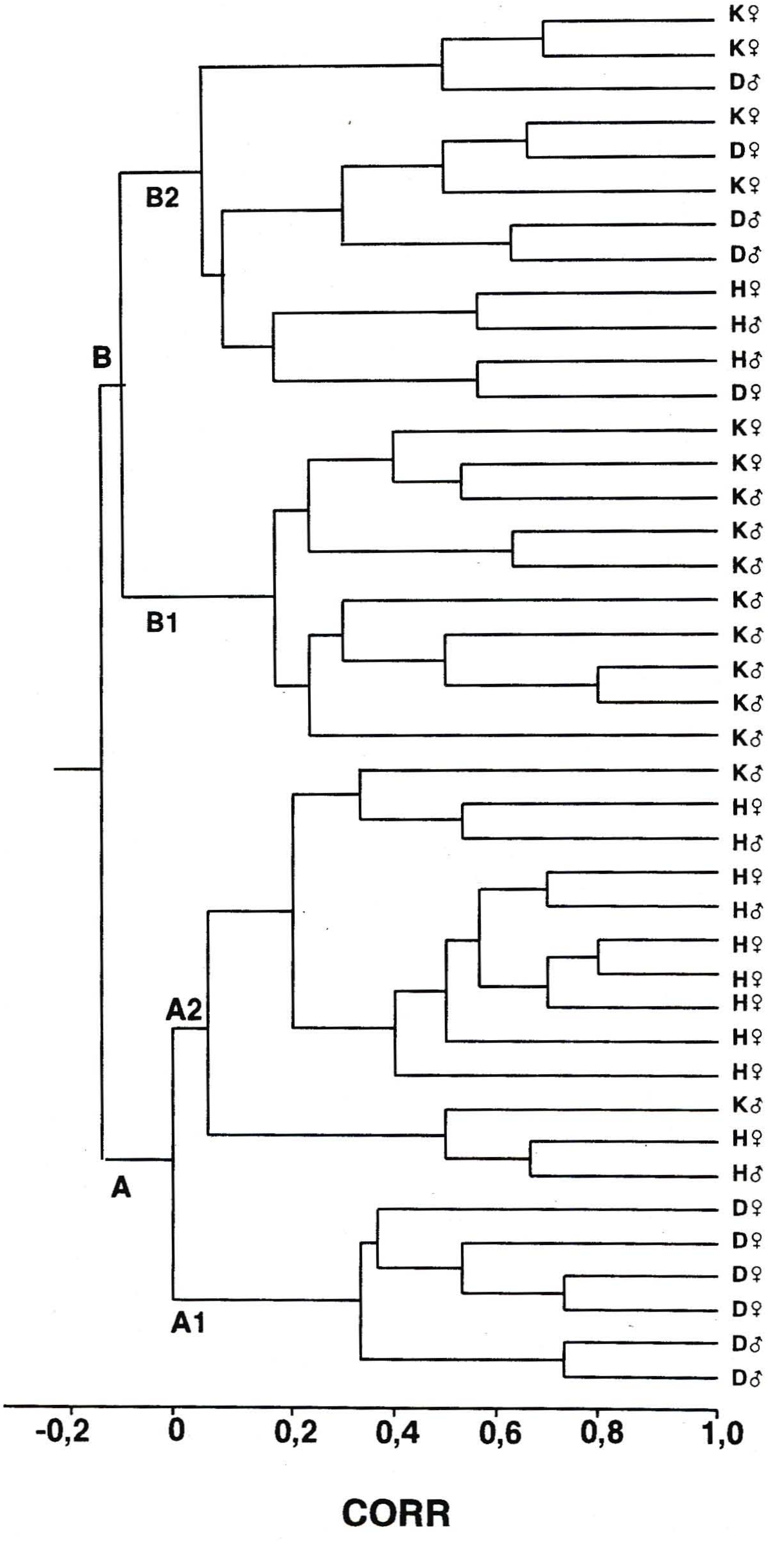
Craniometric variability within *A. corriae* thus involves significant sexual dimorphism, geographic divergence in both size and shape, and synergistic interaction between these sources of variation. To gauge the extent of geographic variation in this species accurately, it was thus necessary to control for the influence of sex on cranial morphology, by standardizing the male and female samples independently (Cheverud 1982). Scatterplots of the first two axes from a resulting principal components analysis revealed broad overlap of the samples from the three localities (Fig. 6.4c). The geographic component of craniometric variation in *A. corriae* is not, therefore, sufficiently pronounced to warrant the recognition of any subspecies.

6.3.6 *Amblysomus septentrionalis*

This cryptic species, which is phenotypically very similar to both *A. hottentotus* and *Amblysomus Species A*, is known from montane vleis in the vicinity of Wakkerstroom and Ermelo on the Mpumalanga highveld. Populations of unknown karyotype from the Heilbron district in the Free State also grouped with this species in ordination analyses (Section 5.3.2.3), suggesting that these forms represent the same species. This possibility is supported by the existence of a single specimen (TM24995) from an intermediate locality (Standerton).

Dental variability is negligible in *A. septentrionalis*. All specimens examined have sectorial first premolars and well-developed molar talonids. Most specimens lack M3, the only exception being one male from Wakkerstroom (TM41600) which shows both M^3 but lacks M_3.

Fig. 6.6. Phenogram based on correlation coefficients (CORR) computed from single-standardized data for *A. corriae* (co-phenetic correlation = 0,592). Population codes are: K - Knysna and George; H - Humansdorp; D - Western Cape (Stellenbosch and Grootvadersbosch).


K♀
K♀
D♂
K♀
D♀
K♀
D♂
D♂
H♀
H♂
H♂
D♀
K♀
K♀
K♂
K♂
K♂
K♂
K♂
K♂
K♂
K♂
K♂
H♀
H♂
H♀
H♂
H♀
H♀
H♀
H♀
H♀
K♂
H♀
H♂
D♀
D♀
D♀
D♀
D♂
D♂
B2
B
B1
A2
A
A1
-0,2
0
0,2
0,4
0,6
0,8
1,0
CORR

Two-way analyses of variance comparing male and female samples from Wakkerstroom, Ermelo and Heilbron showed that sexual dimorphism is pronounced. Males were significantly larger than females in 12 (71%) of the 17 variables analysed (Table 6.7). Geographic variation was even more marked, with 15 (88%) of the measurements differing significantly between the three populations. The order of ranked means was similar in most measurements of both sexes, and reflected a regular pattern of variation whereby the Wakkerstroom OTU was larger than the Ermelo and Heilbron OTUs in most measurements. The Wakkerstroom OTU was characterized by a significantly longer coronoid process (CPL) and mandible (MDL) in both sexes, whereas cranial widths (especially MIO and IPG) were significantly smaller in the Ermelo OTU. The Heilbron female sample was characterized by a significantly shorter palate (PAL) and mandible (MDL) than the other OTUs. The Heilbron specimens, despite their generally smaller size, had wider palates, so that the ratio of P@P:GSL was slightly higher ($\bar{x} \pm 1se = 49{,}0 \pm 1{,}12$) than in the other two samples (Ermelo: $\bar{x} \pm 1se = 47{,}5 \pm 0{,}74$; Wakkerstroom: $\bar{x} \pm 1se = 47{,}1 \pm 0{,}89$).

Multivariate analysis of variance, based on a reduced suite of 14 measurements, showed that differences between the six sex/locality groups were highly significant ($F_{(70,127)} = 2{,}39$, $p < 0{,}001$). However, multiple discriminant functions analysis resulted in an overall *a posteriori* classification of only 80%. Misidentifications involved specimens of either sex from the same locality, and between the Wakkerstroom and Ermelo groups, indicating that these OTUs are not well differentiated from each other. This was further supported by pairwise comparison of the first two canonical variate axes (Fig. 6.7), in which the Heilbron specimens clustered apart from others along CV I, while the sexes within each geographic group tended to plot apart along CV II. CV I was influenced most strongly by P@P, so separation of the Heilbron specimens along this axis to a large degree reflected the tendency for palate width to be relatively larger at this locality than in the other OTUs.

In scatterplots comparing the first two axes from a principal components analysis based on single-standardized data, the sex samples from each locality separated along PC I (Fig. 6.8a). Within each sex, the Heilbron samples tended to plot above the others along PC II, a trend that was particularly evident among the female samples. PC I was a general size vector, as shown by the high, positive eigenvector coefficients

Table 6.7

Summary statistics and results of two-way analyses of variance to test for sexual dimorphism and geographic variation in adult (TW 2-4) *A. septentrionalis* specimens representing three populations (HB = Heilbron; ER = Ermelo; WS = Wakkerstroom). $\overline{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size; * and $^{\#}$ denote significant *F* values at $p \leq 0{,}05$ and $p \leq 0{,}01$ respectively.

OTU	STAT	BCW	ARB	MIO	ZMB	IOW	GSL	GSH	P@P	PBM	PAL	MTL	IPG	PPL	BBW	CPL	APW	MDL
HB♂	$\overline{x}$	5,82	5,21	9,39	17,98	7,99	28,73	13,96	8,06	5,11	14,47	7,21	2,34	9,23	12,51	7,95	5,18	17,89
	sd	0,09	0,19	0,21	0,37	0,36	0,70	0,15	0,29	0,23	0,24	0,16	0,13	0,40	0,49	0,33	0,30	0,55
	Min	5,72	5,01	9,11	17,53	7,60	27,78	13,86	7,69	4,83	14,12	7,02	2,15	8,67	11,93	7,46	4,73	17,08
	Max	5,89	5,44	9,55	18,35	8,44	29,36	14,17	8,30	5,30	14,67	7,39	2,43	9,62	13,11	8,18	5,37	18,31
	n	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
HB♀	$\overline{x}$	5,28	4,89	8,96	16,80	7,59	27,10	13,33	7,59	4,82	13,43	6,80	2,27	8,60	11,73	7,28	4,63	16,67
	sd	0,17	0,21	0,30	0,60	0,28	1,15	0,38	0,21	0,29	0,57	0,36	0,12	0,42	0,58	0,39	0,38	0,72
	Min	4,99	4,55	8,47	16,09	7,16	26,19	12,94	7,37	4,36	12,86	6,38	2,11	8,07	10,84	6,81	4,73	15,91
	Max	5,42	5,11	9,35	17,85	7,95	29,36	13,88	7,98	5,13	14,52	7,39	2,43	9,35	12,63	8,00	5,37	18,00
	n	5	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
WS♂	$\overline{x}$	6,33	5,25	9,29	18,29	8,01	29,44	14,09	7,83	4,99	14,87	7,10	2,36	9,17	12,92	8,11	5,45	18,39
	sd	0,22	0,24	0,28	0,61	0,20	0,54	0,29	0,28	0,13	0,37	0,27	0,14	0,19	0,30	0,23	0,36	0,40
	Min	5,99	4,95	8,89	17,39	7,72	28,76	13,84	7,48	4,83	14,39	6,59	2,16	8,19	12,51	7,71	4,93	17,88
	Max	6,61	5,60	9,69	19,98	8,31	30,48	14,72	8,25	5,16	15,62	7,43	2,60	9,48	13,29	8,48	5,95	18,92
	n	6	8	8	8	3	8	8	8	8	8	8	8	8	8	8	8	8
WS♀	$\overline{x}$	5,73	5,04	9,01	17,16	7,63	28,51	13,47	7,57	4,86	14,25	6,88	2,22	8,97	12,15	7,66	4,99	17,71
	sd	0,27	0,22	0,32	0,73	0,26	0,88	0,49	0,38	0,30	0,53	0,22	0,12	0,29	0,56	0,32	0,29	0,52
	Min	5,21	4,65	8,47	16,16	7,29	26,55	12,79	6,07	4,37	12,86	6,54	2,05	8,49	11,07	7,28	4,33	16,39
	Max	6,10	5,44	9,56	18,95	8,10	29,95	14,43	8,21	5,47	14,91	7,17	2,52	9,39	12,95	8,33	5,43	18,69
	n	10	15	15	15	15	15	15	15	15	14	15	15	15	15	15	15	14
ER♂	$\overline{x}$	6,05	5,01	8,98	17,42	7,71	28,43	13,56	7,57	4,66	14,32	6,76	2,04	9,10	12,38	7,69	5,04	17,59
	sd	0,56	0,39	0,39	0,36	0,28	1,48	0,82	0,44	0,21	0,73	0,40	0,08	0,60	0,65	0,65	0,60	1,05
	Min	5,39	4,53	8,57	17,00	7,40	26,57	12,26	7,04	4,37	13,24	6,23	1,93	8,45	11,55	6,90	4,27	16,16
	Max	6,63	5,45	9,47	17,64	8,07	29,81	14,19	8,10	4,96	14,79	7,29	2,13	9,99	13,13	8,52	5,67	18,52
	n	9	11	11	10	11	10	10	10	10	9	10	10	11	11	10		
ER♀	$\overline{x}$	5,58	4,84	8,65	17,03	7,56	28,06	13,16	7,35	4,87	14,08	6,79	2,21	8,77	11,65	7,43	4,80	17,46
	sd	0,40	0,22	0,48	0,71	0,30	0,90	0,40	0,37	0,38	0,52	0,24	0,15	0,30	0,57	0,29	0,28	0,78
	Min	5,09	4,61	8,01	16,27	7,05	27,07	12,56	6,78	4,26	13,41	6,39	1,98	8,34	10,96	6,97	4,41	16,67
	Max	6,13	5,23	9,47	18,36	7,92	29,17	13,56	7,83	5,35	14,73	7,15	2,48	9,25	12,71	7,76	5,21	18,62
	n	8	9	9	9	9	6	9	9	8	9	9	9	9	9	9	9	9
SEX	*F*	5,35*	3,28*	5,07*	1,85	1,41	5,20$^{\#}$	3,36*	3,37*	1,04	5,48$^{\#}$	2,25	4,67*	1,40	4,85*	3,80*	3,59*	5,87$^{\#}$
OTU	*F*	23,28$^{\#}$	8,74$^{\#}$	10,13$^{\#}$	22,68$^{\#}$	14,33$^{\#}$	9,63$^{\#}$	17,19$^{\#}$	8,12$^{\#}$	0,66	14,55$^{\#}$	5,37*	0,64	9,83$^{\#}$	21,82$^{\#}$	15,85$^{\#}$	14,39$^{\#}$	9,66$^{\#}$
INT	*F*	0,14	0,29	0,20	1,33	0,91	1,23	0,28	0,41	2,38	1,62	1,96	6,20*	1,32	0,06	0,85	0,66	2,03

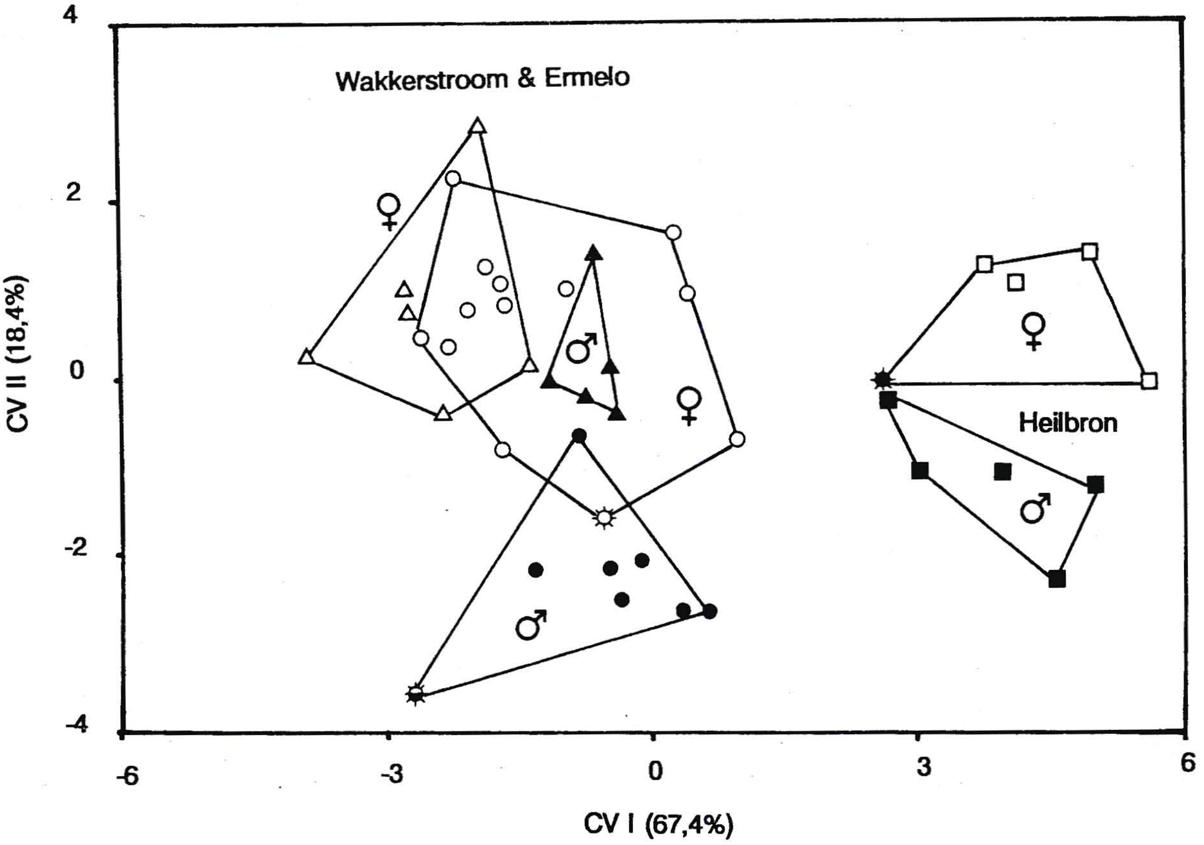
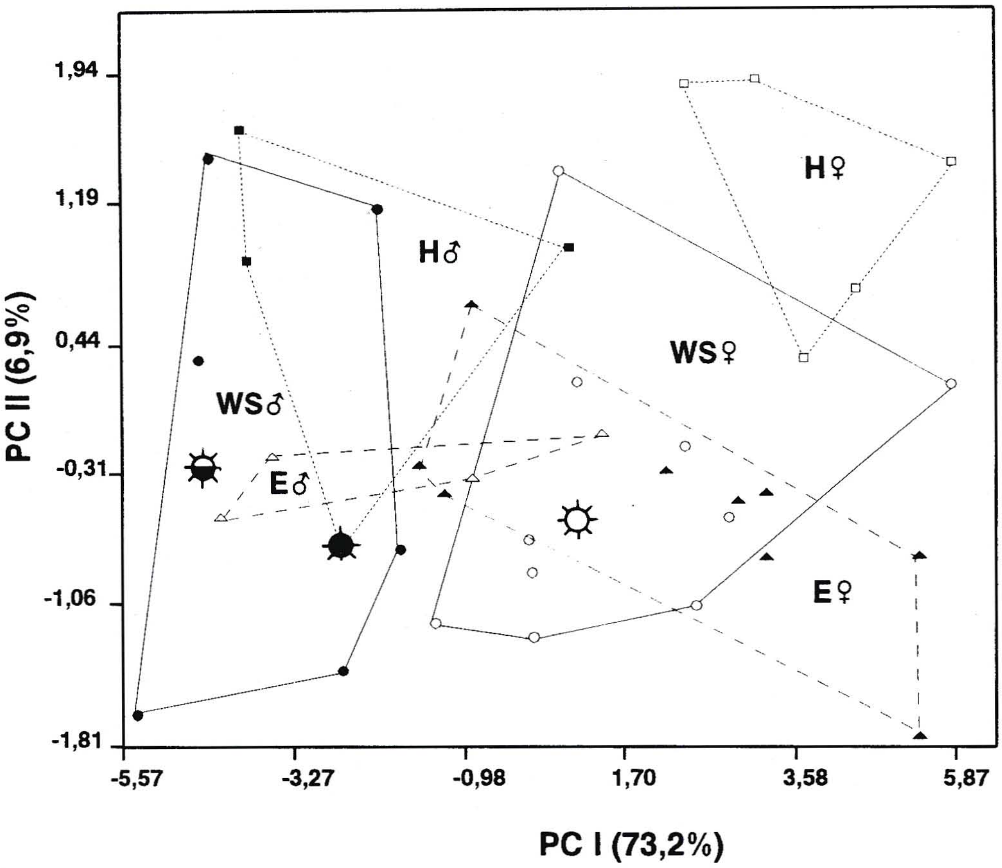
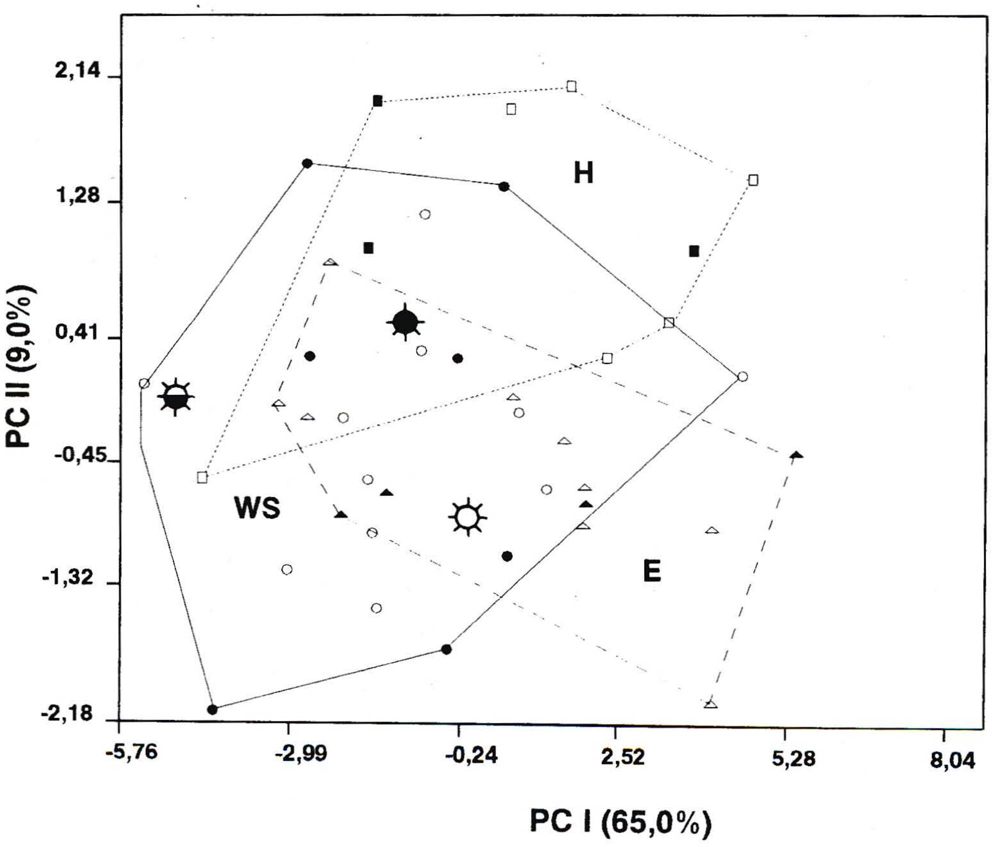


Fig. 6.7. Pairwise comparison of the first two canonical variate axes computed from a six group discriminant functions analysis of *A. septentrionalis* individuals representing three populations. Open (females) and solid (males) symbols indicate: (□) - Heilbron; (△) - Ermelo; (○) - Wakkerstroom; (✺) - holotype of *A. h. drakensbergensis*; (✹) - holotype of *A. h. orangensis*; (☼) -holotype of *A. septentrionalis*.

Fig. 6.8. Results of ordination analyses of male and female *A. septentrionalis* from three localities. Population codes are: H - Heilbron; E - Ermelo; WS - Wakkerstroom. a) scatterplot of the first two principal component axes, based on single standardized data (co-phenetic correlation = 0,911); b) scatterplot of the first two principal compoonent axes computed from data standardized independently by sex (co-phenetic correlation = 0,869). Solid and open symbols denote male and female specimens respectively. Symbols indicate: (■) - Heilbron; (▲) - Ermelo; (●) - Wakkerstroom; (✹) - holotype of *A. s. orangensis*; (✸) - holotype of *A. septentrionalis*; (☼) - holotype of *A. s. drakensbergensis*.


1,94
1,19
0,44
-0,31
-1,06
-1,81
-5,57
-3,27
-0,98
1,70
3,58
5,87
PC II (6,9%)
PC I (73,2%)
H♀
H♂
WS♀
WS♂
E♂
E♀


2,14
1,28
0,41
-0,45
-1,32
-2,18
-5,76
-2,99
-0,24
2,52
5,28
8,04
PC II (9,0%)
PC I (65,0%)
H
WS
E

for all variables (Table 6.8). Separation of the sex samples along this axis was thus due largely to differences in size, which tended to decrease from left to right. PC II was influenced most strongly by measurements summarizing medial cranial width (MIO, IOW), palate width (P@P) and palate length (PAL). Separation along PC II reflected the trend, already noted above, for the palate to be comparatively broader in the Heilbron specimens than in the other demes. This was evident also from an analysis based on data standardized independently by sex to remove the influence of size dimorphism. Although there was broad overlap between the three locality samples, most of the Heilbron specimens tended to plot apart along PC II (Fig. 6.8b), thereby confirming the existence of subtle geographic divergence within *A. septentrionalis*.

The uniqueness of the Heilbron OTU was corroborated also by a phenogram based on correlation coefficients (Fig. 6.9), in which most of the specimens from this OTU grouped (Phenon A) apart from the Wakkerstroom and Ermelo specimens, which fell into three clusters (Clusters B - D) without any clear pattern of separation according to locality. However, the type specimen of *A. h. orangensis*, which was collected from Heilbron, did not cluster with the other Heilbron specimens, but with specimens from Wakkerstroom and Ermelo, including the type of *A. septentrionalis*.

6.4 TAXONOMIC CONCLUSIONS

Sexual dimorphism is pronounced in all *Amblysomus* species except *A. gunningi* and *A. marleyi*. The apparent lack of sexual dimorphism in these species may, however, be an artefact resulting from the pooling of samples from different localities, and therefore masking of intra-population differences by geographic variation.

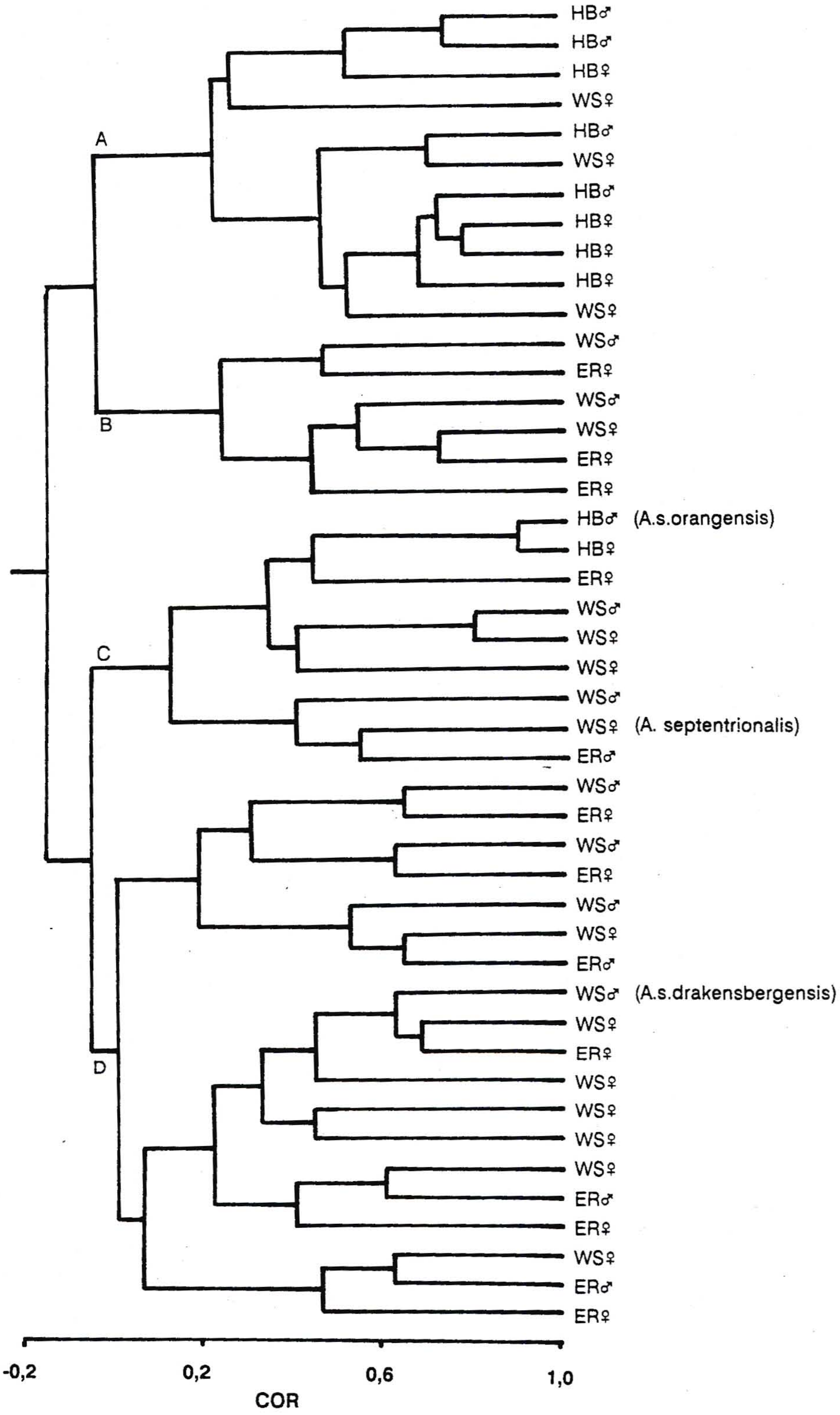
Geographic and sex-related variation is pronounced in *A. corriae*. But, when the influence of sex is controlled for, the three populations analysed do not differ sufficiently in cranial shape to warrant the recognition of subspecies. The George/Knysna and Humandorp populations are situated only about 200 km apart, and are probably geographically continuous since an intermediate deme occurs at Nature's Valley. Given the resemblance of specimens from these OTUs also in fur colour, which is uniformly reddish-black (10R 1,7/1; Section 5.4.4), these OTUs probably represent only craniometric extremes of nominotypical *A. corriae*. The

Table 6.8

Eigenvector coefficients for the first three axes from a principal components analysis based on single standardized craniometric data of male and female *A. septentrionalis* from three localities (see Fig. 6.8). Variables participating strongly in each axis are indicated in boldface.

VARIABLE	PCI	PCII	PCIII
ARB	**0,798**	0,238	**0,375**
MIO	**0,766**	**0,415**	-0,124
ZMB	**0,884**	0,156	0,113
IOW	**0,719**	**0,536**	-0,117
GSL	**0,929**	-0,245	0,031
GSH	**0,895**	-0,008	-0,017
P@P	**0,820**	**0,311**	-0,258
PAL	**0,890**	**-0,261**	-0,051
MTL	**0,685**	**-0,271**	**-0,596**
PPL	**0,870**	-0,137	-0,026
BBW	**0,933**	-0,014	0,069
CPL	**0,931**	-0,156	0,128
APW	**0,878**	-0,204	0,281
MDL	**0,920**	-0,189	0,027

Fig. 6.9 Phenogram based on cluster analysis (UPGMA) of correlation coefficients computed from pooled data for male and female *A. septentrionalis* after individual standardization of the sexes. The co-phenetic correlation is 0,575. Population codes are: HB - Heilbron; WS - Wakkerstroom; ER - Ermelo. Names of type specimens are given in parentheses.


A
B
C
D
HB♂
HB♂
HB♀
WS♀
HB♂
WS♀
HB♂
HB♀
HB♀
HB♀
WS♀
WS♂
ER♀
WS♂
WS♀
ER♀
ER♀
HB♂ (A.s.orangensis)
HB♀
ER♀
WS♂
WS♀
WS♀
WS♂
WS♀ (A. septentrionalis)
ER♂
WS♂
ER♀
WS♂
ER♀
WS♂
WS♀
ER♂
WS♂ (A.s.drakensbergensis)
WS♀
ER♀
WS♀
WS♀
WS♀
WS♀
ER♂
ER♀
WS♀
ER♂
ER♀
-0,2
0,2
0,6
1,0
COR

Stellenbosch/Grootvadersbosch populations, however, occur much further to the west, and differ in fur colour, which is reddish-black mid-dorsally, but becomes progressively redder towards the flanks and abdomen, which are reddish brown (5YR 4-6/4-6). Since these OTUs differ significantly from populations to the east also in cranial width (IOW), they should be relegated to a distinct subspecies, for which the name *A. c. devilliersi* is available.

Geographic and sex-related variation in cranial size is pronounced also in *A. septentrionalis*, but when isometric variation associated with sexual dimorphism is removed from the data the three populations analysed do not appear to be sufficiently differentiated in terms of overall size to warrant taxonomic separation. The Heilbron specimens have broader and shorter palates than those from Wakkerstroom and Ermelo, and indirect evidence (from a discriminant functions analysis) suggests that there are no morphological intermediates (hybrids) between this population and those further to the east. However, the broad overlap of locality samples in principal components analyses suggests that geographic variation in *A. septentrionalis* may be largely clinal, with subtle allometric differences accompanying an increase in overall size from west (Heilbron) to east (Wakkerstroom and Ermelo). Until more specimens from intermediate localities (such as Standerton) are available to allow a more detailed assessment of geographic variation, the Heilbron and Wakkerstroom/Ermelo OTUS should thus be viewed as only craniometric extremes of a monotypic species.

Although craniometric variation in *A. julianae* was not assessed, the colour and dental differences between the Pretoria/Nylsvley and Kruger Park populations are constant, suggesting that these demes represent different subspecies. However, taxonomic separation must await the analysis of more specimens, especially from intermediate localities, should these be found in the future.

Variability in the morphology of the canines and first premolars in negligible within all species examined, but the presence/absence of M3 and molar talonids is more variable. Ellerman *et al.* (1953) argued that the variable presence of M3 in *A. gunningi* showed that dental formula is not a valid character for distinguishing genera among chrysochlorids. This is not necessarily so, because while the presence of M3 is variable within this species, the vast majority of *A. gunningi* specimens have M3, whereas in most other species these teeth are present in only a small minority

(<3%) of individuals. The only species in which M3 occurs variably with an incidence exceeding 5% is *A. julianae*, but this variability has a geographic basis and is restricted to a single population (Kruger National Park) in which M_3 is invariably present. Similarly, well-developed molar talonids are present in most specimens of *A. hottentotus*, *A. corriae*, *A. septentrionalis*, *A. marleyi* and *Amblysomus Species A*, but are invariably absent in *A. julianae* and *A. gunningi*. In most species, therefore, more than 95% of specimens have dental characters that are typical for the species. These dental characters, although perhaps too variable within some species to be used exclusively for diagnostic purposes, thus do have taxonomic value.

CHAPTER 7

INTRA-SPECIFIC MORPHOMETRIC AND DENTAL VARIATION IN THREE *Chlorotalpa* SPECIES FROM SOUTHERN AFRICA

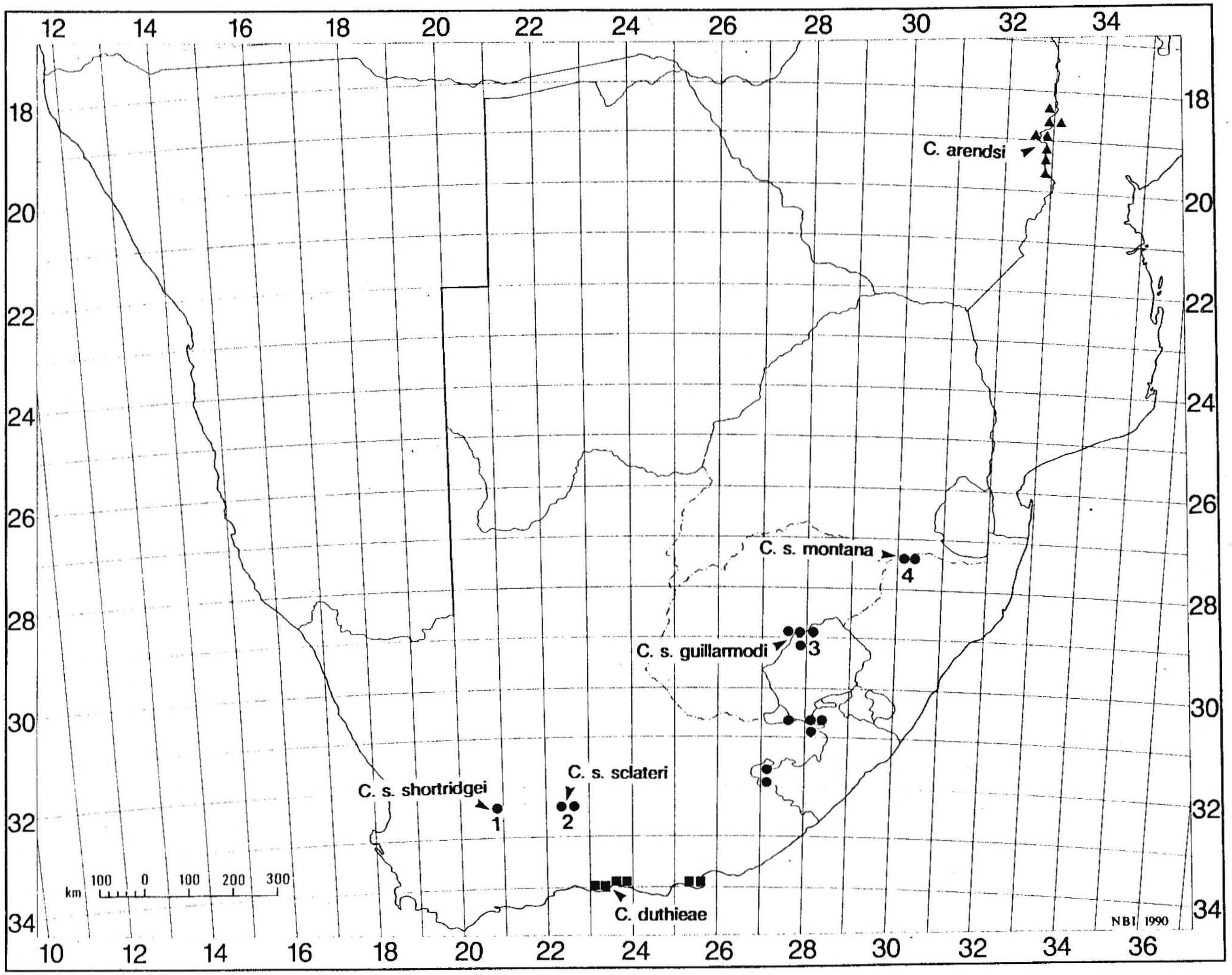
7.1 INTRODUCTION

Ellerman *et al.* (1953) argued against the use of dental formulae for diagnosing genera among chrysochlorids, and thus synonymized *Chlorotalpa* with *Amblysomus*, a treatment endorsed by Petter (1981). Meester (1974), however, regarded the dental differences between these taxa as sufficient to warrant generic separation, and recognized five species within *Chlorotalpa*. Of these, three (*C. duthieae*, *C. sclateri* and *C. arendsi*) are endemic to southern Africa. The two extralimital species are poorly known and have been recorded from only a few, scattered localities. *C. leucorhina* is the only species of golden mole that occurs in the equatorial forests of western central Africa (from Angola to Cameroon), while *C. tytonis* is known from only the partially-complete type specimen collected in Somalian woodland (Simonetta 1968).

Two of the southern African species are restricted to forest habitats along either the eastern coast (*C. duthieae*), or the eastern Zimbabwe escarpment (*C. arendsi*). Owing to their limited ranges (Fig. 7.1), most previous authors considered them to be monotypic species. *C. sclateri* is more widespread, and occurs from the Western Cape northeastwards through Lesotho and the eastern Free State to Wakkerstroom in the Mpumalanga highveld (Rautenbach 1982), with a marginal extension into western KwaZulu-Natal (Taylor *et al.* 1994). But, within this broad range the distribution of demes is clumped, owing to this species' preference for montane grasslands or forested kloofs - habitats that occur in disjunct patches, especially in the southern parts of its range where mountain ranges are separated by wide expanses of semi-arid Karoo. Four species were originally described on the basis of colour and size variation (Broom 1907b, 1946, 1950; Roberts 1924), but these are now considered to represent only subspecies, the validity of which is in need of review (Meester *et al.* 1986).

This chapter examines sexual and geographic morphometric variation in the three southern African species, sample sizes for the extra-limital taxa being too small

Fig. 7.1. The distribution of *Chlorotalpa arendsi* (▲), *C. duthieae* (■) and *C. sclateri* (●) in southern Africa. Arrows indicate type localities, whereas numbers indicate localities pooled for the analysis of geographic variation within species, as specified in Table 7.1.


C. arendsi
C. s. montana
4
C. s. guillarmodi
3
C. s. shortridgei
1
C. s. sclateri
2
C. duthieae
km 100 0 100 200 300
NBI 1990

for statistical analysis, and reviews the validity of the four described subspecies in *C. sclateri*. Patterns of interspecific variation and the generic affinities of these taxa are examined further in Chapter 9.

7.2 MATERIALS AND METHODS

Ninety-eight specimens from various museums (Chapter 2) were examined and measured. Owing to small sample sizes, analyses of non-geographic variation were restricted to statistical comparisons of the sexes (TW2-4 specimens combined) in single or pooled locality samples (Table 7.1) using single or two-way analyses of variance. Patterns of geographic variation in *C. duthieae* and *C. sclateri* were examined using ordination techniques (principal components and discriminant functions analyses) and cluster analysis (UPGMA) of correlation and average taxonomic distance coefficients. Data for the sexes were analysed either separately, or pooled following independent standardization to correct for size dimorphism. Where necessary, certain measurements (particularly EAM, PBM, IPG and FML) were omitted from analyses to maximize sample sizes.

7.3 RESULTS AND DISCUSSION

7.3.1 *Chlorotalpa arendsi*

Lundholm (1955) separated this species from *C. duthieae* and *C. sclateri* in the subgenus *Carpitalpa* on the basis of P_1 morphology (semi-molariform *cf.* sectorial) and ear characters (malleus elongated *cf.* rounded). Simonetta (1968) considered these differences sufficient to raise *Carpitalpa* to generic level, in contrast to Meester (1974) who argued that differences between the species in *Chlorotalpa* do not warrant subgeneric distinction.

All of the *C. arendsi* specimens examined lack protocones on the first upper premolar. P1 are invariably semi-molariform in both the upper and lower toothrows, and a small, molariform M3 is always present. The only dental characters which appears to vary intraspecifically is the presence and development of talonids on the lower cheekteeth. Of the 15 specimens examined, 12 lack talonids, traces of which are however evident in three individuals from toothwear classes TW2 and TW3.

Two-way analysis of variance based on samples pooled by sex regardless of locality indicated that while males were generally slightly larger than females in most

Table 7.1

Localities pooled as Operational Taxonomic Units (OTUs) for the analysis of intra-specific variation in three *Chlorotalpa* species. OTU Names are acronyms referred to in the text. Details of specimens examined are given in Chapter 11; see the Gazetteer for precise locality information.

Species	OTU Name	Pooled localities
C. arendsi	CAR	Mozambique: Villa Gouveia Zimbabwe: Inyanga - Pungwe Falls, Pamushana Farm, Rhodes Estate, Trout Research Centre, Mtarazi Falls; Mutare; Vumba - Bunga Forest, Cloudlands, Vumba Mountain; Hondi Valley; Melsetter.
C. duthieae	KNY	R.S.A., Western Cape Province: Knysna - Town and Forest; Plettenberg Bay.
	PE	R.S.A., Eastern Cape Province: Port Elizabeth - City, Walmer, Baakens Vlei.
C. sclateri	CSH	R.S.A., Western Cape Province: Sutherland.
	CSS	R.S.A., Western Cape Province: Beaufort West - Karoo National Park, Matjiesvlei.
	CSG	R.S.A., Free State: Gumtree; Clocolan; Ficksburg; Lesotho: Leribe; Mamathes.
	CSM	R.S.A., Mpumalanga: Wakkerstroom, Kastrol Nek (= Farm Tafelkop).

measurements, differences between the sexes were statistically non-significant (Table 7.2). In a scatterplot comparing the first two axes from a principal components analysis (Fig. 7.2a) the sex samples overlapped broadly along both axes, and no sex-related pattern of separation was evident in phenograms based on either correlation coefficients (Fig. 7.2b) or average taxonomic distance coefficients. The small samples available thus suggest that sexual differences in cranial size and shape are negligible in *C. arendsi*. Substantially larger samples are, however, needed to demonstrate this conclusively.

7.3.2 *Chlorotalpa duthieae*

This species, the epithet of which is widely mis-quoted as *duthiae*, was considered only subspecifically distinct from *C. sclateri* by Ellerman *et al.* (1953). But, there are several constant dissimilarities indicating that these taxa are not conspecific. These include differences in: dorsal fur colour, which is reddish brown (5YR 3-5\3-6) in *C. sclateri*, and reddish black (10R 2\2) or brownish black (5YR 2\2) in *C. duthieae*; hyoid morphology (Section 3.3.4); chromosomal properties (Section 4.3.1); and their apparent preference for quite dissimilar ecotypes (coastal forests *versus* montane grasslands).

Protocones are always present on P^1, which are semi-molariform in all of the 37 specimens examined. Talonids are invariably present and well-developed on the lower cheekteeth, while M3 are molariform but smaller than the other cheekteeth.

Two-way analysis of variance of the sexes from two pooled locality samples (Knysna and Port Elizabeth) from the extremes of this species' range showed that sexual size dimorphism is pronounced, with males being significantly larger than females in 11 of the 15 variables examined (Table 7.3). Geographic variation is less pronounced, the Knysna specimens being slightly larger in most measurements, and significantly larger in GSL, IPG, CPL and MDL.

Discriminant functions analysis revealed, however, that the locality groups were not well differentiated from each other. Although a 100% *a posteriori* classification was achieved, with no overlap of scores between the sexes along CV I, differences among the sexes and locality samples were not significant (MANOVA: $F_{(15,3)} = 5{,}03$; $p = 0, 104$). In scatterplots comparing the first two principal component axes, the

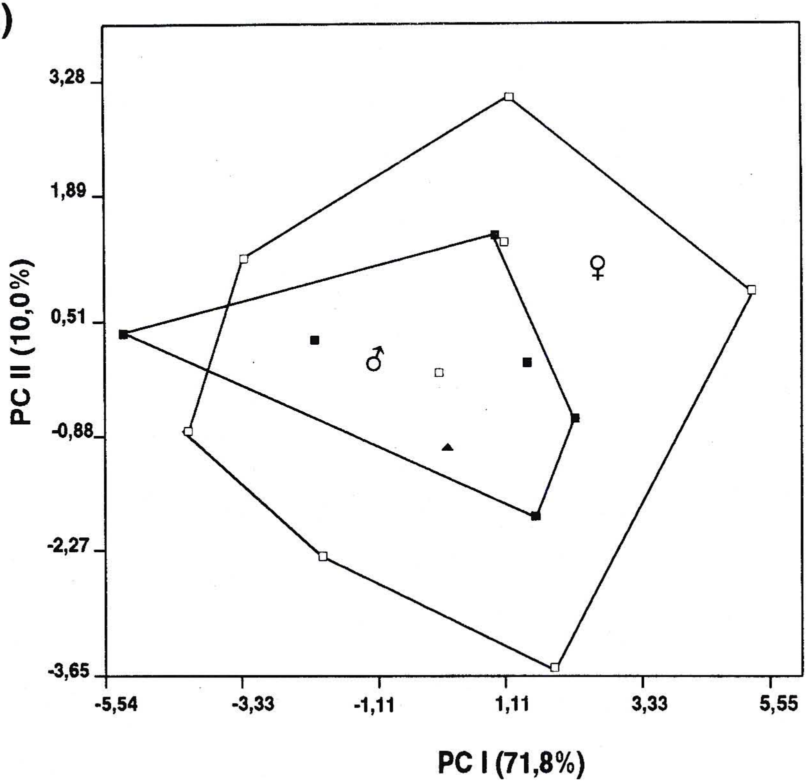
Table 7.2

Summary statistics and results of single-classification analysis of variance to test for sexual dimorphism in adult (TW 2-4) *C. arendsi* from eastern Zimbabwe. $\overline{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size. No significant *F* values were computed.

OTU	STAT	BCW	ARB	MIO	ZMB	IOW	GSL	GSH	P@P	PBM	PAL	MTL	IPG	PPL	BBW	CPL	APW	MDL
♂	$\overline{x}$	4,33	4,90	7,83	16,75	7,46	27,70	12,77	7,85	4,31	14,42	7,14	2,08	8,36	11,79	6,90	4,20	17,00
	sd	0,13	0,20	0,26	0,46	0,25	0,72	0,32	0,21	0,12	0,60	0,35	0,09	0,28	0,50	0,34	0,30	0,59
	Min	4,13	4,69	7,49	16,15	7,16	26,84	12,33	7,64	4,06	13,93	6,52	2,00	7,81	11,12	6,52	3,90	16,41
	Max	4,48	5,17	8,30	17,49	7,93	28,97	13,13	8,24	4,42	15,64	7,60	2,27	8,67	12,68	7,39	4,69	17,85
	n	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7
♀	$\overline{x}$	4,38	4,92	7,84	16,61	7,59	27,31	12,86	7,85	4,33	14,27	7,31	2,17	8,39	11,42	6,91	4,11	17,05
	sd	0,35	0,16	0,25	0,49	0,27	1,16	0,35	0,35	0,37	0,70	0,25	0,09	0,28	0,24	0,37	0,31	0,64
	Min	4,00	4,70	7,43	15,79	7,07	25,28	12,46	7,35	3,63	13,12	6,89	2,03	7,93	11,04	6,22	3,70	16,02
	Max	4,94	5,13	8,25	17,18	8,01	28,60	13,38	8,36	4,63	15,17	7,68	2,30	8,77	11,87	7,33	4,62	17,97
	n	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
SEX	*F*	0,13	0,02	0,01	0,35	0,99	0,59	0,27	0,01	0,01	0,20	1,14	2,80	0,04	3,54	0,01	0,29	0,02

Fig. 7.2. Phenetic relationships among specimens of *C. arendsi* from eastern Zimbabwe, as indicated by: a) pairwise comparison of the first two principal component axes (co-phenetic correlation = 0,782); and b) cluster analysis of correlation coefficients computed from single-standardized data (co-phenetic correlation = 0,594). Open and closed squares represent female and male specimens, respectively. The holotype of *C. arendsi* is indicated by a triangle (▲).

a)


3,28
1,89
0,51
-0,88
-2,27
-3,65
-5,54
-3,33
-1,11
1,11
3,33
5,55
PC II (10,0%)
PC I (71,8%)
♂
♀

b)

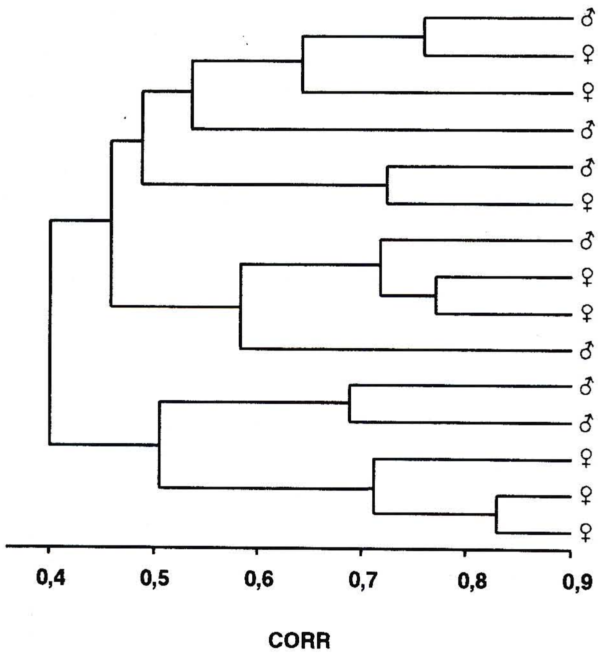

♂
♀
♀
♂
♂
♀
♂
♀
♀
♂
♂
♂
♀
♀
♀
0,4
0,5
0,6
0,7
0,8
0,9
CORR

Table 7.3

Summary statistics and results of two-way analyses of variance to test for sexual dimorphism and geographic variation in adult (TW 2-4) *C. duthieae* specimens representing two populations (Kny = Knysna and PE = Port Elizabeth). $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size; * and # denote significant *F* values at $p \leq 0,05$ and $p \leq 0,01$ respectively. No measurements showed significant interactive *F* values.

OTU	STAT	BCW	ARB	MIO	ZMB	IOW	GSL	GSH	P@P	PAL	IPG	PPL	BBW	CPL	APW	MDL
KNY♀	$\bar{x}$	3,60	4,13	7,00	14,19	6,71	22,97	10,84	6,74	11,84	1,75	7,22	10,13	5,75	3,33	14,21
	sd	0,18	0,10	0,34	0,59	0,51	0,32	0,28	0,54	0,27	0,18	0,13	0,45	0,34	0,09	0,49
	Min	3,40	4,05	6,78	13,69	6,29	22,61	10,59	6,19	11,54	1,61	7,12	9,71	5,47	3,25	13,73
	Max	3,71	4,23	7,39	14,84	7,27	23,23	11,15	7,27	12,07	1,95	7,36	10,61	6,13	3,43	14,70
	n	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
KNY♂	$\bar{x}$	3,74	4,45	7,28	15,08	7,01	24,18	11,42	6,97	12,68	1,87	7,62	10,64	5,93	3,62	14,80
	sd	0,19	0,16	0,27	0,72	0,39	0,47	0,20	0,36	0,56	0,06	0,31	0,39	0,18	0,09	0,40
	Min	3,52	4,23	6,95	14,38	6,59	23,47	11,27	6,60	11,98	1,79	7,31	10,15	5,75	3,52	14,28
	Max	3,96	4,59	7,56	15,79	7,37	24,47	11,71	7,47	13,35	1,91	8,04	10,95	6,15	3,71	15,14
	n	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
PE♀	$\bar{x}$	3,46	4,23	6,83	14,30	6,82	22,75	10,94	6,77	11,85	1,62	7,00	9,97	5,45	3,35	13,82
	sd	0,17	0,16	0,26	0,46	0,22	0,63	0,34	0,11	0,34	0,07	0,27	0,38	0,23	0,23	0,34
	Min	3,25	4,09	6,65	13,80	6,60	22,02	10,69	6,64	11,46	1,52	6,74	9,41	5,24	3,08	13,46
	Max	3,74	4,55	7,40	15,20	7,24	23,19	11,63	6,95	12,47	1,74	7,51	10,59	5,92	3,78	14,46
	n	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7
PE♂	$\bar{x}$	3,61	4,39	7,03	14,85	7,00	23,42	11,24	6,87	12,18	1,65	7,34	10,54	5,77	3,59	14,48
	sd	0,12	0,35	0,23	0,32	0,20	0,46	0,23	0,10	0,42	0,04	0,18	0,44	0,16	0,16	0,35
	Min	3,50	3,95	6,79	14,55	6,72	22,92	10,92	6,76	11,74	1,60	7,18	10,00	5,55	3,35	14,15
	Max	3,78	4,81	7,26	15,28	7,20	23,85	11,49	6,97	12,67	1,68	7,59	11,02	5,92	3,70	14,96
	n	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
OTU	*F*	4,15	0,07	3,63	0,63	0,01	6,96*	0,79	0,24	3,18	19,29#	8,384*	1,65	6,63*	0,45	7,16*
SEX	*F*	4,33	4,87*	4,30	7,92*	1,90	15,61#	9,48#	1,40	9,12*	5,67*	14,03*	8,88*	8,09*	9,22*	15,43#

sexes separated along PC I (Fig. 7.3a), but the Knysna and Port Elizabeth samples of like sex overlapped broadly along both axes. PC I was an overall size vector (as indicated by high, positive loadings for all variables) that accounted for over 70% of the sample variance, indicating that craniometric variation in *C. duthieae* is dominated by sexual differences in overall size. However, these size differences are not absolute, since in phenograms based on average taxonomic distance coefficients (Fig. 7.3b) the specimens grouped into two main clusters, but each contained individuals of either sex or locality. A similar result was indicated in phenograms based on correlation coefficients (Fig. 7.3c), where some influence of both sex and locality on clustering was evident, but specimens of both populations were included in each subcluster. Intrapopulational differences in cranial size and shape are thus negligible, and interpopulational variation is not sufficiently marked to distinguish any geographic groups in *C. duthieae*.

7.3.3. ***Chlorotalpa sclateri***

Of 36 specimens examined, all lack protocones on P^1, and have semi-molariform P_1 and small, molariform M3. Only one specimen (NMB6866, *C.s. guillarmodi* from Ficksburg) lacks well-developed molar talonids.

The only population sample sufficiently large for statistical analysis of intra-population variation was from Ficksburg (Free State), and represented the subspecies *C. s. guillarmodi*. Single classification analysis of variance indicated that males were significantly larger in six of the 17 variables considered (Table 7.4). Sexual size dimorphism is, therefore, also quite pronounced in this species, but apparently not to the extent displayed by *C. duthieae*.

To maximize sample sizes for analyses of geographic variation, PBM and the six variables that differed significantly between the sexes were excluded, so that data for males and females of each subspecies could be pooled. Single classification analysis of variance showed that the four subspecies differed significantly in only three measurements (Table 7.5). Overall size was largest in the *C. s. shortridgei* OTU, which was distinguished by a significantly greater rostral breadth (ARB) than the other samples. The *C. s. guillarmodi* OTU was characterized by a significantly shorter palate (PAL) than the other taxa, and the *C. s. sclateri* sample by a significantly wider

Fig. 7.3. Phenetic relationships among specimens of *C. duthieae*, based on analyses of single-standardized data: a) pairwise comparison of the first two principal component axes (co-phenetic correlation = 0,991); b) phenogram based on average taxonomic distance (ATD) coefficients (co-phenetic correlation = 0,731); c) phenogram based on correlation coefficients (co-phenetic correlation = 0,634). Open (females) and solid (males) symbols, and acronyms indicate: (△) - Knysna and George (KNY); (○) - Port Elizabeth (PE).

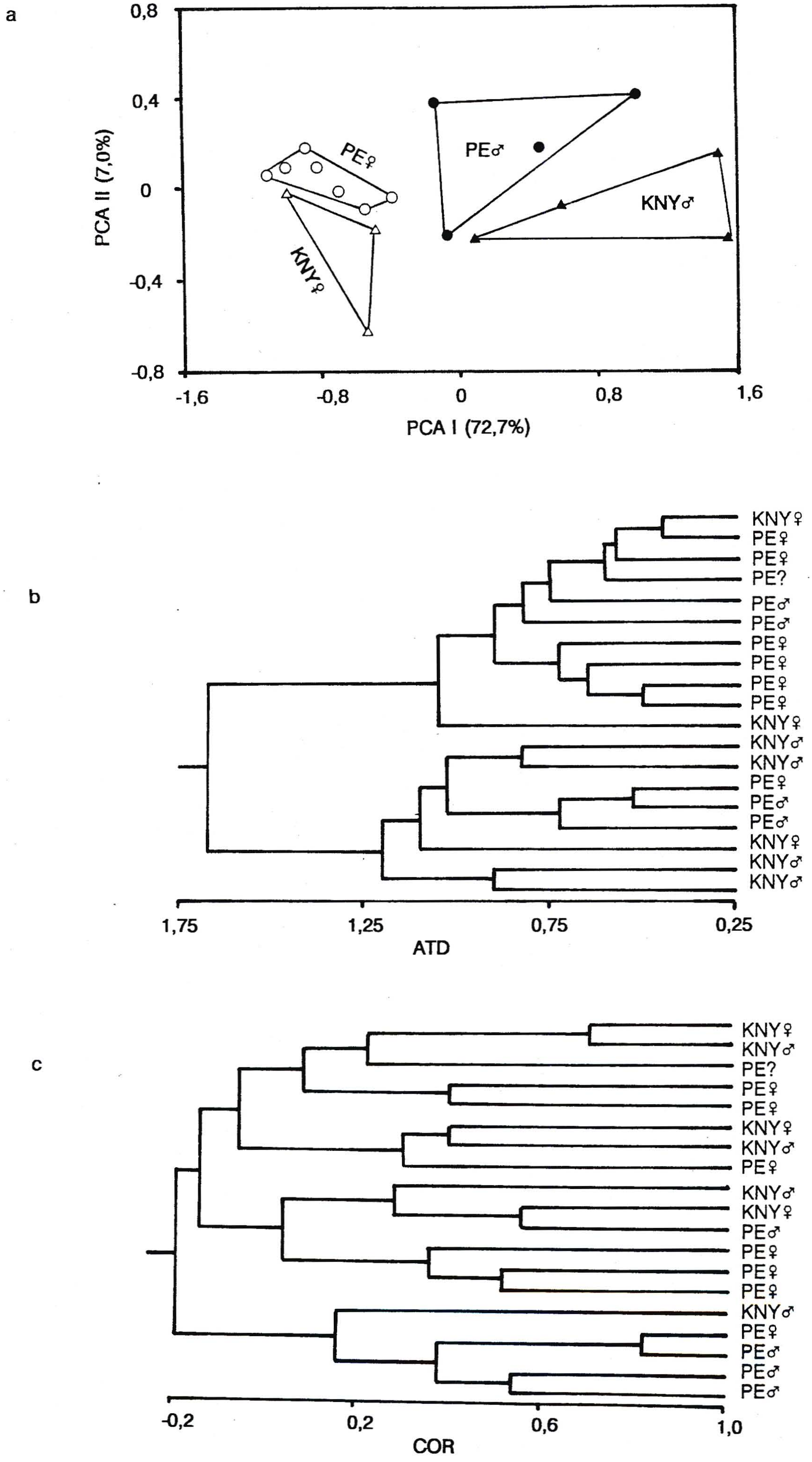

a
0,8
0,4
0
-0,4
-0,8
PCA II (7,0%)
-1,6
-0,8
0
0,8
1,6
PCA I (72,7%)
PE♀
KNY♀
PE♂
KNY♂
b
KNY♀
PE♀
PE♀
PE?
PE♂
PE♂
PE♀
PE♀
PE♀
PE♀
KNY♀
KNY♂
KNY♂
PE♀
PE♂
PE♂
KNY♀
KNY♂
KNY♂
1,75
1,25
0,75
0,25
ATD
c
KNY♀
KNY♂
PE?
PE♀
PE♀
KNY♀
KNY♂
PE♀
KNY♂
KNY♀
PE♂
PE♀
PE♀
PE♀
KNY♂
PE♀
PE♂
PE♂
PE♂
-0,2
0,2
0,6
1,0
COR

Table 7.4

Summary statistics and results of single-classification analysis of variance to test for sexual dimorphism in adult (TW 2-4) *C. s. guillarmodi* from Ficksburg, Free State. $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size; * - $p \leq 0,05$; $^\#$ - $p \leq 0,001$.

OTU	STAT	BCW	ARB	MIO	ZMB	IOW	GSL	GSH	P@P	PBM	PAL	MTL	IPG	PPL	BBW	CPL	APW	MDL
♂	$\bar{x}$	3,90	4,36	7,27	15,11	6,90	22,96	11,22	6,88	4,01	11,76	6,22	1,78	7,36	10,11	5,82	3,58	14,14
	sd	0,18	0,22	0,23	0,36	0,23	0,53	0,23	0,17	0,12	0,46	0,24	0,14	0,11	0,22	0,15	0,13	0,31
	Min	3,57	3,97	6,91	14,53	6,67	21,81	10,83	6,55	3,70	10,58	5,76	1,40	7,23	9,77	5,49	3,41	13,69
	Max	4,19	4,69	7,66	15,55	7,45	23,60	11,54	7,11	4,11	12,15	6,58	1,95	7,55	10,55	6,08	3,86	14,71
	n	10	10	10	10	11	10	10	11	10	11	10	11	10	8	11	11	11
♀	$\bar{x}$	3,58	4,23	7,07	14,49	6,79	22,02	10,92	6,73	3,96	11,38	5,90	1,79	7,20	9,79	5,53	3,22	13,53
	sd	0,16	0,11	0,12	0,39	0,33	0,86	0,43	0,19	0,17	0,56	0,27	0,06	0,36	0,27	0,25	0,14	0,36
	Min	3,46	4,15	6,95	14,14	6,33	21,12	10,39	6,56	3,78	10,79	5,59	1,71	6,75	9,52	5,30	3,10	13,20
	Max	3,76	4,30	7,23	14,86	7,12	23,04	11,29	6,95	4,16	11,86	6,21	1,86	7,62	10,03	5,78	3,41	13,93
	n	3	2	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
SEX	*F*	7,44*	0,69	2,95	8,27*	0,53	6,42*	2,93	2,23	0,44	1,79	4,47	0,02	1,78	4,80	8,01*	22,00$^\#$	10,72*

Table 7.5

Summary statistics of 10 cranial measurements in four geographic groups of *Chlorotalpa sclateri*, and results of single classification ANOVAs of OTU means. Taxa are: CSS - *C. s. sclateri*; CSH - *C. s. shortridgei*; CSG - *C. s. guillarmodi*; CSM - *C. s. montana*. $\bar{x}$ = sample mean; *sd* = standard deviation; *n* = sample size. Vertical lines denote maximally non-significant subsets from SNK multiple comparisons tests.

ARB (*F* = 4,23; *p* = 0,019)

OTU	$\bar{x}\pm sd(n)$	Range
CSM	4,15±0,23(2)	3,99-4,31
CSG	4,29±0,28(12)	3,81-4,69
CSS	4,51±0,19(4)	4,28-4,74
CSH	4,68±0,10(5)	4,56-4,78

MIO (*F* = 0,85; *p* = 0,512)

OTU	$\bar{x}\pm sd\ (n)$	Range
CSM	7,01±0,08(2)	6,95-7,06
CSG	7,18±0,24(12)	6,71-7,66
CSS	7,20±0,31(4)	6,90-7,57
CSH	7,34±0,33(5)	6,91-7,78

IOW (*F* = 2,11; *p* = 0,132)

OTU	$\bar{x}\pm sd\ (n)$	Range
CSM	6,43±0,23(2)	6,27-6,59
CSG	6,85±0,29(12)	6,26-7,45
CSS	6,88±0,14(4)	6,68-7,01
CSH	6,97±0,25(5)	6,71-7,30

GSH (*F* = 2,16; *p* = 0,126)

OTU	$\bar{x}\pm sd(n)$	Range
CSG	11,06±0,40(12)	10,36-11,54
CSS	11,17±0,26(4)	10,96-11,51
CSH	11,46±0,28(5)	11,00-11,70
CSM	11,52±0,06(2)	11,48-11,56

P@P (*F* = 2,58; *p* = 0,083)

OTU	$\bar{x}\pm sd\ (n)$	Range
CSM	6,41±0,30(2)	6,20-6,62
CSG	6,75±0,27(12)	6,21-7,05
CSS	6,78±0,20(4)	6,48-6,89
CSH	7,05±0,39(5)	6,68-7,61

PAL (*F* = 4,45; *p* = 0,016)

OTU	$\bar{x}\pm sd\ (n)$	Range
CSG	11,51±0,66(12)	10,52-12,15
CSS	12,24±0,32(4)	11,90-12,59
CSH	12,33±0,42(5)	11,61-12,62
CSM	12,59±0,40(2)	12,30-12,87

IPG (*F* = 3,42; *p* = 0,038)

OTU	$\bar{x}\pm sd(n)$	Range
CSS	1,54±0,12(4)	1,39-1,68
CSM	1,69±0,10(2)	1,62-1,76
CSH	1,72±0,09(5)	1,59-1,80
CSG	1,76±0,13(12)	1,45-1,95

PPL (*F* = 1,47; *p* = 0,254)

OTU	$\bar{x}\pm sd\ (n)$	Range
CSS	6,97±0,14(4)	6,83-7,16
CSM	7,22±0,15(2)	7,11-7,32
CSG	7,24±0,24(12)	6,75-7,62
CSH	7,29±0,34(5)	6,95-7,79

BBW (*F* = 2,81; *p* = 0,067)

OTU	$\bar{x}\pm sd\ (n)$	Range
CSG	10,00±0,28(12)	9,52-10,55
CSM	10,07±0,06(2)	10,02-10,11
CSS	10,26±0,26(4)	10,00-10,52
CSH	10,43±0,38(5)	9,88-10,83

FML (*F* = 3,05; *p* = 0,053)

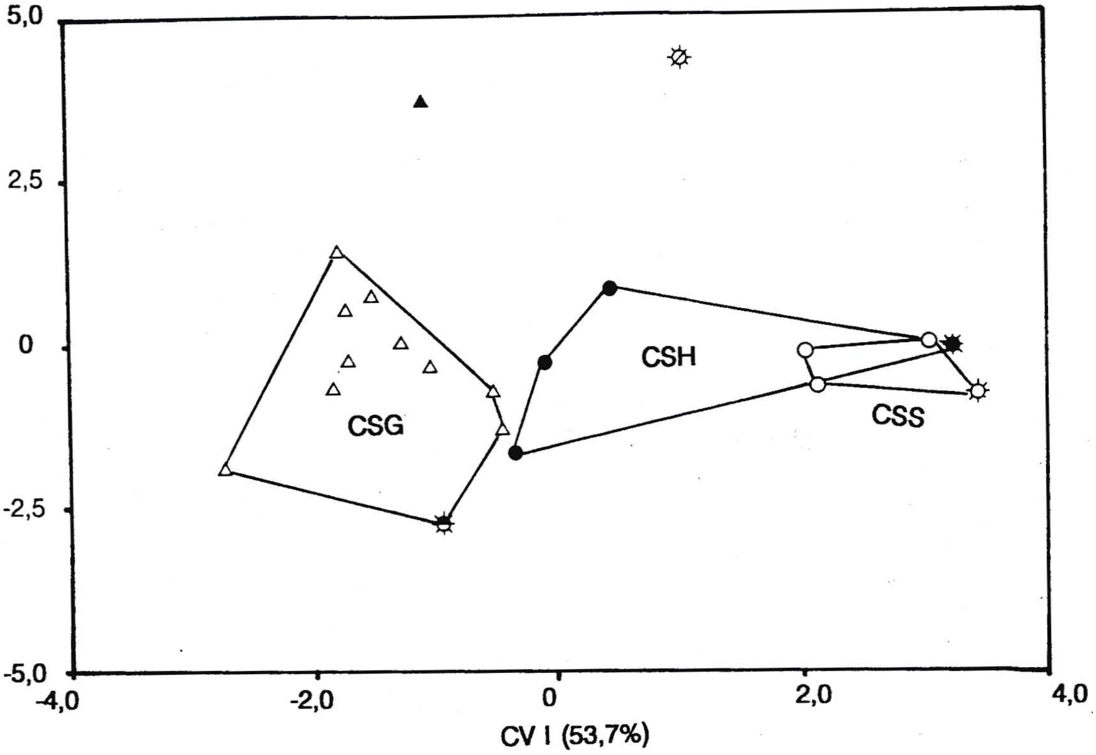
OTU	$\bar{x}\pm sd(n)$	Range
CSG	4,08±0,15(12)	3,83-4,29
CSS	4,17±0,12(4)	4,03-4,33
CSH	4,26±0,11(5)	4,10-4,37
CSM	4,36±0,29(2)	4,15-4,57

posterior palate (IPG). The *C. s. montana* OTU was smallest in most length measurements, but largest in greatest skull height (GSH), foramen magnum diameter (FML) and palatal length (PAL).

Multigroup discriminant functions analysis revealed that differences between the four geographic OTUs were significant ($F_{(30,30)} = 1{,}92$; $p = 0{,}04$) when all measurements are considered simultaneously, and resulted in a 96% correct *a posteriori* classification. The only misidentification involved one specimen of *C. s. shortridgei* which was incorrectly assigned to *C. s. sclateri*. In scatterplots comparing the first three canonical variate axes (Fig. 7.4), *C. s. guillarmodi* tended to plot apart from *C. s. shortridgei* and *C. s. sclateri* along CV I, while the latter two subspecies separated from each other apart along CV III. The two available specimens of *C. s. montana* plotted well above the other subspecies along CV II, and far apart from each other along CV I. CV I was influenced most strongly by interpterygoid width (IPG; Table 7.6), which decreased from left to right, and anterior rostral width (ARB), which showed the opposite trend. The separation of the *C. s guillarmodi* OTU along CV II thus reflected the tendency for specimens from the eastern Free State and adjoining Lesotho to have relatively broader posterior palates, but narrower rostra, than those from other areas. CV II was also influenced strongly by cranial widths (ARB, IOW, IPG), which decreased from bottom to top. The separation of the *C. s. montana* specimens from the others along this axis thus reflected a tendency for skulls to be narrower in the northern part this species' range. CV III was strongly influenced by IOW, P@P, and FML, which tended to increase from bottom to top. Separation of the OTUs along this axis thus indicated a trend for specimens of *C. s. shortridgei* to have broader skulls, and for foramen magnum diameter to be greater in samples from the northern and southern extremes of this species range than in intermediate areas.
IPG also loaded relatively high along CV III, and since this was the only variable that differed significantly between *C. s. shortridgei* and *C. s. sclateri*, separation of these OTUs along CV III reflected a tendency for the posterior palate to be relatively narrower in *C. s. sclateri*.

In phenograms based on average taxonomic distance coefficients, no clear separation of specimens according to subspecies was evident (Fig. 7.5a), indicating that size differences between these taxa are negligible. But, cluster analysis of correlation

Fig. 7.4. Pairwise comparisons of the first three canonical variate axes from a four-group discriminant functions analysis of *C. sclateri* individuals. Symbols and acronyms are: (●) - *C. s. shortridgei* (CSH); (△) - *C. s. guillarmodi* (CSG); (○) - *C. s. sclateri* (CSS); (▲) - *C. s. montana*; (☼) - holotype of *C. s. sclateri*; (✹) - holotype of *C. s. guillarmodi*; (⊘) - holotype of *C. s. montana*; (✸) - holotype of *C. s. shortridgei*.


5,0
2,5
0
-2,5
-5,0
-4,0
-2,0
0
2,0
4,0
CV II (31,6%)
CV I (53,7%)
CSG
CSH
CSS

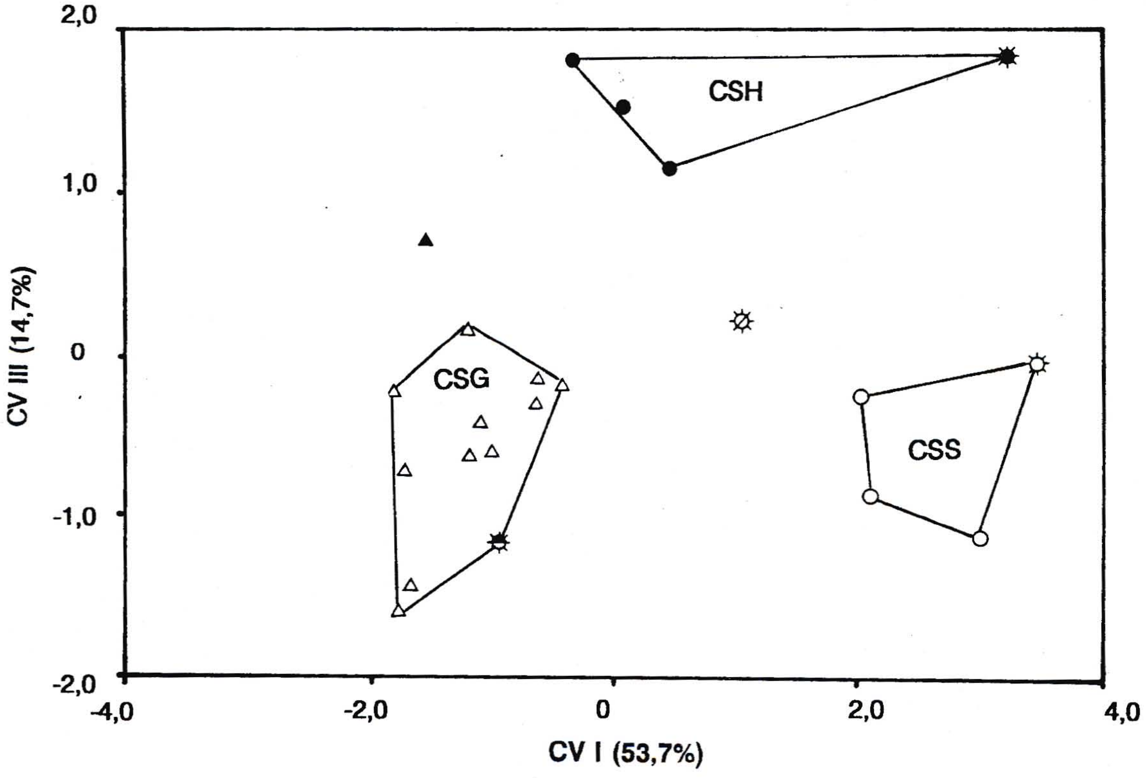
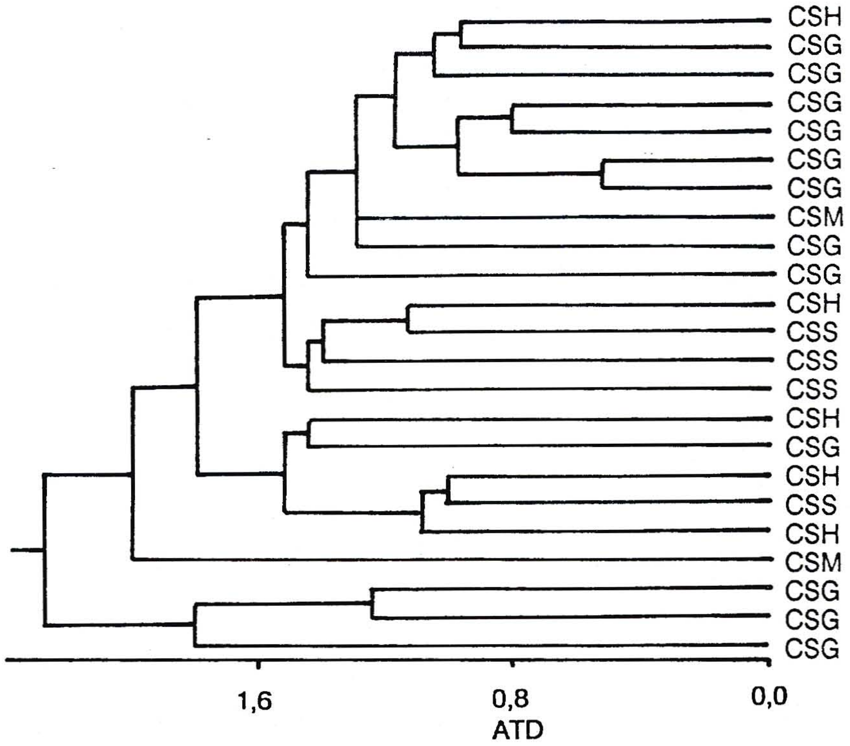

2,0
1,0
0
-1,0
-2,0
-4,0
-2,0
0
2,0
4,0
CV III (14,7%)
CV I (53,7%)
CSH
CSG
CSS

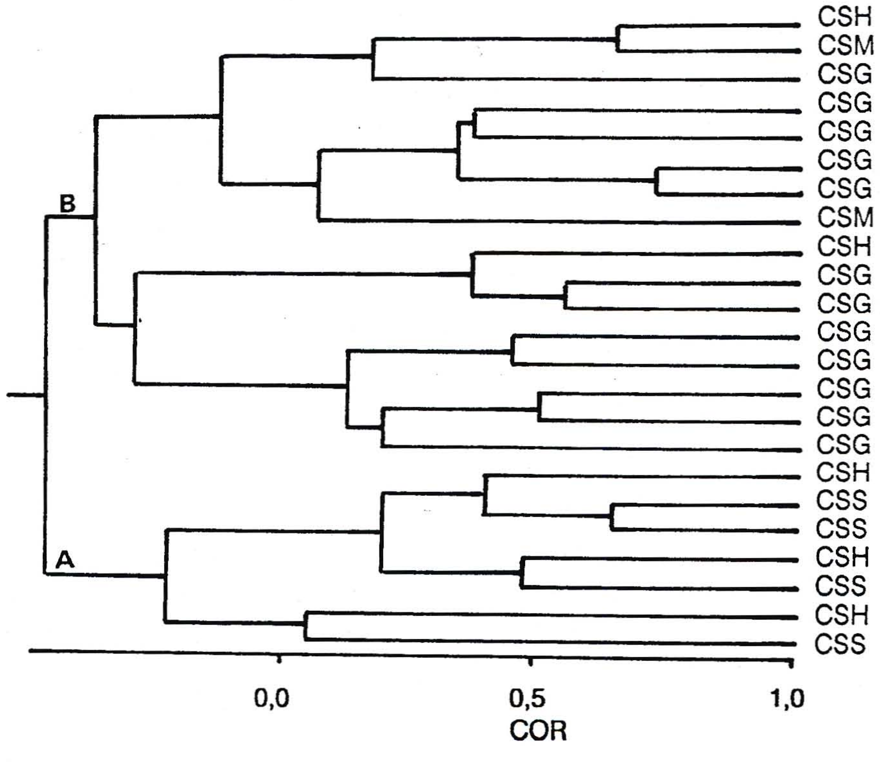
Table 7.6

Factor matrix from a four-group discrminant functions analysis of 10 cranial measurements in *Chlorotalpa sclateri* from South Africa. Boldfaced values indicate strong variable participation in the respective axes.

Variable	CV I	CV II	CV III
ARB	**2,920**	**-3,620**	2,644
MIO	-1,642	2,383	2,100
IOW	1,942	**-3,961**	**-6,073**
GSH	-1,000	2,201	2,170
P@P	-0,439	-0,354	**5,933**
PAL	1,738	0,866	-1,926
IPG	**-7,412**	**3,462**	2,689
PPL	-2,316	-2,066	-0,942
BBW	1,242	-0,593	-2,287
FML	-0,132	**3,117**	**6,269**

Fig. 7.5. Phenetic relationships among specimens of *C. sclateri*, based on cluster analyses (UPGMA) of average taxonomic distance (ATD; co-phenetic correlation = 0,789)) and correlation (COR; co-phenetic correlation = 0,690) coefficients computed from single-standardized data. See Table 7.1 for explanation of acronyms.


CSH
CSG
CSG
CSG
CSG
CSG
CSG
CSM
CSG
CSG
CSH
CSS
CSS
CSS
CSH
CSG
CSH
CSS
CSH
CSM
CSG
CSG
CSG
1,6
0,8
0,0
ATD


CSH
CSM
CSG
CSG
CSG
CSG
CSG
CSM
CSH
CSG
CSG
CSG
CSG
CSG
CSG
CSG
CSH
CSS
CSS
CSH
CSS
CSH
CSS
B
A
0,0
0,5
1,0
COR

coefficients separated the specimens into two main groups (Fig. 7.5b): Cluster A, containing most of the *C. s. shortridgei* and *C. s. sclateri* specimens; and Cluster B, containing all *C. s. guillarmodi*, and the two *C. s. montana* specimens which, however, fell in different subclusters. Subtle differences in cranial shape are thus sufficiently marked to distinguish *C. s. montana* and *C. s. guillarmodi* in the north of the species' range, from *C. s. sclateri* and *C. s. shortridgei* in the south, but do not differentiate between the taxa within either of these two groups.

7.4 TAXONOMIC CONCLUSIONS

The extent of sexual size dimorphism appears to be quite variable among the three species examined, being negligible in *C. arendsi* and most pronounced in *C. duthieae*. However, more specimens need to be analysed to confirm that this variability is a real phenomenon rather than an artefact of small sample sizes.

Dental variability is negligible in all three species. The only species with intraspecific dental variability exceeding 5% was *C. arendsi*, and this variability was restricted to the absence of talonids, traces of which were however present in three specimens.

Although the mesostyle of P^1 tends to be more robust, and P_1 appears somewhat wider than in *C. duthieae* and *C. sclateri*, the differences in P1 morphology between these species appear to be negligible. Lundholm (1955) apparently failed to take toothwear into account when claiming that P_1 is sectorial in *C. duthieae* and *C. sclateri*. This conclusion is supported by the fact that his diagram outlining this difference is based on the type specimen of *C. sclateri guillarmodi* (TM7312), which shows heavy occlusal attrition (= TW4).

Geographic variation in *C. duthieae* is less pronounced than sexual dimorphism, and seems to involve mainly size variation, with specimens of the same sex tending to be larger in the Knysna population than in the Port Elizabeth sample further to the east. Whether or not this is the result of a longitudinal cline in size cannot be established from the limited data available, but since these populations exist in coastal habitats at similar elevations, an altitudinal cline in size - as demonstrated for *A. hottentotus* (Section 5.3.2.2) - seems unlikely. Given the only slight geographic differences in cranial shape, the limited range of this species, and the geographic continuity of coastal forest between Knysna and Port Elizabeth, taxonomic distinction between these populations does not seem warranted.

Geographic variation in *C. sclateri* appears to involve mainly subtle differences in cranial shape, and is sufficiently marked to warrant the recognition of four geographic groups. *C. s. montana* and *C. s. guillarmodi* are quite similar in cranial shape, but differ in dorsal fur colour (Roberts 1951). This colour difference involves mainly the extent of a bright reddish-brown (5YR 5\6) tinge on the flanks, which is pronounced in all but the two specimens of *C. s. montana* from Wakkerstroom. Conversely, *C. s. sclateri* and *C. s. shortridgei* are quite similar in colour and size, but differ subtly in cranial shape. Given the small samples available for analysis, the apparent geographical discontinuity between these taxa, and the isolation of their preferred montane vlei habitats by expanses of seemingly inhospitable terrain, their current subspecific separation seems warranted. However, more sampling is needed to ascertain the range limits of each - particularly of *C. s. sclateri* and *C. s. shortridgei*, which are known from localities only ≈160 km apart. Meester *et al.* (1986) claimed that *C. s. sclateri* ranges as far north as Herschel and Lesotho, but this seems unlikely owing to the intermediate existence of arid Karoo. Four specimens from the vicinity of Herschel and Lady Grey (KM24974-6, NMB4358), and identified as *C. sclateri* on the basis of M3 presence, were excluded from this analysis since in size and other dental characters (P^1_1 morphology = sectorial) they approximate *Amblysomus hottentotus,* a species also recorded from this area. Whether these specimens represent a markedly larger subspecies of *C. sclateri*, or *A. hottentotus* that are dentally atypical, warrants further attention.

CHAPTER 8

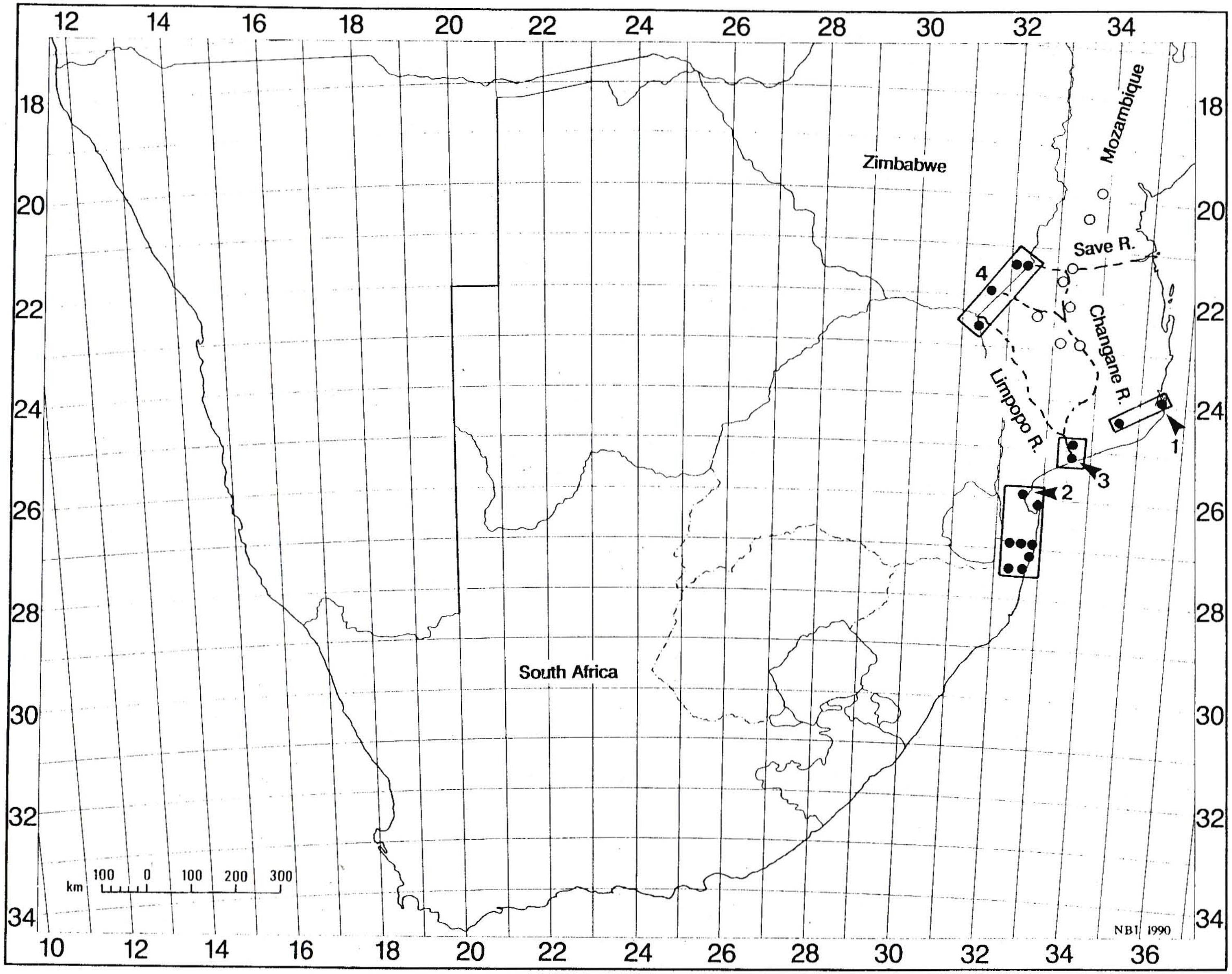
CRANIOMETRIC AND DENTAL VARIATION IN THE GOLDEN MOLE GENUS *Calcochloris*

8.1 INTRODUCTION

Broom (1907a) treated this taxon as a subgenus (*Chrysotricha*) within *Chrysochloris*, whereas Roberts (1951) afforded *Chrysotricha* full generic rank. Ellerman *et al.* (1953) pointed out, however, that the name *Calcochloris* Mivart, 1867 has precedence, and synonymized both with *Amblysomus*, a treatment followed by Simonetta (1968) and Petter (1981). Conversely, Meester (1974) argued that recognition of *Calcochloris* as a distinct genus was justified by its striking fur colour (grizzled-orange colour, wood brown terminally and basally pale whitish with a yellow tinge, *cf.* grey in all other taxa), broader skull and more molariform P1. Known only from coastal Mozambique, northern KwaZulu-Natal and south-eastern Zimbabwe (Fig. 8.1), with a marginal intrusion into the north-eastern Kruger National Park of the Northern Province, these moles appear to favour bushveld habitats supported by loose, sandy soils (Smithers and Lobao-Tello 1976).

Although previous authors disagreed about the generic status of this taxon, they concurred in recognizing only a single species *C. obtusirostris*, comprising three subspecies (Fig. 8.1): *C. o. obtusirostris* from northern coastal Mozambique; *C. o. chrysillus* from southern coastal Mozambique and northern KwaZulu-Natal; and *C. o. limpopoensis* from northern Gaza and Inhambane in Mozambique, ranging to the lowlands of Zimbabwe and the Northern Province of South Africa via the Limpopo and Changane River systems. These taxa are supposedly similar in cranial and dental characters, but differ in size and fur colour. *C. o. obtusirostris* and *C. o. limpopoensis* are similar in size, but differ subtly in the colour of the muzzle region (Roberts 1951). *C. o. chrysillus* is consistently smaller with paler fur, and was regarded as a distinct species by Thomas and Schwann (1905b). But, after examining only four specimens, Broom (1907a) argued that the extent of colour and size variation manifest in this taxon is similar to that shown by other golden mole species, and thus that only subspecific separation was warranted. Subsequent authors followed Broom (1907a), and apparently

Fig. 8.1. The distribution of *Calcochloris obtusirostris* in southern Africa. Numbers refer to OTU codes, as specified in Table 8.1., while broken lines mark rivercourses. Arrows indicate type localities. Open circles denote localities not included in analyses (owing to small sample sizes), or literature records.


Zimbabwe
Mozambique
Save R.
Changane R.
Limpopo R.
South Africa
1
2
3
4
km 100 0 100 200 300
NBI 1990
12 14 16 18 20 22 24 26 28 30 32 34
10 12 14 16 18 20 22 24 26 28 30 32 34 36
18 20 22 24 26 28 30 32 34

made no further attempt to examine patterns of variation in greater detail, probably because of the few specimens available for study. Current taxonomy is, therefore, based on a relatively poor knowledge of phenotypic diversity in this genus.

Small sample sizes notwithstanding, this chapter examines craniometric and dental variation in *C. obtusirostris* to establish if geographic differentiation is sufficiently marked to warrant the taxonomic separation of any known populations.

8.2 MATERIALS AND METHODS

Fifty-eight specimens from various museums (Chapter 2) were examined and measured. Owing to small sample sizes, analyses of non-geographic variation were restricted to statistical comparisons of the sexes (TW2-4 specimens combined) in single or pooled locality samples (Table 8.1) using single or two-way analyses of variance. Patterns of geographic variation were examined by ordination techniques and cluster analyses (UPGMA) of correlation and average taxonomic distance coefficients computed from single-standardized data for the sexes separately, or from pooled sexual samples following independent standardization to correct for sexual size dimorphism. Where necessary, certain measurements (particularly EAM, PBM, IPG and FML) were omitted from analyses to maximize sample sizes.

8.3 RESULTS AND DISCUSSION

8.3.1 Dental variability

All specimens examined have completely molariform first premolars and lack M3, while the canine is distinctly bicuspid with a well-developed mesostyle basin, and resembles the semi-molariform P1 of *Chlorotalpa* and some *Amblysomus*. The presence of protocones on P^1 is, however, more variable, with 36,2% of the specimens showing distinct protocones (Table 8.2), although this may vary between jaw halves. The highest incidence of protocones is found in *C. o. limpopoensis*, whereas the lowest incidence is found in *C. o. obtusirostris*. Similarly, the presence/absence of talonids in quite variable, with 8,7% of the specimens examined showing traces of molar talonids, the incidence of talonids being lowest in *C. o. obtusirostris*.

Table 8.1

Localities pooled as Operational Taxonomic Units (= OTUs) for the analysis of intraspecific variation in *C. obtusirostris*. The first column gives OTU numbers referred to in Fig. 8.1; the second gives names by which OTUs are referred to in other Figures and the text.

OTU No.	**OTU NAME**	**POOLED LOCALITIES**
1	COO	Mozambique: Inhambane; Coguno.
2	COC	Mozambique: Maputo City and Suburbs; Inhaca Island; R.S.A., KwaZulu-Natal: Ndumu Game Reserve; Lake Sibaya; Lalanek Inspection Quarters, Amanzengwenya; Kosi Lake.
3	COL	Mozambique: Maciene.
4	COZ	R.S.A., Northern Province: Nyadu Sandveld, north-eastern Kruger National Park. Zimbabwe: Malugwe Pan; Zinave; Lake Mahembe; Nyaboa; Fisham; Confluence of Save and Lundi Rivers.

Table 8.2

Dental variation among four pooled population samples of *C. obtusirostris*. Values in each column indicate the number of individuals showing each trait; values in parenthesis indicated the incidence of each trait, expressed as a percentage of specimens in each sample. Symbols used are: COO - *C. o. obtusirostris*; COC - *C. o. chrysillus*; COL - *C. o. limpopoensis*; COZ - southeastern Zimbabwe population; *n* - sample size; P1 - first (upper and lower) premolars.

OTU	*n*	**P1 with protocones**	**Lower molars with talonids**	**P1 molariform**
COO	4	0	0	4(100%)
COC	31	13(41,9%)	3(9,7%)	31(100%)
COL	8	4(50%)	1(12,5%)	8(100%)
COZ	15	4(26,7%)	1(6,7%)	15(100%)
Total	58	21(36,2%)	5(8,7%)	58(100%)

8.3.2 Craniometric variability

Only two pooled locality samples (COC = *C. o. chrysillus*; COZ = southeastern Zimbabwe) were sufficiently large for the analysis of sexual dimorphism. Two-way analysis of variance (Table 8.3) revealed that males were significantly larger than females in seven measurements (ARB, GSH, P@P, MTL, CPL, APW, MDL), and thus that sexual size dimorphism is pronounced in this species.

Geographic variation between the two populations is even more pronounced, with the southeastern Zimbabwe sample being significantly smaller than *C. o. chrysillus* in 11 measurements. This was confirmed by univariate analyses of variance of the four pooled population samples, regardless of sex, which showed that all measurements varied significantly on a geographic basis (Table 8.4). The southeastern Zimbabwe sample (COZ) was significantly smaller than others in palatal length (PAL), maxillary toothrow length (MTL) and coronoid process width (APW), whereas the *C. o. limpopoensis* OTU was significantly larger in five measurements summarizing skull/mandible length (GSL, PAL, PPL, APW and MDL) and three variables reflecting cranial width (IOW, IPG and BBW).

A four-group discriminant functions analysis based on nine measurements (sexually dimorphic variables eliminated to allow the pooling of male and female data, PBM and EAM deleted to increase sample sizes) resulted in a 92% overall classification of specimens to their correct *a priori* groups, indicating that the samples were well differentiated from each other. The only misidentifications involved specimens of the *C. o. obtusirostris* and *C. o. chrysillus* OTUs. In a scatterplot comparing the first two canonical variate axes (Fig. 8.2a), these two samples grouped together, indicating that they were similar in size and shape, and plotted apart from the southeastern Zimbabwe (COZ) specimens along CV II. The *C. o. limpopoensis* specimens plotted well to the right of others along CV I. Differences between the group centroids of the population samples were highly significant (MANOVA: $F_{(27,79)}$ = 6,72; $P < 0{,}001$).

Examination of factor loadings (Table 8.5) showed that CV I was influenced most strongly by zygomatic breadth (ZMB), rostral breadth (IOW) and post-palatal length (PPL). Separation along this axis thus reflected the tendency for *C. o. limpopoensis* to be larger, with significantly wider skulls and post-palatal lengths. CV II was strongly influenced by palatal and post-palatal length (PAL, PPL).

Table 8.3

Summary statistics and results of two-way analyses of variance to test for sexual dimorphism and geographic variation in adult (TW 2-4) *C. o. chrysillus* (COC) and *Calcochloris* from southeastern Zimbabwe (COZ). $\bar{x}$ = arithmetic mean; *sd* = standard deviation; *n* = sample size; * and $^{\#}$ denote significant *F* values at $p \leq 0{,}05$ and $p \leq 0{,}01$ respectively.

OTU	STAT	BCW	ARB	MIO	ZMB	IOW	GSL	GSH	P@P	PBM	PAL	MTL	IPG	PPL	BBW	CPL	APW	MDL
COC♀	$\bar{x}$	2,92	5,01	7,16	15,52	6,87	22,01	10,73	7,93	4,06	11,66	5,91	1,86	7,02	10,27	5,89	3,35	14,24
	sd	0,14	0,16	0,29	0,66	0,21	0,73	0,29	0,30	0,15	0,45	0,16	0,09	0,25	0,16	0,24	0,17	0,44
	Min	2,66	4,81	6,64	14,78	6,51	21,03	10,26	7,35	3,83	11,01	5,57	1,75	6,75	9,69	5,68	3,17	13,63
	Max	3,18	5,29	7,62	16,76	7,26	23,60	11,34	8,43	4,29	12,64	6,16	2,05	7,55	11,12	6,53	3,80	15,04
	n	11	11	11	11	11	11	11	11	9	11	10	11	11	9	11	11	11
COC♂	$\bar{x}$	3,06	5,13	7,10	15,82	6,90	22,32	10,95	8,15	4,12	11,75	6,08	1,91	7,11	10,34	6,01	3,36	14,39
	sd	0,12	0,21	0,24	0,40	0,20	0,76	0,22	0,17	0,10	0,44	0,13	0,06	0,21	0,26	0,26	0,15	0,46
	Min	2,88	4,77	6,83	15,37	6,69	21,20	10,58	7,89	3,97	11,03	5,91	1,80	6,82	9,91	5,71	3,18	13,80
	Max	3,23	5,43	7,65	16,62	7,35	23,38	11,25	8,35	4,27	12,36	6,29	2,01	7,36	10,64	6,39	3,59	15,01
	n	9	9	9	9	9	8	8	9	8	8	9	9	7	9	9	9	9
COZ♀	$\bar{x}$	2,93	4,78	7,10	15,30	6,70	20,77	10,33	7,26	4,07	10,59	5,37	1,75	6,82	10,03	5,38	2,90	13,02
	sd	0,26	0,21	0,27	0,80	0,49	0,91	0,45	0,39	0,13	0,43	0,26	0,14	0,26	0,48	0,33	0,14	0,63
	Min	2,51	4,52	6,62	13,88	5,88	18,98	9,61	6,62	3,91	9,68	4,81	1,53	6,46	9,36	4,75	2,70	11,84
	Max	3,19	5,16	7,44	16,12	7,27	21,60	10,90	7,74	4,27	11,07	5,65	1,98	7,18	10,54	5,74	3,09	13,63
	n	7	8	7	8	8	7	8	8	7	8	8	8	8	7	8	8	8
COZ♂	$\bar{x}$	2,95	4,92	7,19	15,97	6,86	21,34	10,68	7,81	4,10	10,70	5,44	1,81	6,92	10,45	5,83	3,42	13,67
	sd	0,14	0,24	0,41	0,17	0,14	0,50	0,27	0,19	0,15	0,55	0,35	0,08	0,20	0,42	0,33	0,30	0,46
	Min	2,78	4,71	6,80	15,83	6,66	20,76	10,46	7,68	3,95	10,08	5,11	1,68	6,74	10,16	5,46	3,11	13,05
	Max	3,10	5,26	7,70	16,20	6,98	21,65	11,04	8,03	4,24	11,13	5,80	1,85	7,17	11,07	6,17	3,84	14,14
	n	4	4	4	4	4	3	4	3	3	3	3	4	4	4	4	4	4
OTU	*F*	0,48	10,85$^{\#}$	0,02	0,36	1,49	15,76$^{\#}$	10,21$^{\#}$	32,11$^{\#}$	0,06	39,92$^{\#}$	59,34$^{\#}$	9,98$^{\#}$	5,36*	0,71	16,34$^{\#}$	18,83$^{\#}$	34,03$^{\#}$
SEX	*F*	2,50	4,53*	0,05	4,13	0,67	3,18	6,42*	15,04$^{\#}$	0,98	2,21	10,69$^{\#}$	3,34	1,23	2,24	7,59$^{\#}$	11,80$^{\#}$	6,05*
INT	*F*	0,85	0,18	0,56	0,71	0,41	0,40	0,36	3,20	0,13	0,89	2,81	0,16	0,03	1,35	2,73	14,96$^{\#}$	2,22

Table 8.4

Summary statistics of one external (BCW) and 15 cranial measurements in four geographic groups of *Calcochloris obtusirostris*, and results of single classification ANOVAs of OTU means. Taxa are: COO - *C. o. obtusirostris*; COC - *C. o. chrysillus*; COL - *C. o. limpopoensis*; COZ - *C. obtusirostris* from southeastern Zimbabwe and Northern Province, South Africa. $\bar{x}$ = sample mean; *sd* = standard deviation; *n* = sample size. Vertical lines denote maximally non-significant subsets from SNK multiple comparisons tests.

BCW (*F* = 0,36; *p* = 0,788)

OTU	$\bar{x}\pm sd(n)$		Range
COC	2,99±0,12(15)	│	2,88-3,23
COZ	2,99±0,15(12)	│	2,71-3,19
COO	3,05±0,03(2)	│	3,02-3,07
COL	3,06±0,29(5)	│	2,99-3,46

ARB (*F* = 1,04; *p* = 0,395)

OTU	$\bar{x}\pm sd\ (n)$		Range
COZ	4,89±0,22(12)	│	4,73-5,26
COO	4,94±0,08(2)	│	4,86-5,01
COC	5,08±0,17(19)	│	4,77-5,43
COL	5,09±0,18(8)	│	4,92-5,25

MIO (*F* = 6,24; *p* = 0,002)

OTU	$\bar{x}\pm sd\ (n)$		Range
COC	7,13±0,22(19)	│	6,83-7,65
COZ	7,17±0,24(11)	│	6,80-7,77
COO	7,25±0,13(2)	││	7,12-7,37
COL	7,51±0,09(8)	│	7,40-7,56

ZMB (*F* = 5,11; *p* = 0,007)

OTU	$\bar{x}\pm sd(n)$		Range
COC	15,70±0,50(19)	│	15,04-16,76
COZ	15,85±0,51(11)	│	14,59-16,48
COO	16,31±0,21(2)	││	16,10-16,51
COL	16,45±0,33(8)	│	16,12-16,80

IOW (*F* = 19,52; *p* <0,001)

OTU	$\bar{x}\pm sd\ (n)$		Range
COC	6,88±0,16(19)	│	6,69-7,35
COZ	6,90±0,25(11)	│	6,30-7,27
COO	7,19±0,10(2)	│	7,09-7,29
COL	7,51±0,20(8)		7,14-7,59

GSL (*F* = 20,69; *p* < 0,001)

OTU	$\bar{x}\pm sd\ (n)$		Range
COZ	21,10±0,46(8)	│	20,28-21,65
COC	22,07±0,27(2)	│	21,08-23,60
COO	22,14±0,70(17)	│	21,80-22,33
COL	23,60±0,84(8)		21,60-24,15

GSH (*F* = 2,56; *p* = 0,077)

TU	$\bar{x}\pm sd(n)$		Range
COZ	10,62±0,28(8)	│	10,05-11,04
COC	10,84±0,24(17)	│	10,53-11,34
COO	10,92±0,02(2)	│	10,90-10,94
COL	10,96±0,22(8)	│	10,45-11,16

P@P (*F* = 8,95; *p* < 0,001)

OTU	$\bar{x}\pm sd\ (n)$		Range
COZ	7,49±0,38(7)	│	6,85-8,03
COO	7,80±0,29(2)	││	7,51-8,08
COC	8,03±0,25(17)	│	7,79-8,43
COL	8,26±0,48(8)	│	7,30-8,86

PAL (*F* = 24,45; *p* < 0,001)

OTU	$\bar{x}\pm sd\ (n)$		Range
COZ	10,82±0,20(7)		10,56-11,13
COC	11,66±0,44(16)	│	11,01-12,64
COO	11,64±0,22(2)	│	11,41-11,86
COL	12,35±0,60(8)		10,95-12,66

MTL (*F* = 13,23; *p* < 0,001)

OTU	$\bar{x}\pm sd(n)$		Range
COZ	5,52±0,16(7)		5,41-5,80
COO	5,97 (1)	│	/
COC	5,98±0,20(16)	│	5,51-6,29
COL	6,11±0,29(8)	│	5,47-6,42

IPG (*F* = 18,26; *p* < 0,001)

OTU	$\bar{x}\pm sd\ (n)$		Range
COZ	1,80±0,06(7)	│	1,69-1,84
COO	1,86±0,05(2)	││	1,81-1,91
COC	1,88±0,07(16)	│	1,75-2,01
COL	2,04±0,10(8)		1,87-2,08

PPL (*F* = 19,94; *p* < 0,001)

OTU	$\bar{x}\pm sd\ (n)$		Range
COZ	7,00±0,17(7)	│	6,63-7,18
COC	7,03±0,19(16)	│	6,75-7,36
COO	7,34±0,03(2)	│	7,31-7,36
COL	7,67±0,40(8)		6,77-8,20

BBW (*F* = 13,83; *p* < 0,001)

OTU	$\bar{x}\pm sd(n)$		Range
COZ	7,60±0,30(6)	│	7,35-8,35
COC	7,99±0,23(16)	│	7,60-8,03
COO	7,80±0,29(2)	│	7,51-8,08
COL	8,27±0,48(8)		7,30-8,87

CPW (*F* = 9,62; *p* < 0,001)

OTU	$\bar{x}\pm sd\ (n)$		Range
COZ	5,77±0,26(6)	│	5,56-6,17
COC	5,89±0,18(16)	│	5,69-6,34
COO	6,00±0,01(2)	││	5,99-6,01
COL	6,28±0,30(8)	│	5,57-6,55

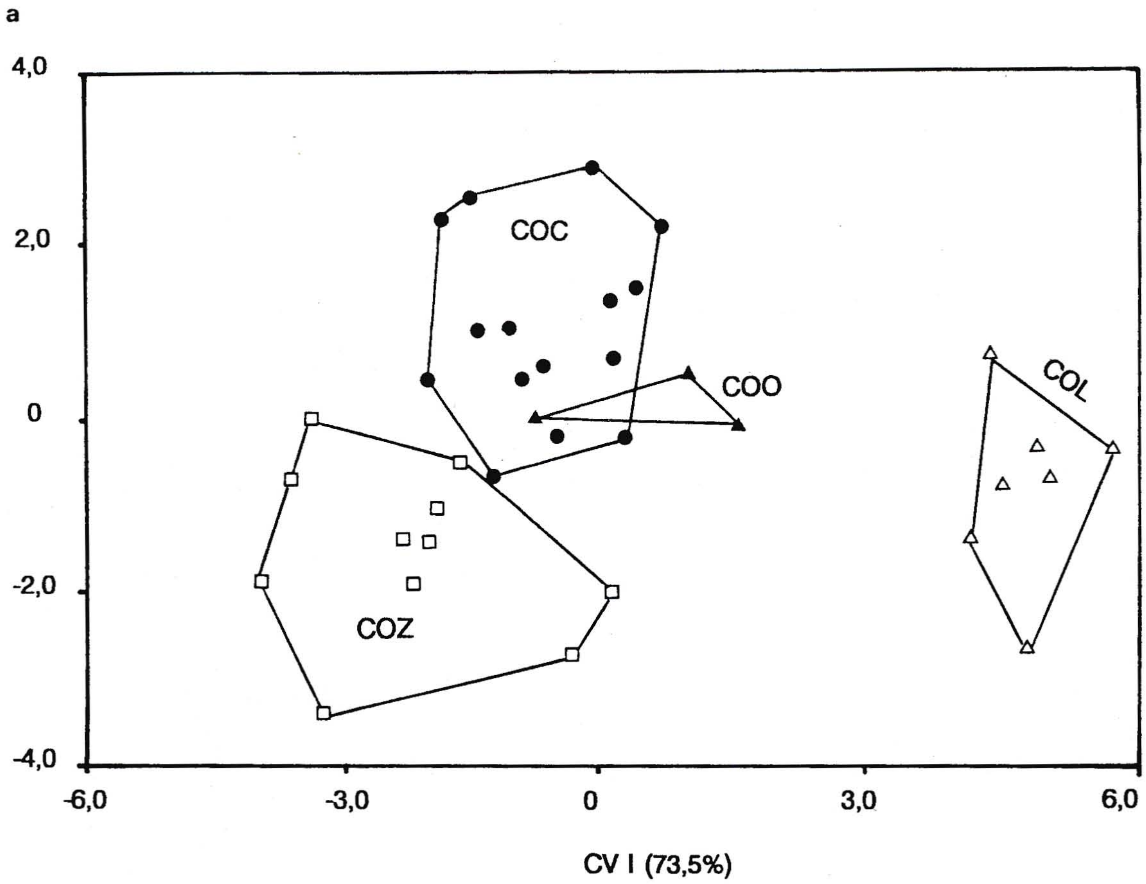
APW (*F* = 14,60; *p* < 0,001)

OTU	$\bar{x}\pm sd\ (n)$		Range
COZ	3,08±0,22(6)		2,85-3,07
COC	3,35±0,12(16)	│	3,18-3,55
COO	3,40±0,05(2)	│	3,35-3,44
COL	3,59±0,26(8)		3,09-3,92

MDL (*F* = 26,57; *p* < 0,001)

OTU	$\bar{x}\pm sd\ (n)$		Range
COZ	13,55±0,36(6)	│	13,02-14,14
COO	14,10±0,49(2)	││	13,61-14,58
COC	14,21±0,37(16)	│	13,63-14,98
COL	15,24±0,65(8)		13,63-15,82

Fig. 8.2. Phenetic relationships among specimens of *Calcochloris obtusirostris*, as indicated: a) pairwise comparison of the first two canonical variate axes from a four-group discriminant functions analysis; and b) pairwise comparison of the first two principal component axes from an analysis based on single-standardized data (co-phenetic correlation = 0,963). Symbols and acronyms used are: (▲) - *C. o. obtusirostris* (COO); (●) - *C. o. chrysillus* (COC); (△) - *C. o. limpopoensis* (COL); (□) - *C. obtusirostris* (COZ) from south-eastern Zimbabwe and north-eastern Kruger National Park.


a
4,0
2,0
0
-2,0
-4,0
-6,0
-3,0
0
3,0
6,0
CV II (18,3%)
CV I (73,5%)
COC
COO
COL
COZ

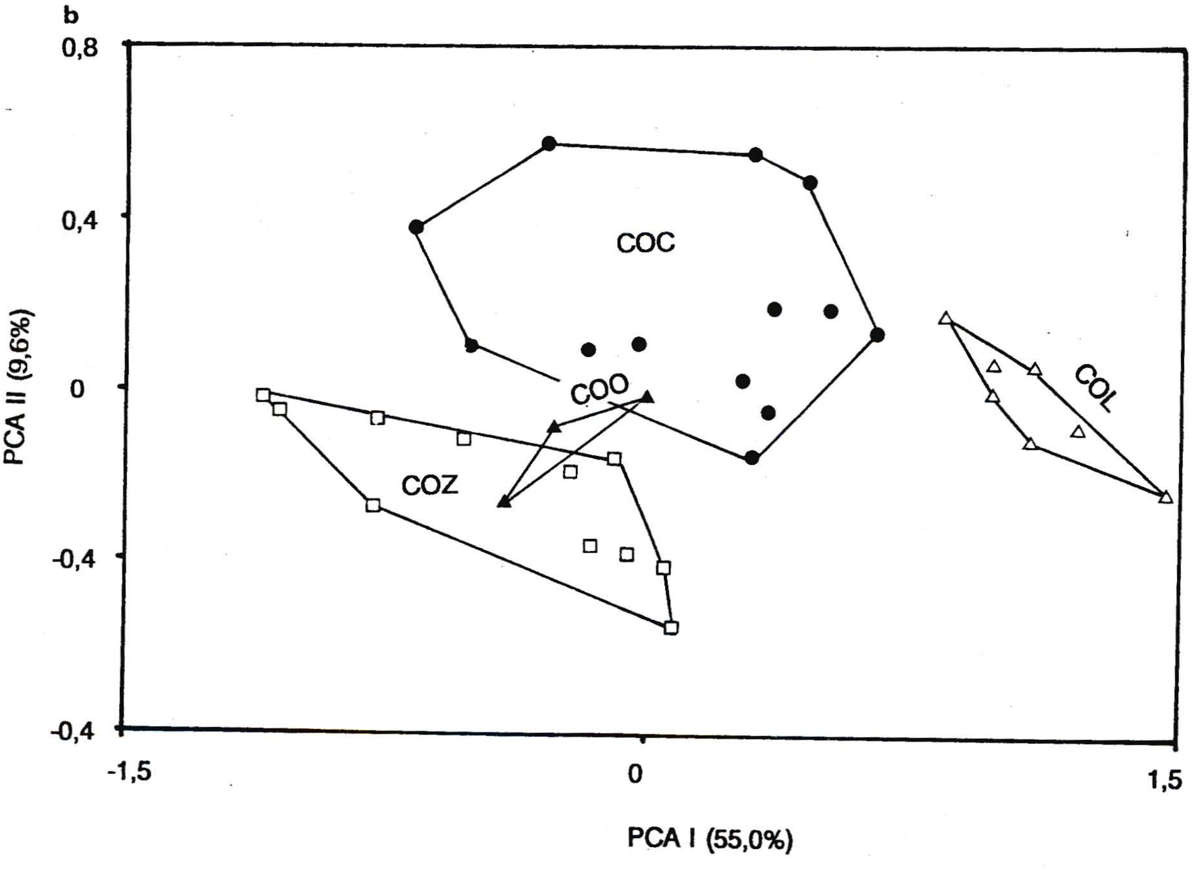

b
0,8
0,4
0
-0,4
-0,4
-1,5
0
1,5
PCA II (9,6%)
PCA I (55,0%)
COC
COO
COL
COZ

Table 8.5

Factor matrix showing measurement loadings for the first three canonical variate axes from a multiple discriminant functions analysis of *C. obtusirostris* specimens representing four pooled population samples. Boldfaced loadings indicated strong variable participation in the respective axes.

Measurement	**CV I**	**CV II**	**CV III**
BCW	-1,798	0,070	-0,544
MIO	-0,296	-0,969	**-2,047**
ZMB	**-2,074**	0,789	1,484
IOW	**2,675**	-0,416	1,869
GSL	-0,168	-0,731	**-2,322**
PAL	1,041	**4,036**	1,947
IPG	0,444	0,696	**2,287**
PPL	**3,584**	**-2,929**	0,657
BBW	1,967	-1,977	-0,182

Separation along this axis thus largely reflected the tendency for palatal length to be significantly smaller in southeastern Zimbabwe than elsewhere (Table 8.4).

Pairwise comparison of the first two principal component axes (using an 18 measurement suite with data for males and females pooled after individual standardization to correct for sexual dimorphism) revealed a similar pattern of variation. The *C. o. limpopoensis* specimens plotted well to the right of others along PCA I (Fig. 8.2b), while the *C. o. chrysillus* and southeastern Zimbabwe (COZ) samples plotted apart along PCA II, with the three *C. o. obtusirostris* specimens intermediately.

PCA I was a general size vector (as indicated by the high, positive loading for most variables; Table 8.6a), but BCW loaded relatively low. Separation along PC I thus indicated a tendency for BCW to become relatively narrower (as indicated by the ratio BCW:GSL) as overall size increased from left to right (Table 8.6b). PCA II contrasted skull widths (MIO, ZMB, IOW) with palate dimensions (PAL, MTL, P@P), so that increasing scores along this axis corresponded with a relative increase in palate width (as indicated by the ratio P@P:MIO) and length (as indicated by the ratio PAL:ZMB). As MIO and ZMB did not vary significantly between *C. o. chrysillus* and the southeastern Zimbabwe samples (Table 8.4), separation of these OTUs along PCA II largely reflected the tendency for palates to be shorter and narrower in the latter, their similarity in overall size notwithstanding.

Cluster analysis based on average taxonomic distance coefficients (Fig. 8.3a) clearly differentiated the *C. o. limpopoensis* specimens (Cluster A), owing to their larger size. Similarly, most of the *C. o. chrysillus* specimens grouped together in two distinct clusters (B and C1), and were well separated from the south-eastern Zimbabwe specimens, which fell in a distinct subcluster (C2) that included also the two *C. o. obtusirostris* specimens. In a phenogram based on correlation coefficients, the *C. o. limpopoensis*, *C. o. chrysillus* and south-eastern Zimbabwe specimens also tended to group apart in distinct clusters (A - D). Phenetic analyses thus showed that the four populations are well-differentiated from each other in both cranial size and shape, as follows: *C. o. limpopoensis* - overall size larger, but with relatively more feeble claws (BCW) relative to the other OTUs; *C. o. chrysillus* - overall size smaller, but with relatively wider and longer palates (P@P, PAL) than the southeastern Zimbabwe

Table 8.6

Results of a principal components analysis of *C. obtusirostris* specimens representing four pooled population samples. a) Factor matrix showing measurement loadings for the first three principal component axes. Boldfaced loadings indicated strong variable participation in the respective axes; b) Morphometric ratios indicating shape differences between the four populations. Sample acronyms are: COO - *C. o. obtusirostris*; COC - *C. o. chrysillus*; COL - *C. o. limpopoensis*; COZ - southeastern Zimbabwe population.

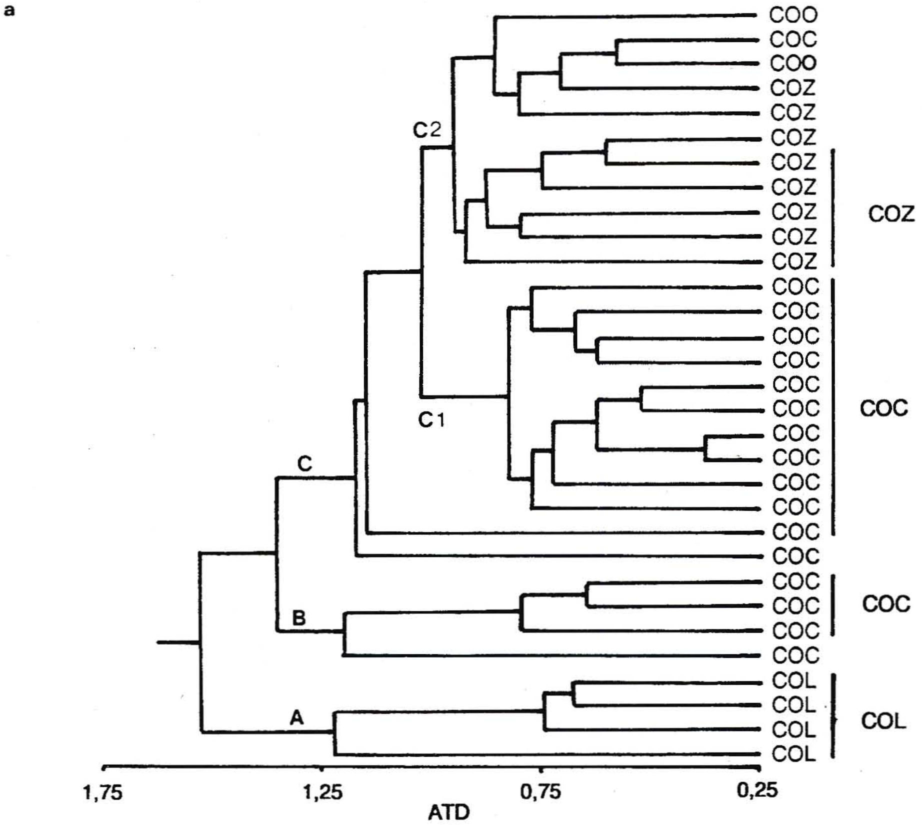
a) Factor matrix

Measurement	PCA I	PCA II	PCA III
BCW	0,359	-0,458	-0,482
ARB	**0,508**	-0,012	**-0,630**
MIO	**0,558**	**-0,614**	-0,044
ZMB	**0,670**	**-0,566**	0,227
IOW	**0,678**	**-0,464**	0,293
GSL	**0,919**	0,206	0,076
GSH	**0,580**	-0,103	-0,370
P@P	**0,746**	**0,364**	-0,149
PBM	**0,547**	-0,207	-0,287
PAL	**0,854**	**0,412**	-0,067
MTL	**0,724**	**0,503**	-0,159
IPG	**0,786**	-0,127	-0,083
PPL	**0,787**	-0,127	0,025
BBW	**0,700**	-0,204	**0,410**
CPL	**0,863**	0,173	0,197
APW	**0,535**	0,145	**0,464**
MDL	**0,883**	0,321	0,080

b) Morphometric ratios

	RATIOS (X 100)		
OTU	BCW:GSL	P@P:MIO	PAL:ZMB
COZ	14,1±0,7	105,1±5,3	68,2±2,3
COO	13,8±0,1	107,6±2,9	71,4±2,8
COC	13,5±0,7	112,4±4,8	74,5±2,8
COL	12,9±1,0	111,7±4,4	75,0±3,1

Fig. 8.3. Phenetic relationships among specimens of *C. obtusirostris* based on cluster analyses of: a) average taxonomic distance coefficients (co-phenetic correlation = 0,701); and b) correlation coefficients (co-phenetic correlation = 0,640). Locality acronyms are explained in Table 8.1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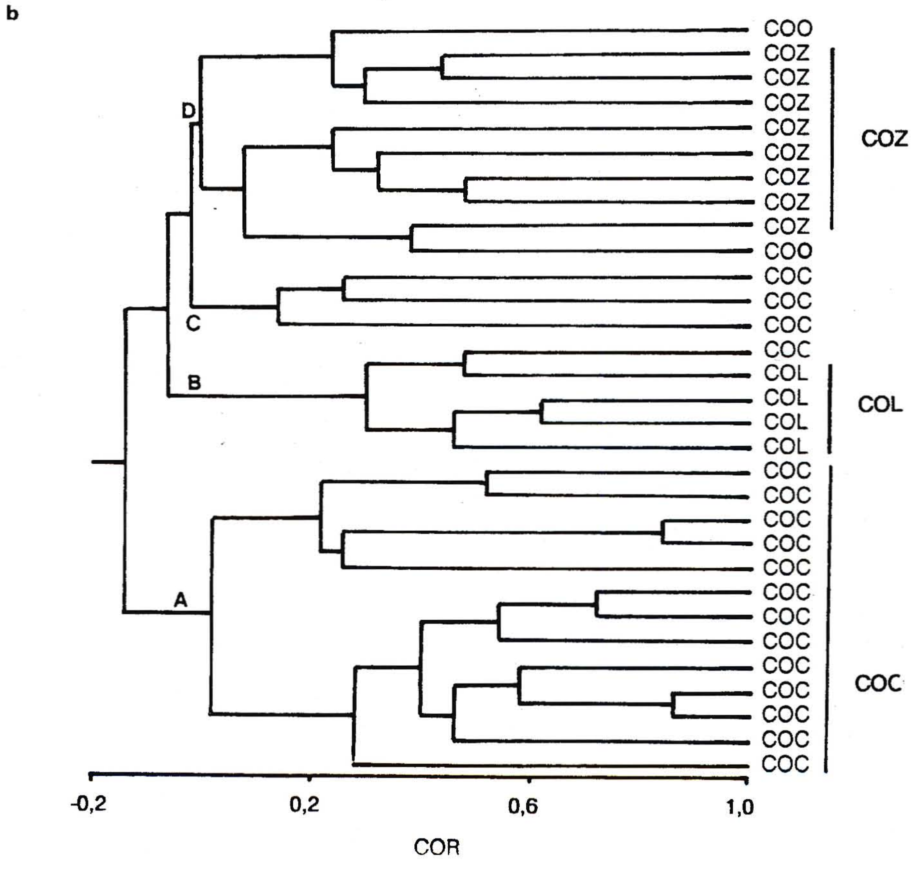
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specimens, and narrower posterior palates (IPG) than the *C. o. obtusirostris* sample; *C. o. obtusirostris* - similar to the southeastern Zimbabwe sample in cranial shape and overall size, but with significantly longer palates (PAL in Table 8.4); and the southeastern Zimbabwe OTU, which is characterized by a significantly narrower and shorter palate, but relatively more robust claws.

8.4 TAXONOMIC CONCLUSIONS

Calcochloris obtusirostris is unique in that, while all specimens have molariform P1, protocones are more commonly found on P^1 than in any other chrysochlorid taxon examined. The occurrence of P^1 protocones in this species seems too great to be explained by the presence of deciduous and permanent teeth with differing morphologies in the same toothrow, as I suggested may be the case in *Amblysomus* species (Section 5.3.2.1).

Lundholm (1955:287) first noted that while the absence of talonids has been used as a generic character distinguishing *Calcochloris* (Forcart 1942; Roberts 1951), talonids are present quite often on the molars. My analyses support this finding, and show that variability in this character in *Calcochloris* is similar in magnitude to that within *Chlorotalpa* and some *Amblysomus* species.

Dental variation, in respect of the presence/absence of protocones and molar talonids, appears to be most pronounced in *C. o. limpopoensis* and least pronounced in *C. o. obtusirostris*. The apparent dental uniformity of the latter population is, however, probably due to only three specimens being available for study. It seems likely that variability of a similar magnitude to that observed in other populations will become manifest once more specimens are examined.

Sexual size dimorphism is pronounced in *C. obtusirostris*, and similar in magnitude to that observed in most other chrysochlorid species. Sample sizes were too small to evaluate whether this variation is essentially allometric or isometric.

Geographic variation in *C. obtusirostris* is more pronounced than sexual size dimorphism. *C. o. limpopoensis* and *C. o. chrysillus* are clearly distinguished from the other two populations analysed by both cranial size and shape, indicating that the current subspecific distinction between these OTUs is warranted. The southeastern Zimbabwe population is well differentiated from both of these subspecies, and thus cannot be assigned to *C. o. limpopoensis*, as treated by Meester (1974) and Meester *et al* (1986). *C. o. obtusirostris* and the southeastern Zimbabwe populations differ in only minor respects, despite their wide geographic separation (Fig. 8.1). This suggests that gene flow occurs between these populations, and thus that they should be referred, albeit provisionally, to the same subspecies. Such gene flow may occur via the intermediate demes found along the Changane river system, which Meester (1974) postulated to be the link between the coastal Mozambique and inland Zimbabwe populations.

PART IV

RECLASSIFICATION OF SPECIES

CHAPTER 9

SYSTEMATIC RELATIONSHIPS AMONG THIRTEEN CHRYSOCHLORID SPECIES: A SYNTHESIS OF CONFLICTING DATA SUITES

9.1. INTRODUCTION

Owing to their reliance on small numbers of specimens, often contradictory data suites and largely omnispective analytical approaches, previous authors differed considerably in their treatment of the genera *Amblysomus*, *Chlorotalpa* and *Calcochloris*. Consequently, generic and inter-specific relationships have been obscured rather than clarified (Chapter 1). Of the three most recent classifications proposed for the Chrysochloridae, that of Simonetta (1968) was essentially monothetic, since it was based primarily on malleus and epitympanic recess morphology. Petter's (1981) treatment was epistemological, in that it placed greater emphasis on classificatory expedience than on reflecting phylogenetic relationships. Meester's (1974) classification was polythetic in that it considered cranial, dental, malleus and fur colour characteristics, and would thus seem preferable. This treatment was largely intuitive, however, and offered little in the way of supporting evidence (beyond a few measurements given in diagnostic keys) that can be used by other researchers to assess the validity of conclusions.

As a reviewer, I was thus not able to assume that any of the generic divisions proposed by recent authors are valid. In this chapter, I therefore consider both inter-specific and inter-generic relationships among species traditionally referred to *Amblysomus*, *Chlorotalpa* and *Calcochloris*. As *Chrysochloris stuhlmanni* was also included in this complex by Simonetta (1968), samples of this species, and of *Chrysochloris asiatica*, were also examined to assess the generic affinity of the former.

By integrating craniometric data with hyoid, malleus and dental characters using mainly phenetic and numerical cladistic techniques, and taking into account also chromosomal properties (if known) for these taxa, I attempted to resolve the following issues in particular:

1) Should *C. stuhlmanni* be assigned to *Chrysochloris* (Meester 1974; Petter 1981) or another genus (Simonetta 1968)?;

2) Are *Chlorotalpa* and *Calcochloris* valid genera (Meester 1974; Simonetta 1968) or merely synonyms of *Amblysomus* (Ellerman *et al.* 1953; Petter 1981)?;

3) Are *Carpitalpa* and *Kilimatalpa*, proposed for the species *C. arendsi* and *C. stuhlmanni* respectively, valid taxa (*sensu* Lundholm 1955)?; if so, should these be afforded subgeneric rank in *Chlorotalpa*, or should *Carpitalpa* be elevated to generic rank to include *Kilimatalpa* (*sensu* Simonetta 1968)?;

4) Is *Neamblysomus* a valid taxon (Allen 1939; Roberts 1924), and if so, what rank should it be afforded?

5) Should *C. leucorhina* from central Africa be included in *Chlorotalpa* (Meester 1974), *Amblysomus* (Ellerman *et al.* 1953; Petter 1981) or the subgenus *Huetia* within *Chrysochloris* (Forcart 1942)?;

9.2. MATERIALS AND METHODS

9.2.1. General

Seven hundred and sixty-two specimens were analysed. Of the 19 measurements identified for use (Chapter 2), maxillary toothrow length (MTL) and palate width between M2 (PBM) were excluded, since these are not homologous across all species (owing to the variable presence of M3). To increase sample sizes, particularly of the central-African *C. leucorhina* and *C. stuhlmanni*, three measurements (IPG, EAM and FML) were excluded from most analyses

Specimens were grouped into 13 OTUs (Table 9.1) according to species, as recognized by Meester (1974), but with the addition of several taxa shown to be worthy of specific rank in Chapter 5. Codes in square brackets ([ ]) in the text refer to these OTUs, as specified in Table 9.1.

Data for specimens in TW 2 - 4 were pooled within each species, this being a practical necessity owing to small sample sizes. The underlying assumption that age variation is negligible was verified in *A. hottentotus* (Section 5.3.1.3). While possibly more pronounced in other species, it is unlikely that such variation is sufficiently marked to obscure patterns of inter-specific variability.

Table 9.1

Species and subspecies samples used as Operational Taxonomic Units (OTUs) for the analysis of interspecific and generic patterns of craniometric variation. The generic classification used is that of Meester (1974). See Chapters 5 - 8 for details of localities pooled for each OTU.

Genus	Species	Species Acronym	Subspecies	Subspecies Acronym
Amblysomus	*corriae*	AC	*corriae*	ACC
			devilliersi	ACD
	gunningi	AG	/	/
	hottentotus	AH	*hottentotus*	AHH
			pondoliae	AHP
			iris	AHI
			longiceps	AHL
			subspecies A	AHA
	julianae	AJ	/	/
	marleyi	AM	/	/
	septentrionalis	AS	/	/
	Species A	AA	/	/
Chlorotalpa	*arendsi*	CA	/	/
	duthieae	CD	/	/
	leucorhina	CL	/	/
	sclateri	CS	*sclateri*	CSS
			shortridgei	CSH
			guillarmodi	CSG
			montana	CSM
Calcochloris	*obtusirostris*	CO	*obtusirostris*	COO
			chrysillus	COC
			limpopoensis	COL
Chrysochloris	*asiatica*	CAS	/	/
	stuhlmanni	CST	/	/

9.2.2 Phenetic analyses

Since most species show significant sexual differences in cranial size, males and females were studied separately in univariate and discriminant functions analyses. As the available samples of *C. leucorhina* and *C. stuhlmanni* were small, and the sexes of most specimens were not recorded by collectors, no attempt was made to divide the specimens into male and female OTUs. Similarly, the single OTU of *Chrysochloris asiatica* used in initial exploratory analyses deliberately included specimens of both sexes, and from various localities, to ensure that the sample adequately circumscribed sexual and geographic variation in this species.

Cluster and principal components analyses of craniometric data were based on the means of male and female samples, following independent standardization by sex to correct for sexual size dimorphism (Cheverud 1982). To increase the number of OTUs, samples for polytypic species were divided into subspecies OTUs (Table 9.1).

Craniometric data and qualitative characters (Table 9.2) were integrated directly by cluster analyses based on Gower's General Similarity Coefficient - the only association index appropriate for mixed-mode data (Pimentel and Smith 1986).

9.2.3 Cladistic analyses

Strict parsimony cladograms were generated with Hennig86 Version 1.5 (Farris 1988) and PAUP Version 3.2 (Swofford 1991), using six qualitative characters, and nine gap-coded cranial ratios reflecting differences in cranial shape (Table 9.2; determined by examining variable participation in ordination axes). Gap-coding was performed using an interval of one within-OTU standard deviation to delimit character states (Table 9.3), as suggested by Thorpe (1984). *Chrysochloris asiatica* was used as the outgroup for all analyses, since this species represents a clearly distinct line of descent from the OTUs considered here (Broom 1907a; Simonetta 1968; Roberts 1951).

Characters were weighted either equally, or differentially using the WEIGHTS option of PAUP, and the 'ccode' option of Hennig86. Cranial characters not showing a linear sequence of transformation were treated as unordered, as suggested by Swofford (1985). For each weighting regime, all minimum length trees were identified by the exhaustive search option (ie*) of Hennig86, as recommended by Fitzhugh (1989), and the branch-and-bound (BB) exact option of PAUP. Strict consensus trees were derived from multiple equally parsimonious trees with the CONTREE algorithm of PAUP, and the 'Nelsen' command in Hennig86.

To test if the data contained a phylogenetic signal, the $g1$ (skewness) statistic of tree lengths were computed from a 1000 randomly generated trees using the RANDTREES option of PAUP, and evaluated for significance using the probability tables of Hillis and Huelsenbeck (1992).

The extent of homoplasy associated with a cladogram was measured using the consistency index (*CI*) of Kluge and Farris (1969), Farris's (1989) retention index (*RI*), and Archie's (1989) homoplasy excess ratio (*HSR*). Since these indices are affected by the number of taxa included in an analysis, and to a lesser extent also by the number of characters, the rescaled consistency index (*RCI*) was used for comparing the relative merits of different cladograms (Klassen *et al.* 1991).

The relative stability of each internal node was assessed by bootstrapping (BOOTSTRAP option of PAUP) either the single trees produced by branch-and-bound searching, or the consensus tree if more than one equally parsimonious tree was generated. Confidence limits associated with each internode were inferred from bootstrap values on a 50% majority-rule consensus tree (Hillis and Bull 1993) computed using 1000 iterations (Hedges 1992).

9.2.4. Qualitative data suites

The data matrix used for mixed-mode phenetic and cladistic analyses is shown in Table 9.2. The six qualitative characters used were scored for each species after examining character-state distributions within and among taxa, as detailed below.

9.2.4.1. Dental characters.

Of the dental characters identified in Chapter 2, incisor morphology was rejected out of hand since this is apparently influenced heavily by toothwear. As *Calcochloris obtusirostris* is the only species showing semi-molariform canines, this character is an autapomorphy that conveys no information about inter-specific relationships, and was excluded from further analysis. Variability in the other dental characters examined is summarized in Table 9.4.

Protocones are absent on P^1 in eight OTUs, and occur only variably in the other

Table 9.2

Character-states for nine gap-coded craniometric ratios and six qualitative characters in 14 chrysochlorid species, and the alphabetic codes by which they are referred to in cladograms. *Chrysochloris asiatica* [CAS] was used as the outgroup for cladistic analyses. See Table 9.1 for an explanation of OTU codes, Table 9.3 for actual craniometric ratios, and the text for an explanation of qualitative character codings. Missing values are denoted by question marks (?), which was the code entered for incomplete data in phylogenetic analyses.

	CRANIAL RATIOS									QUALITATIVE CHARACTERS					
OTU	P@P	ARB	MIO	PAL	BCW	IPG	P@P	APW	ZMB	M3	I:M	SH	NORs	C15	C11
	GSL	GSL	P@P	MIO	GSL	P@P	PPL	ZMB	GSL						
CODE	A	B	C	D	E	F	G	H	O	I	J	K	L	M	N
CO	2	1	0	1	0	0	2	0	1	0	0	0	1	1	1
CS	1	0	1	2	1	0	1	1	0	2	1	1	1	0	1
CD	1	0	1	2	1	0	1	1	0	2	1	1	1	0	1
CA	1	0	1	3	1	0	1	2	0	2	2	3	?	?	?
CL	1	1	2	0	0	2	0	0	1	2	0	?	?	?	?
CST	0	0	2	2	0	2	0	3	0	2	3	?	?	?	?
AG	1	0	1	3	1	0	1	2	0	1	0	4	1	1	0
AJ	1	0	1	1	1	0	1	0	1	1	0	4	1	1	0
AM	0	0	1	2	2	1	0	3	0	0	0	4	2	1	2
AH	0	0	2	1	3	1	0	3	0	0	0	4	2	1	2
AC	0	0	2	2	3	1	0	4	0	0	0	4	2	1	2
AS	0	0	2	1	3	1	0	4	0	0	0	4	3	1	2
AA	0	0	2	1	3	1	0	3	0	0	0	4	3	1	2
CAS	1	0	1	2	1	0	2	0	2	2	4	2	0	0	1

Table 9.3

Selected cranial ratios (expressed as percentages ± one standard deviation) for 14 chrysochlorid species, chosen after examining variable loadings in ordination analyses of species OTUs, and character-states (CH) afforded to each OTU after gap-coding (Thorpe 1984b), for use in cladistic analyses. *Chrysochloris asiatica* [CAS] was used as an outgroup for cladistic analyses.

OTU	P@P:GSL		ARB:GSL		MIO:P@P		PAL:MIO		BCW:GSL		IPG:P@P		P@P:PPL		APW:ZMB		ZMB:GSL	
	RATIO	CH	RATIO	CH	RATIO	CH	RATIO	CH	RATIO	CH	RATIO	CH	RATIO	CH	RATIO	CH	RATIO	CH
CO	35,8±0,6	2	22,7±0,6	1	91,6±3,3	0	158,7±7,4	1	13,6±0,4	0	23,8±0,4	0	110,3±3,2	2	21,0±1,0	0	71,0±2,2	1
CL	30,6±1,5	1	22,9±0,9	1	115,8±5,6	2	139,4±5,7	0	12,8±0,6	0	33,4±2,9	2	85,2±4,5	0	21,4±1,5	0	72,2±0,1	1
CS	29,5±1,3	1	19,0±0,8	0	105,9±1,7	1	167,8±6,4	2	16,4±0,4	1	25,0±1,4	0	94,4±3,0	1	23,7±1,0	1	64,8±2,0	0
CD	29,4±0,3	1	18,4±0,3	0	102,6±1,3	1	172,4±2,4	2	15,4±0,2	1	25,0±0,8	0	94,2±1,8	1	23,7±0,3	1	62,5±0,5	0
CA	28,5±0,2	1	17,8±0,2	0	100,1±0,3	1	182,3±0,3	3	15,9±0,2	1	27,1±0,6	0	93,4±0,2	1	25,0±0,3	2	60,9±0,1	0
AJ	31,6±0,3	1	19,8±0,4	0	99,5±2,3	1	159,1±1,5	1	16,4±0,1	1	26,3±0,3	0	97,4±0,7	1	21,2±0,4	0	68,4±0,2	1
AM	28,1±0,3	0	18,6±0,5	0	104,9±1,6	1	166,5±0,4	2	17,2±0,6	2	30,9±0,6	1	84,9±0,6	0	27,7±0,1	3	62,9±1,1	0
AG	29,1±0,1	1	17,3±0,3	0	98,4±0,6	1	183,1±0,7	3	16,4±0,2	1	26,3±0,8	0	92,7±0,3	1	25,5±0,4	2	60,8±0,4	0
AH	28,0±0,9	0	18,6±0,2	0	112,2±4,6	2	159,0±3,9	1	19,8±1,0	3	29,2±1,1	1	86,4±2,8	0	26,9±1,4	3	62,1±0,6	0
AS	26,9±0,1	0	17,7±0,1	0	118,1±0,4	2	157,9±0,9	1	20,4±0,6	3	29,6±0,1	1	85,3±0,2	0	28,8±0,5	4	61,4±0,6	0
AA	26,8±0,3	0	18,2±0,3	0	118,5±1,1	2	157,8±1,7	1	21,3±0,9	3	29,0±0,5	1	84,4±0,4	0	27,6±0,2	3	62,0±0,7	0
AC	26,1±0,6	0	17,5±0,4	0	114,9±3,4	2	167,3±3,6	2	18,5±0,5	3	29,8±0,6	1	80,4±1,7	0	29,1±1,5	4	58,1±0,1	0
CST	27,1±0,6	0	17,9±0,4	0	114,0±3,5	2	163,6±7,8	2	13,3±1,6	0	31,7±2,7	2	83,0±4,0	0	26,4±1,2	3	60,9±1,3	0
CAS	30,8±0,7	1	20,7±0,7	0	104,6±1,9	1	163,5±2,3	2	16,5±0,8	1	23,2±2,9	0	108,4±1,3	2	22,9±0,2	0	75,2±1,2	2

five, perhaps because of dental differences between deciduous and permanent teeth present in the same toothrow. Since the intra-specific variability of this character exceeded 5% (in *C. obtusirostris* and *C. stuhlmanni*), I excluded it from further analysis.

Intra-specific variability in the morphology of P1 exceeds 5% in *Amblysomus Species A*, and is even higher (7,5%) within the Durban population of *A. hottentotus* (Section 5.3.1.2). This character is also difficult to score accurately, since there is appreciable intergradation between the pseudo- and semi-molariform states resulting from differential toothwear (Section 5.3.1.2). Conversely, the molariform morphology of P1 in *C. obtusirostris* is clearcut, even in specimens showing extremely heavy toothwear (TW5). However, this character is autapomorphic, and therefore conveys no information about inter-specific relationships. P1 morphology was thus also excluded from further analyses.

The presence and development of molar talonids also varies within four species. Regardless of toothwear, molar talonids are invariably present and well-developed in all *C. duthieae* examined, and also in most *Amblysomus* specimens, but are feeble or absent in *C. leucorhina*, *A. gunningi* and *A julianae*. In *C. sclateri*, well-developed talonids occur on M_1 in the majority (97%) of specimens, but are absent on M_2 in a few older individuals. Similarly, while all of the *C. stuhlmanni* I examined possess well-developed molar talonids, St. Leger (1931) reported that molar talonids are reduced to a feeble ledge in some specimens from the Ruwenzori mountains. Conversely, in *C. arendsi* and *C. obtusirostris* the molar talonids are always feeble, but occur in only a few specimens, all of which belong to TW2 or TW3.

These data suggest that there may be interspecific differences in the presence and development of molar talonids, but also that this character is significantly influenced also by the extent of occlusal attrition, thereby casting doubt on its reliability as a taxonomic indicator. Since intra-specific variability exceeded 5% in some of the species examined, this character was excluded from further analysis.

Much of the variability in the dental characters considered so far may be the result of deciduous and permanent teeth with different morphologies occurring in the same toothrow (Broom 1916b). Intra-specific variation in the presence/absence and morphology of M3 cannot, however, be attributed to differences between deciduous and

Table 9.4

Variation in the incidence of protocones on P^1, molar talonids, M3 and P1 morphology amongst 13 chrysochlorid species, as indicated by the percentage of specimens showing each character state. See Table 9.1 for an explanation of OTU codes.

	Protocone on P^1		P1 morphology			Molar talonids		M3	
	Present	Absent	Sectorial	Pseudo- or Semi-molariform	Molariform	Present	Absent	Present	Absent
CO	36	64	0	0	100	9*	91	0	100
CA	0	100	0	100	0	12*	88	100	0
CD	8	92	0	100	0	100	0	100	0
CS	3	97	0	100	0	97	3	100	0
CL	0	100	0	100	0	0	100	100	0
AG	0	100	0	100	0	0	100	75	25
AM	0	100	100	0	0	100	0	0	100
AJ	6	94	0	100	0	0	100	18	82
AH	0	100	97	3	0	100	0	1	99
AC	0	100	100	0	0	100	0	0	100
AS	0	100	96	4	0	100	0	2	98
AA	0	100	100	0	0	100	0	0	100
CST	22	78	0	100	0	100**	0	100	0

* - although present, talonids are only weakly-developed

** - but are reduced to feeble ledges in some specimens (St. Leger 1931) permanent dentitions, since molars are by definition permanent teeth. As the morphology of M3 (peg-like *cf.* molariform) varies with toothwear in some species (Section 5.3.2.1), this character was not considered further.

The variable presence of M3 within some species might likewise seem sufficient justification to eliminate this character from analysis, but as demonstrated in Chapter 6, this character has systematic value. There appear to be two trends amongst chrysochlorids, whereby this tooth is either retained in all specimens (*Chlorotalpa* species and *Chrysochloris stuhlmanni*, each with an incidence of 100%), or lost in the majority of individuals (*Calcochloris* and most *Amblysomus* species, with an incidence of < 3%). Only *A. gunningi* and *A. julianae* are intermediate, M3 being present variably with an incidence exceeding 10%. This character was thus included in analyses, and was scored as: State 0 - M3 present in < 5% of specimens examined; State 2 - M3 present variably with an incidence of >5% and <80%; and State 3 - M3 present in > 95% of specimens.

Of the seven dental traits which previous authors treated as diagnostic (Section 2.2.3), only one - the presence/absence of an M3 - appeared to be constant enough to warrant its use in inter-specific analyses. This supports the warning, voiced independently by Ellerman *et al.* (1953) and St. Leger (1931), that most dental characters are too variable to serve as valid indicators of systematic relationships among chrysochlorids.

9.2.4.2 Hyoid morphology

Of the various hyoid characters assessed in Chapter 2, stylohyal shape displayed the greatest inter-specific variability. Since these analyses were completed, a single specimen (NM695) of *C. arendsi* with a stylohyal bone attached to the dentary was traced. The stylohyal in this species is more bulbous than in either of the two other *Chlorotalpa* species or *C. asiatica*, but not as robust as in *Amblysomus*, and thus must be regarded as intermediate in morphology. Stylohyal morphology was thus scored as (Table 9.2): State 0 - slender with a well-developed articular surface situated proximally (*C. obtusirostris*); State 1 - slender or semi-bulbous with a well-developed medial articular surface (*C. duthieae*, *C. sclateri*); State 2 - bulbous with a distinct and slightly elevated articular surface (*C. asiatica*); State 3 - bulbous with a high medial articular surface, but not robust (*C. arendsi*); and State 4 - robust and bulbous with a high medial articular surface (*Amblysomus*).

9.2.4.3. Malleus morphology

Forster-Cooper (1928:278) first showed that malleus morphology in chrysochlorids can be categorized as either: hypertrophied and "pea-shaped"; elongated and "pear-shaped"; or "normal". He did not, however, accept this as evidence for generic distinction since "these three types are not absolute, in that there are forms transitional both in size and shape from the small ossicles to the large pea and pear-shapes respectively". Roux (1947) and Simonetta (1956, 1957), on the other hand, demonstrated that the shape and development of the malleus affects the morphology of the whole temporal region in the skull. They therefore argued that the unusual middle ear characteristics of some chrysochlorids must be considered taxonomically important.

Lundholm (1955) used malleus morphology as a benchmark for describing the subgenera *Carpitalpa* and *Kilimatalpa* in *Chlorotalpa*. Similarly, Simonetta (1968) placed prime emphasis on this character, and argued that even within those species with "normal" mallei, the size and development of the epitympanic recess (which houses the head of the malleus) varies conspicuously. He argued that chrysochlorids should be classified into three subfamilies: Amblysominae - malleus "normal" and epitympanic recess absent; Chrysochlorinae - malleus enlarged to varying degrees so that the epitympanic recess is either large and visible as a temporal bulla (*Chrysochloris*), or large but not showing conspicuously as a temporal bulla (*Carpitalpa*), or small and not visible as a temporal bullae (*Chlorotalpa*); and Eremitalpinae - malleus spherical so that the epitympanic recess is enormous but entirely concealed within the braincase.

This classification is not satisfactory, for several reasons. First, Simonetta's (1968) account of epitympanic recess variation was somewhat vague. In the absence of accurate descriptions or diagrams, it is difficult to either identify or objectively assess the relative size and development of the epitympanic recess in the various species. Second, variation in malleus and epitympanic recess morphology, both within and between species, has not been adequately studied since it is almost impossible to examine these characters in undamaged skulls. Simonetta's (1968) classification was derived after studying only relatively few specimens, and while he claimed that the epitympanic recess is clearly visible through the foramen magnum, this allows at best only a cursory examination. While X-ray's allow one to indirectly visualize the development of both the recess and the malleus, this technique is too expensive to use for large numbers of specimens. Since museums generally do not permit their material to be deliberately damaged, only crania that have been accidentally damaged in the past can be used, with the result that sample sizes are too small to accurately gauge the degree of intra-specific or even inter-specific variation. And third, Simonetta (1968) classified *Eremitalpa* and *Chrysospalax* together in the same family on the grounds that both have "spherical" mallei, notwithstanding the many morphological differences which negate the prospect that these genera are closely related, and despite the fact that the malleus in *Eremitalpa* is intermediate between the "pea" and "pear" shapes (Forster-Cooper 1928).

The systematic importance of middle ear morphology in chrysochlorids will be established only once the functional role played by the unusual auditory ossicles of some species is better understood. Previous authors presumed that the unusual auditory morphology of golden moles is related to prey detection by hearing, a sense thought to be particularly well-developed in chrysochlorids owing to their blindness (Forster-Cooper 1928; Roberts 1951). However, this functional relationship has not been unequivocally demonstrated. In collaboration with Dr. E. Sarmiento[1], I thus initiated a study on the functional auditory anatomy of golden moles, results of which are detailed in publications by two post-graduate students (O'Brien 1991; Von Mayer 1992; Von Mayer *et al.* 1995).

This study showed that the middle ear in chrysochlorids is generally specialized for detecting low-frequency sounds, and that middle ear specializations are probably adaptations to life in the subterrestrial environment where high frequency sounds are markedly attenuated along burrow walls. Inter-specific variation in total ossicular mass varies markedly between and within species, and is due mainly to variation in the size of the malleus (Table 9.5). The ratio of incus:malleus mass also varies considerably on an inter-specific basis, but is relatively constant within species (as indicated by low standard deviations). Based on these data, it appears that malleus size is inversely

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[1] Dr. E. Sarmiento, Department of General Anatomy, University of the Witwatersrand, P. O. Wits, 2050

Table 9.5

Summary of middle ear characteristics in 11 chrysochlorid species, based on data in Forster-Cooper (1928), and Von Mayer *et al.* (1995). Mass and ratios are given as arithmetic means ± one standard deviation. Sample sizes are indicated in parentheses. Slashes indicate a lack of data for a species. $\bar{x}$ = group mean; *se* = standard error.

Species	Malleus appearance	Mean ossicular mass (mg)	Malleus mass (% of total)	Incus:Malleus (mg) (X100)	Malleus:Incus Arm Ratio	Footplate ratio
Amblysomus hottentotus	"normal"	1,87±0,13(5)	47,5	104,9±16,0(5)	1,05±0,11(5)	13,61:1(1)
Amblysomus corriae	"normal"	1,90±0,16(4)	51,6	86,8±9,6(4)	1,07±0,11(3)	15,69:1(1)
Amblysomus gunningi	/	3,67(1)	57,3	71,7(1)	/	/
Calcochloris obtusirostris	"normal"	1,78±0,20(2)	55,5	75,4±0,2(2)	1,08±0,07(2)	12,66:1(1)
Group $\bar{x}\pm 1se$	------	**2,30±0,91**	**52,9±4,4**	**84,7±14,9**	**1,07±0,02**	**13,98±1,5**
Chlorotalpa sclateri	"small pear"	4,23±0,74(5)	75,4	29,0±4,9(5)	1,04±0,12(8)	7,93-8,46:1(2)
Chlorotalpa duthieae	"small pear"	4,46±0,68(4)	74,9	29,4±7,6(4)	1,07±0,04(3)	7,43-9,66:1(2)
Chlorotalpa arendsi	/	4,29±0,01(2)	/	13,0±0,1(2)	/	/
Group $\bar{x}\pm 1se$	------	4,33±0,12	75,2±0,4	23,8±9,4	1,06±0,02	8,37±0,96
Chrysochloris asiatica	"long pear"	18,56±10,67(10)	92,4	6,9±1,6(10)	0,78±0,75(7)	4,75-6,23:1(2)
Chrysospalax trevelyani	"large pea"	148,67±16,89(2)	92,5	7,3±0,5(4)	/	/
Chrysospalax villosus	"large pea"	142,67±54,77(2)	92,8	7,2±0,6(2)	0,68±0,003(2)	4,36:1(1)
Eremitalpa granti	"round pear"	46,64±15,55(4)	96,8	2,5±0,5(4)	0,65(1)	/

correlated with both malleus:incus lever arm ratios ($y = -0{,}715x + 1{,}47$; $p = 0{,}03$), and tympanic membrane:stapes footplate ratios ($y = -0.22x + 25{,}27$; $p = 0{,}02$). Among mammals, the tympanic membrane:stapes footplate ratio is high in low frequency hearers, whereas high incudomallear ratios are associated with low frequency detection, and *vice-versa* (Webster 1961). This suggests that the enlarged mallei found in some chrysochlorid species are adaptations for detecting higher frequencies, a possibility supported by the trend by taxa with the largest mallei (*Eremitalpa* and *Chrysospalax*) to forage largely above ground (Hickman 1990), which requires a greater sensitivity to higher frequencies (Von Mayer 1992). The unusual auditory morphologies found in some species are, therefore, probably adaptations for selecting different frequency ranges associated with divergent foraging styles.

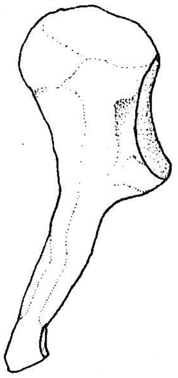
Given that middle ear morphology is relatively constant in other mammals regardless of differences in size, habit, environment and physiology (Fleischer 1978), and that the skull is greatly modified in those chrysochlorid taxa with enlarged mallei, middle ear characters in golden moles must be regarded as taxonomically important. But, another important finding of this study is that similarities in epitympanic recess morphology in *Eremitalpa* and *Chrysospalax* are probably parallelisms (Von Mayer *et al.* 1995). In *Eremitalpa*, the epitympanic recess is situated well medial to the glenoid joint and has a large contribution from the alisphenoid, whereas in *Chrysospalax* the recess surrounds the glenoid and receives a large contribution from the mastoid. Middle ear structure in these genera is thus dissimilar, despite their superficial resemblance in malleus morphology. Categorizing malleus morphology in golden moles as "normal", "pear-shaped" or "pea-shaped" is, therefore, too simplistic. Also, apparent resemblances in middle ear morphology may be the result of parallel evolution rather than common ancestry.

Variation in the malleus morphology of the species examined here is shown in Fig. 9.1. In most of the *Amblysomus* species, *C. obtusirostris* and *C. leucorhina* the malleus is small and unspecialized. The incudomallear facet is relatively large, and located mediolaterally so that most of the mass of the malleus is distal to the articulation. The malleus of *C. leucorhina* is not hypertrophied as in the other *Chlorotalpa* species, and has a more elongated shape, while that of *A. gunningi* is

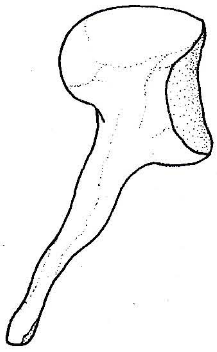
Figure 9.1. Morphology of the malleus in 14 chrysochlorid species (magnification = 16X).

Calcochloris

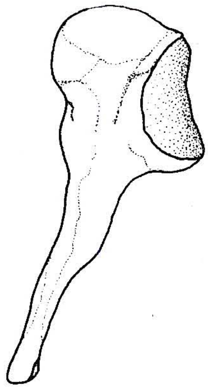
Amblysomus



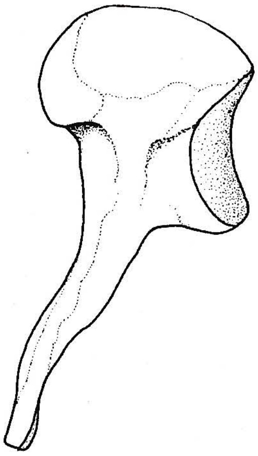
C. obtusirostris



A. julianae

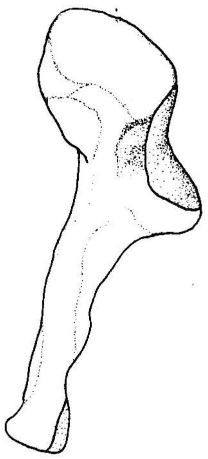


A. hottentotus

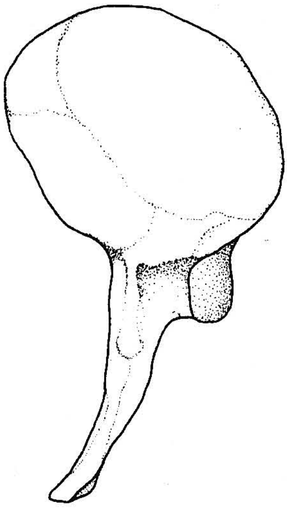


A. gunningi

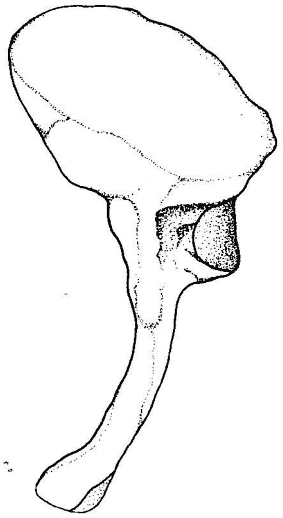
Chlorotalpa



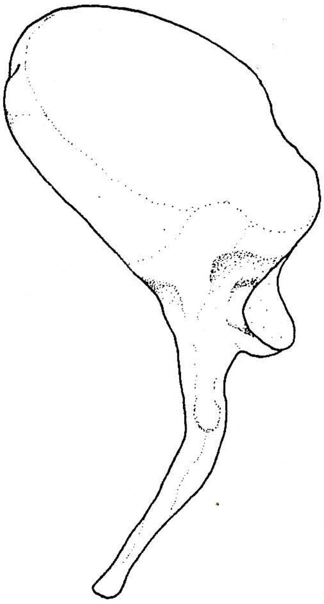
C. leucorhina



C. sclateri

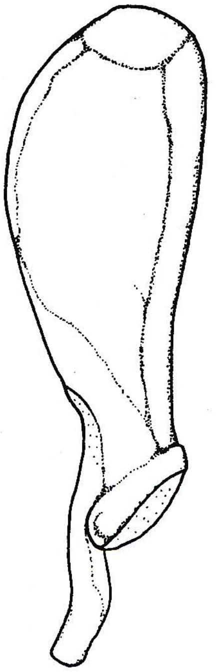


C. duthieae

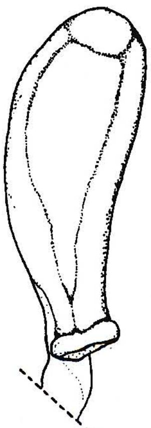


C. arendsi

Chrysochloris



C. asiatica



C. stuhlmanni

peculiar in that the caput is more inflated than in other *Amblysomus*. The incudomallear ratio in all of these species, however, exceeds 70% (Table 9.5), so they were afforded the same character state (State 0). In *Chlorotalpa* (excluding *C. leucorhina*) the caput of the malleus is expanded to varying degrees. The incudomallear facet is relatively smaller, and is located superoinferiorly and mediolaterally, so that the majority of the mass of the malleus is diagonal to the articulation. In *C. sclateri* and *C. duthieae*, the head of the malleus is moderately expanded, so that the incudomallear ratio is reduced to approximately 29% (State 1), while in *C. arendsi* the caput is markedly inflated in a distal plane, so that the incudomallear ratio is even lower (13%; State 2).

The malleus of *Chrysochloris asiatica* is club-shaped ("long pear" *sensu* Forster-Cooper 1928), and greatly inflated, so that the incudomallear ratio is extremely low (6,9±1,6%). The incudomallear facet is approximately the same size as in *Chlorotalpa*, but is located inferiorly at the junction of the caput and neck. Most of the mass of the malleus is thus superior to the articulation. Although it was not possible to accurately figure or measure the malleus of *C. stuhlmanni*, I traced two specimens (BM31.11.1.3 and KMT 37096) with dislocated, partially damaged mallei which appear to be expanded even more than in *C. arendsi*, and have an elongate shape as in *Chrysochloris asiatica*. The incudomallear facet is also located basally, so that the majority of the mass of the malleus is superior to the articulation. However, the malleus in *C. stuhlmanni* is considerably smaller than in *C. asiatica*, while the epitympanic recess is visible on the external surface of the skull as only a small sub-temporal bulla (as in *C. arendsi*), in contrast to the prominent temporal bulla observed in *C. asiatica*. These differences appear to be constant throughout the ranges of both species, and are not simply allometric, since *C. stuhlmanni* is larger than *C. asiatica* in overall size, but has a markedly smaller malleus and temporal bulla. For coding purposes, the malleus of *C. stuhlmanni* was, therefore, regarded as intermediate between that of *C. arendsi* and *C. asiatica* (Simonetta 1968), and was scored as State 3, while that of the latter was scored as State 4.

9.2.4.4. Guard hair morphology

Based on a pilot microscopy study of guard hair cross-sectional shapes and cuticular scale patterns in golden moles, Tonkin (1984) constructed a tentative key for the Chrysochloridae, but warned that further study was necessary to assess individual and geographic variation within species. Timms (1985) subsequently reported that cuticular scale patterns vary considerably between different parts of the body in *A. hottentotus*, and concluded that only cross-sectional shape has any taxonomic value. As guard hair cross-sectional shape is similar (concavo-convex) in all of the species except *C. obtusirostris* (oblong; Tonkin 1984), this character is autapomorphic, and conveys no information about inter-specific relationships. Guard hair morphology was not, therefore, included in analyses.

9.2.4.5 Chromosomal data

Seven chromosomes differ in morphology between species (Section 4.3). However, the submetacentric morphology of chromosome 1 in *C. obtusirostris*, and chromosome 7 in *C. sclateri*, were autapomorphic among members of the ingroup, and was thus not considered further. Similarly, the morphology of chromosome 3 was excluded since this chromosome is submetacentric/subtelocentric in all OTUs except *C. obtusirostris*, while the morphology of chromosome 14 was rejected because this chromosome is apparently absent in *C. obtusirostris*.

Only three chromosomal characters were thus included in phylogenetic analyses. The morphology of chromosome 11 was scored as either subtelocentric (State 0), submetacentric (State 1), or metacentric (State 2), while that of chromosome 15 was scored as either metacentric (State 0) or acrocentric (State 1). The number of nucleolar organizer regions, which is probably the most important chromosomal character from a systematic perspective, was scored as: State 0 - two NORs present, apparently on the long arm of chromosome 12 and the short arm of chromosome 13; State 1 - two NORs present, apparently on the short arms of chromosomes 12 and 13; State 2 - two NORs present, on the short arms of chromosomes 8 and 11; and State 3 - three NORs present, apparently on the short arms of chromosomes 8, 9 and 11.

9.3 RESULTS AND DISCUSSION

9.3.1 Phenetic analyses

9.3.1.1. Univariate analyses

Summary statistics and the results of one-way analyses of variance for 14 measurements in the 13 species examined are given in Tables 9.6 and 9.7. In both sexes, all measurements differed significantly ($p < 0,001$) among the OTUs. The order of ranked means was similar in most measurements of both sexes, and reflected a regular pattern of variation whereby two groups of OTUs that differed significantly in size were evident.

Size group I included five *Amblysomus* species (*A. corriae* [AC], *A. hottentotus* [AH], *A. gunningi* [AG], *A. septentrionalis* [AS], *Amblysomus Species A* [AA]), *C. arendsi* [CA] and *C. stuhlmanni* [CST]. These OTUs were generally larger in most measurements in both sexes, and significantly larger than the other OTUs in greatest skull length (GSL), height (GSH), palatal length (PAL) and mandible length (MDL). Within this group, *C. stuhlmanni* [CST] was the smallest in overall size (as reflected by GSL, GSH and MDL), and was characterized by a significantly narrower palate (P@P) in both sexes, and smaller skull height (GSH) and mandible length (MDL) in females. *Amblysomus Species A* [AA] and *A. septentrionalis* [AS] were the largest in overall size, and differed significantly from the other OTUs in two measurements (MIO, APW) in both sexes, as well as post-palatal length (PPL) and coronoid process length (CPL) in males. Zygomatic breadth (ZMB) and mandible length (MDL) were significantly larger in *Amblysomus Species A* [AA] than in the other OTUs in this group. *C. arendsi* [CA], which was fourth largest in overall size, showed the smallest post-palatal length (PPL) in this size group. Despite being only third largest in overall size, *A. gunningi* [AG] had the widest and longest palate (P@P, PAL), but resembled *A. corriae* in having a relatively narrow rostrum (ARB).

Size Group II comprised six species (*C. duthieae* [CD], *C. sclateri* [CS], *C. leucorhina* [CL]; *A.julianae* [AJ], *A. marleyi* [AM]; *C. obtusirostris* [CO]) that were smaller in most measurements in both sexes. Within this phenon, most measurements (in particular GSL, GSH and MDL) showed broadly overlapping non-significant

Table 9.6

Summary statistics of one external (BCW) and 13 cranial measurements in 14 OTUs. OTU codes are those given in Table 9.1, and represent male samples for the following species (*n* = sample sizes in parentheses): AC - *Amblysomus corriae* (*n*=23); AG - *A. gunningi* (*n*=9); AH - *A.hottentotus* (*n*=132); AJ - *A. julianae* (*n*=6); AM - *A. marleyi* (*n*=4); AS - *A. septentrionalis* (*n*=16); AA - *Amblysomus Species A* (*n*=6); CA - *Chlorotalpa arendsi* (*n*=7); CD - *Chlorotalpa duthieae* (*n*=8); CL - *Chlorotalpa leucorhina* (*n*=6); CS - *Chlorotalpa sclateri* (*n*=23); CO - *Calcochloris obtusirostris* (*n*=16); CST - *Chrysochloris stuhlmanni* (*n*=7). ANOVA of OTU means resulted in highly significantly ($p < 0{,}001$) *F* statistics for all measurements. $\bar{x}$ = sample mean; *sd* = standard deviation. Vertical lines denote maximally non-significant subsets indicated by SNK multiple comparisons tests at 95% probability level.

Table 9.6

BCW

OTU	$\bar{x}\pm sd$	Range
CL	2,81±0,12	2,63-2,97
CO	3,05±0,16	2,64-3,46
CST	3,63±0,52	2,73-4,28
CD	3,67±0,16	3,50-3,96
CS	3,84±0,19	3,46-4,14
AJ	3,86±0,13	3,60-4,01
AM	4,25±0,01	4,12-4,37
CA	4,41±0,21	4,13-4,85
AG	4,74±0,14	4,54-4,94
AC	4,85±0,35	4,20-5,55
AH	5,52±0,42	4,45-6,57
AS	6,09±0,35	5,51-6,63
AA	6,86±0,25	6,49-7,19

ARB

OTU	$\bar{x}\pm sd$	Range
CS	4,40±0,28	3,81-4,78
CD	4,42±0,24	3,95-4,81
AM	4,56±0,09	4,47-4,71
AC	4,64±0,32	4,10-5,25
AJ	4,72±0,13	4,50-4,87
CST	4,90±0,42	4,36-5,69
CA	4,96±0,23	4,69-5,30
AG	5,01±0,19	4,70-5,30
CO	5,07±0,19	4,77-5,43
CL	5,11±0,21	4,78-5,39
AH	5,12±0,28	4,32-5,96
AS	5,16±0,25	4,75-5,60
AA	5,69±0,12	5,55-5,89

MIO

OTU	$\bar{x}\pm sd$	Range
AM	7,11±0,23	6,88-7,08
CD	7,15±0,25	6,79-7,56
CS	7,21±0,26	6,71-7,78
CO	7,33±0,28	6,83-7,77
AJ	7,44±0,21	7,20-7,79
CL	7,65±0,20	7,42-8,05
CA	7,92±0,31	7,49-8,45
AC	8,06±0,23	7,75-8,51
CST	8,22±0,19	7,90-8,51
AG	8,22±0,36	7,61-8,74
AH	8,40±0,43	7,52-9,76
AS	9,17±0,35	8,48-9,69
AA	9,79±0,35	9,57-10,56

ZMB

OTU	$\bar{x}\pm sd$	Range
CD	14,96±0,49	14,38-15,79
CS	15,00±0,52	14,01-15,93
AM	15,32±0,51	14,75-16,00
AC	15,74±0,49	14,90-16,85
CL	15,83±0,26	15,36-16,17
AJ	16,02±0,45	15,44-16,65
CO	16,14±0,46	15,37-16,80
CST	16,17±0,80	14,73-17,22
AH	16,97±0,81	15,30-19,36
CA	17,04±0,57	16,36-18,15
AG	17,45±0,66	16,12-18,20
AS	17,95±0,63	16,81-19,48
AA	19,34±0,55	18,83-20,43

IOW

OTU	$\bar{x}\pm sd$	Range
CS	6,84±0,27	6,26-7,45
AM	6,92±0,13	6,77-7,12
CD	6,99±0,27	6,59-7,37
AC	7,06±0,29	6,66-7,54
CL	7,08±0,21	6,65-7,33
CO	7,14±0,36	6,69-7,79
CST	7,43±0,37	6,80-7,80
AJ	7,46±0,16	7,17-7,63
AH	7,51±0,35	6,64-8,26
CA	7,64±0,39	7,33-8,47
AG	7,90±0,29	7,56-8,34
AS	7,92±0,28	7,40-8,44
AA	8,34±0,24	7,96-8,67

GSL

OTU	$\bar{x}\pm sd$	Range
CL	21,82±0,56	21,22-22,83
CO	22,76±1,01	21,20-24,15
CS	22,96±0,87	21,12-24,43
AJ	23,35±0,25	22,88-23,62
CD	23,80±0,56	22,92-24,47
AM	23,94±0,60	23,06-24,58
CST	26,87±1,30	24,81-28,91
AC	27,08±0,88	25,34-28,88
AH	27,17±1,07	24,95-30,84
CA	27,76±0,70	26,84-28,97
AG	28,49±0,64	27,13-29,33
AS	28,99±0,84	27,22-30,48
AA	30,84±0,63	29,92-31,96

GSH

OTU	$\bar{x}\pm sd$	Range
CL	10,55±0,29	10,13-11,07
CO	10,96±0,17	10,58-11,25
CS	11,21±0,36	10,36-11,70
CD	11,33±0,21	10,92-11,71
AJ	11,50±0,10	11,39-11,69
AM	11,63±0,30	11,25-12,09
CST	12,20±0,64	11,37-13,19
AC	12,56±0,43	11,75-13,42
CA	12,92±0,35	12,33-13,48
AH	13,21±0,53	11,83-14,75
AG	13,33±0,32	12,76-13,83
AS	13,94±0,37	13,00-14,72
AA	14,73±0,39	14,26-15,26

P@P

OTU	$\bar{x}\pm sd$	Range
CL	6,64±0,36	6,09-7,20
AM	6,67±0,23	6,34-6,93
CS	6,79±0,32	6,20-7,61
AC	6,89±0,32	6,38-7,42
CD	6,92±0,24	6,60-7,47
CST	7,19±0,25	6,82-7,54
AJ	7,31±0,18	7,03-7,58
AH	7,60±0,36	6,46-8,75
AS	7,79±0,39	6,95-8,30
CA	7,88±0,18	7,64-8,24
CO	8,16±0,27	7,68-8,87
AA	8,18±0,22	7,80-8,52
AG	8,31±0,27	7,96-8,73

PAL

OTU	$\bar{x}\pm sd$	Range
CL	10,74±0,49	9,93-11,26
AJ	11,73±0,21	11,38-12,08
AM	11,81±0,52	11,07-12,41
CS	11,91±0,66	10,52-12,87
CO	11,93±0,61	10,88-12,86
CD	12,43±0,49	11,74-13,35
AH	13,55±0,65	11,70-15,31
AC	13,55±0,57	12,28-14,39
CST	13,61±0,86	12,48-14,79
CA	14,42±0,56	13,93-15,64
AS	14,57±0,52	13,24-15,62
AG	14,99±0,42	14,02-15,44
AA	15,62±0,42	15,06-16,16

PPL

OTU	$\bar{x}\pm sd$	Range
CS	7,20±0,25	6,75-7,79
CO	7,38±0,38	6,82-8,20
CD	7,48±0,26	7,18-8,04
AJ	7,56±0,18	7,30-7,76
AM	7,80±0,26	7,48-8,16
CL	7,85±0,41	7,21-8,26
CA	8,43±0,32	7,81-8,92
AC	8,78±0,27	8,40-10,10
CST	8,82±0,53	8,32-9,34
AH	8,83±0,41	7,88-9,69
AG	8,93±0,31	7,82-9,76
AS	9,16±0,31	8,51-9,34
AA	9,72±0,27	9,33-10,00

BBW

OTU	$\bar{x}\pm sd$	Range
CS	10,14±0,32	9,52-10,83
CL	10,54±0,47	10,10-11,46
CD	10,59±0,36	10,00-11,02
AJ	10,67±0,35	10,20-11,23
AM	10,84±0,49	10,23-11,56
CO	10,84±0,58	9,91-11,87
AC	11,25±0,40	10,56-11,98
CST	11,39±0,80	10,31-12,46
CA	11,89±0,54	11,12-12,68
AH	12,11±0,69	10,52-13,90
AG	12,27±0,51	11,44-13,19
AS	12,57±0,57	11,24-13,28
AA	13,29±0,47	12,81-14,07

CPL

OTU	$\bar{x}\pm sd$	Range
CL	5,79±0,24	5,48-6,11
CS	5,81±0,25	5,33-6,23
CD	5,85±0,17	5,55-6,15
AJ	6,05±0,12	5,83-6,17
CO	6,17±0,25	5,71-6,55
CST	6,58±0,50	5,79-7,36
AM	6,85±0,29	6,45-7,27
CA	7,00±0,35	6,52-7,39
AC	7,21±0,43	6,58-8,35
AH	7,32±0,43	6,18-8,60
AG	7,44±0,35	6,85-8,13
AS	7,92±0,40	6,93-8,48
AA	8,28±0,17	8,04-8,51

APW

OTU	$\bar{x}\pm sd$	Range
AJ	3,45±0,13	3,23-3,62
CO	3,51±0,21	3,18-3,92
CL	3,53±0,26	3,10-3,91
CS	3,53±0,20	3,15-3,92
CD	3,60±0,11	3,35-3,71
AM	4,27±0,21	4,09-4,59
CA	4,30±0,29	3,90-4,69
CST	4,36±0,44	3,58-5,12
AG	4,52±0,21	4,16-4,83
AC	4,52±0,36	3,94-5,27
AH	4,62±0,47	3,92-5,72
AS	5,27±0,40	4,60-5,95
AA	5,38±0,24	5,12-5,75

MDL

OTU	$\bar{x}\pm sd$	Range
CL	13,60±0,38	13,11-14,21
CS	14,04±0,56	12,76-15,07
AJ	14,55±0,24	14,14-14,97
CD	12,64±0,36	14,15-15,14
CO	14,74±0,68	13,78-15,82
AM	15,20±0,55	14,39-15,72
CST	16,04±0,92	14,60-17,21
AC	16,59±0,70	15,22-18,01
AH	17,06±0,71	15,51-19,55
CA	17,25±0,70	16,41-18,40
AG	17,73±0,50	16,66-18,57
AS	18,06±0,61	16,83-18,92
AA	19,37±0,38	18,96-19,95

Table 9.7

Summary statistics of one external (BCW) and 13 cranial measurements in 14 OTUs. OTU codes are those given in Table 9.1, and represent female samples for the following species (n = sample sizes in parentheses): AC - *Amblysomus corriae* ($n=22$): AG - *A. gunningi* ($n=7$); AH - *A.hottentotus* ($n=102$); AJ - *A. julianae* ($n=8$); AM - *A. marleyi* ($n=7$); AS - *A. septentrionalis* ($n=25$); AA - *Amblysomus Species A* ($n=12$); CA - *Chlorotalpa arendsi* ($n=6$); CD - *Chlorotalpa duthieae* ($n=10$); CL - *Chlorotalpa leucorhina* ($n=4$); CS - *Chlorotalpa sclateri* ($n=8$); CO - *Calcochloris obtusirostris* ($n=15$); CST - *Chrysochloris stuhlmanni* ($n=6$). ANOVA of OTU means resulted in highly significantly ($p < 0{,}001$) F statistics for all measurements. $\bar{x}$ = sample mean; sd = standard deviation. Vertical lines denote maximally non-significant subsets indicated by SNK multiple comparisons tests at the 95% probability level.

Table 9.7

BCW

OTU	$\bar{x}\pm sd$	Range
CL	2,71±0,09	2,63-2,81
CO	2,89±0,18	2,51-3,19
CST	3,16±0,38	2,73-3,41
CD	3,51±0,18	3,25-3,74
AJ	3,81±0,23	3,64-4,30
AM	3,91±0,17	3,70-4,20
CS	3,97±0,22	3,95-4,29
CA	4,29±0,31	4,00-4,89
AG	4,58±0,24	4,31-5,01
AC	5,02±0,36	4,39-5,94
AH	5,22±0,40	4,27-6,58
AS	5,58±0,35	4,99-6,31
AA	5,88±0,27	5,26-6,19

ARB

OTU	$\bar{x}\pm sd$	Range
CD	4,20±0,14	4,03-4,55
AM	4,26±0,22	3,87-4,51
AJ	4,39±0,16	4,14-4,55
CST	4,57±0,29	4,36-5,13
CS	4,60±0,29	3,99-4,97
AC	4,70±0,24	4,29-5,13
AG	4,73±0,15	4,59-5,00
CL	4,89±0,21	4,64-5,12
CO	4,90±0,20	4,52-5,29
AH	4,91±0,28	4,26-5,68
CA	4,95±0,14	4,71-5,13
AS	4,97±0,23	4,55-5,44
AA	5,15±0,22	4,75-5,55

MIO

OTU	$\bar{x}\pm sd$	Range
CD	6,88±0,26	6,65-7,40
AM	6,89±0,26	6,51-7,19
AJ	7,00±0,40	6,37-7,58
CO	7,06±0,23	6,62-7,47
CS	7,49±0,38	7,04-8,18
CL	7,69±0,31	7,42-8,12
CA	7,80±0,25	7,43-8,25
AG	7,88±0,20	7,63-8,28
CST	7,99±0,14	7,77-8,18
AC	8,21±0,37	7,51-8,83
AH	8,32±0,50	7,04-9,79
AS	8,97±0,31	8,47-9,56
AA	9,18±0,36	8,21-9,63

ZMB

OTU	$\bar{x}\pm sd$	Range
CD	14,27±0,44	13,69-15,20
AM	14,52±0,52	13,91-15,48
CO	15,34±0,67	13,88-16,76
AJ	15,38±0,50	14,69-16,19
CS	15,50±0,75	14,37-16,93
AC	15,67±0,49	14,90-16,90
CST	15,78±0,83	14,33-17,22
CL	16,04±0,62	15,29-16,78
AH	16,38±0,78	15,07-18,07
CA	16,56±0,50	15,79-17,18
AG	16,76±0,61	15,85-18,03
AS	17,12±0,67	16,09-18,95
AA	17,68±0,48	16,76-18,24

IOW

OTU	$\bar{x}\pm sd$	Range
AM	6,76±0,29	6,47-7,22
CO	6,77±0,33	5,88-7,27
CD	6,79±0,29	6,29-7,27
AC	6,99±0,25	6,52-7,63
CS	7,04±0,28	6,59-7,49
AJ	7,13±0,21	6,82-7,47
CST	7,13±0,27	6,80-7,57
CL	7,17±0,32	6,82-7,56
AH	7,32±0,36	6,51-8,68
CA	7,59±0,29	7,07-8,01
AS	7,65±0,24	7,16-8,10
AG	7,67±0,21	7,41-8,12
AA	7,93±0,31	7,25-8,34

GSL

OTU	$\bar{x}\pm sd$	Range
CO	21,44±1,02	18,98-23,60
CL	22,20±0,87	21,05-23,14
AJ	22,52±0,54	21,83-23,52
CD	22,82±0,51	22,02-23,91
AM	23,49±0,75	22,40-24,76
CS	24,22±1,32	22,38-26,70
CST	25,92±1,43	24,31-28,30
AH	26,53±1,17	24,25-29,91
AC	26,90±0,81	25,70-28,59
CA	27,09±1,12	25,28-28,59
AG	27,76±0,63	27,01-29,12
AS	28,18±1,05	26,19-29,95
AA	28,83±0,83	27,21-29,67

GSH

OTU	$\bar{x}\pm sd$	Range
CL	10,44±0,37	9,89-10,68
CO	10,58±0,38	9,61-11,34
CD	10,91±0,29	10,59-11,63
AJ	11,16±0,20	10,76-11,45
AM	11,30±0,34	10,67-11,70
CST	11,70±0,75	11,18-13,19
CS	11,82±0,53	11,29-12,76
AC	12,63±0,43	12,02-13,76
CA	12,78±0,30	12,46-13,38
AH	12,85±0,60	11,52-14,56
AG	12,99±0,29	12,60-13,49
AS	13,40±0,38	12,79-14,43
AA	13,74±0,26	13,09-14,08

P@P

OTU	$\bar{x}\pm sd$	Range
AM	6,67±0,38	6,10-7,20
CL	6,71±0,33	6,45-7,20
CD	6,76±0,25	6,19-7,27
CST	6,93±0,31	6,54-7,47
AC	7,08±0,21	6,59-7,47
CS	7,14±0,38	6,62-7,70
AJ	7,20±0,10	7,01-7,31
AH	7,40±0,34	6,29-8,42
AS	7,57±0,30	6,67-8,21
CO	7,72±0,50	6,62-8,43
CA	7,74±0,28	7,35-8,23
AA	7,83±0,31	7,31-8,27
AG	8,06±0,19	7,66-8,32

PAL

OTU	$\bar{x}\pm sd$	Range
CL	10,89±0,45	10,30-11,38
CO	11,22±0,69	9,68-12,64
AJ	11,24±0,33	10,64-11,71
AM	11,50±0,45	10,78-12,25
CD	11,85±0,29	11,46-12,47
CS	12,79±0,77	11,86-14,27
CST	13,14±0,96	12,08-14,74
AH	13,20±0,69	11,94-15,25
AC	13,45±0,58	12,15-14,34
AS	14,09±0,60	12,86-14,91
CA	14,16±0,69	13,12-15,17
AA	14,34±0,51	13,04-14,98
AG	14,49±0,32	14,00-14,92

PPL

OTU	$\bar{x}\pm sd$	Range
CO	6,94±0,21	6,52-7,27
CD	7,04±0,25	6,74-7,51
AJ	7,34±0,24	6,99-7,71
CS	7,48±0,39	6,99-8,29
CL	7,88±0,12	7,74-8,10
AM	7,91±0,24	7,48-8,27
CA	8,36±0,29	7,93-8,77
CST	8,41±0,38	7,88 8,81
AH	8,61±0,43	7,59-9,65
AG	8,72±0,22	8,51-9,12
AC	8,75±0,28	8,35-9,37
AS	8,86±0,33	8,07-9,39
AA	9,23±0,36	8,69-9,61

BBW

OTU	$\bar{x}\pm sd$	Range
CD	10,02±0,37	9,41-10,61
CO	10,14±0,43	9,36-11,12
AJ	10,48±0,22	10,10-10,84
AM	10,53±0,41	10,05-11,33
CS	10,62±0,48	10,02-11,48
CL	10,94±0,58	10,27-11,46
CST	11,11±0,82	10,31-12,46
AC	11,39±0,45	10,65-12,45
CA	11,42±0,26	11,04-11,87
AH	11,63±0,60	10,46-13,19
AS	11,99±0,56	10,84-12,95
AG	12,06±0,37	11,70-12,76
AA	12,14±0,71	10,95-13,23

CPL

OTU	$\bar{x}\pm sd$	Range
CD	5,54±0,27	5,24-6,13
CO	5,70±0,37	4,75-6,53
AJ	5,75±0,16	5,48-6,01
CL	5,82±0,43	5,21-6,20
CS	6,13±0,33	5,76-6,66
CST	6,31±0,48	5,79-7,03
AM	6,42±0,30	5,87-6,89
CA	6,86±0,36	6,22-7,25
AH	7,05±0,44	5,91-8,11
AG	7,08±0,31	6,68-7,64
AC	7,27±0,28	6,87-7,80
AS	7,49±0,38	6,50-8,33
AA	7,65±0,18	7,33-7,96

APW

OTU	$\bar{x}\pm sd$	Range
CO	3,16±0,27	2,70-3,80
AJ	3,20±0,12	2,99-3,35
CD	3,34±0,19	3,08-3,78
CL	3,41±0,50	2,97-4,08
CS	3,72±0,25	3,41-4,07
AM	4,01±0,27	3,68-4,51
CA	4,04±0,25	3,70-4,35
CST	4,11±0,41	3,58-4,51
AG	4,21±0,24	3,95-4,73
AH	4,44±0,41	3,28-5,44
AC	4,46±0,25	4,00-4,88
AA	4,85±0,21	4,35-5,14
AS	4,85±0,33	4,25-5,43

MDL

OTU	$\bar{x}\pm sd$	Range
CO	13,72±0,73	11,84-14,73
AJ	13,93±0,27	13,52-14,40
CD	13,94±0,39	13,46-14,70
CL	14,02±0,55	13,21-14,44
AM	14,70±0,54	13,88-15,65
CS	14,85±0,91	13,73-16,38
CST	15,22±0,83	14,39-16,62
AH	16,69±0,82	14,68-18,80
AC	16,72±0,62	15,83-18,08
CA	16,90±0,56	16,02-17,72
AG	17,14±0,31	16,84-17,67
AS	17,49±0,73	15,91-18,69
AA	18,17±0,40	17,47-18,87

subsets, indicating that size variation is gradual rather than discontinuous. *C. leucorhina* [CL] and *C. obtusirostris* [CO] were generally smaller than the other four OTUs, and had significantly narrower claws (BCW), but relatively wider rostra (ARB). These species differed significantly from each other in palatal width (P@P), which was significantly wider in *C. obtusirostris* [CO] than in any of the other five OTUs. Palatal length (PAL) was significantly smaller in male *C. leucorhina* [CL], but not in females, which may be an artefact of the small samples available (*n* = 6 and *n* = 4, respectively). Despite their similarity in overall size, *A. julianae* [AJ] and *A. marleyi* [AM] differed significantly in ascending process width (APW) and palatal width (P@P). The former OTU had relatively the widest palate (P@P) among OTUs in this size group, whereas *A. marleyi* tended to have the narrowest interorbital region (MIO).

9.3.2. Multivariate analyses

9.3.2.1. Discriminant functions analyses

Multiple discriminant functions analyses based on individuals representing the 13 OTUs, and a sample of *C. asiatica* that was included for exploratory purposes, resulted in an overall *a posteriori* classification of 92% for males, and 95% for females (Table 9.8). All OTUs except *A. septentrionalis* [AS] and *Amblysomus Species A* [AA] were characterized by high (>80%) accuracy of correct specimen assignment in both sexes, indicating that they are morphologically well differentiated from each other. Six OTUs [CO, CL, CAS, AM, AG, AJ] showed a 100% *a posteriori* classification in both sexes, and a further three OTUs (♂: [CST]; ♀: [CD], [AC]) showed 100% classification accuracy in either sex, indicating that these samples were particularly distinctive. Within each sex, most misidentifications involved specimens of the cryptic species traditionally included wholly (*A. septentrionalis* [AS], *Amblysomus Species A* [AA]) or partly (*A. corriae* [AC]) in *A. hottentotus* [AH], and to a lesser extent, specimens representing congeneric species within *Chlorotalpa*. Misclassifications to the incorrect *a priori* groups involved specimens of: *A. gunningi* [AG] and *C. arendsi* [CA] (both sexes): *C. stuhlmanni* [CST] and *A. hottentotus* [AH] (females only): or *C. sclateri* [CS] and *A. marleyi* [AM] (males only).

Table 9.8

A posteriori Geisser classification summary based on discriminant functions analyses of males and females representing 14 OTUs, showing the percentage assignment of specimens to the various species. Samples characterized by particularly high (> 95%) accuracy of specimen assignment to the correct *a priori* groups are shown in bold on the diagonal.

SEX	OTU	CO	CS	CD	CA	AC	AG	AJ	AH	AM	AS	AA	CL	CST	CAS
♂:	CO	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0
	CS	0	**96**	0	0	0	0	0	0	4	0	0	0	0	0
	CD	0	12	88	0	0	0	0	0	0	0	0	0	0	0
	CA	0	0	0	86	0	14	0	0	0	0	0	0	0	0
	AC	0	0	0	0	**96**	0	0	4	0	0	0	0	0	0
	AG	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0
	AJ	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0
	AH	0	0	0	0	2	0	0	94	0	4	0	0	0	0
	AM	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0
	AS	0	0	0	0	0	0	0	13	0	81	6	0	0	0
	AA	0	0	0	0	0	0	0	0	0	33	67	0	0	0
	CL	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0
	CST	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0
	CAS	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**
♀:	CO	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0
	CS	0	88	0	12	0	0	0	0	0	0	0	0	0	0
	CD	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0
	CA	0	0	0	83	0	17	0	0	0	0	0	0	0	0
	AC	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0
	AG	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0
	AJ	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0
	AH	0	0	0	0	0	0	0	**99**	0	1	0	0	0	0
	AM	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0
	AS	0	0	0	0	0	0	0	14	0	72	14	0	0	0
	AA	0	0	0	0	0	0	0	8	0	8	84	0	0	0
	CL	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0
	CST	0	0	0	0	0	0	0	14	0	0	0	0	86	0
	CAS	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**

In a scatterplot of the first two canonical variate axes (Fig. 9.2a), the 14 male OTUs grouped into four major phena (A-D) along CV I, primarily on the basis of size. This was borne out by cluster analyses of euclidean distances between group centroids (Fig. 9.3) separated the OTUs into two major size groups, identical to those discerned from univariate analyses: Size Group I - large to medium sized OTUs, with GSL $(\bar{x} \pm 1sd)$ exceeding 25mm (Phena A and B); and Size Group II - smaller sized OTUs, with GSL $(\bar{x} \pm 1sd)$ less than 25 mm (Phena C and D).

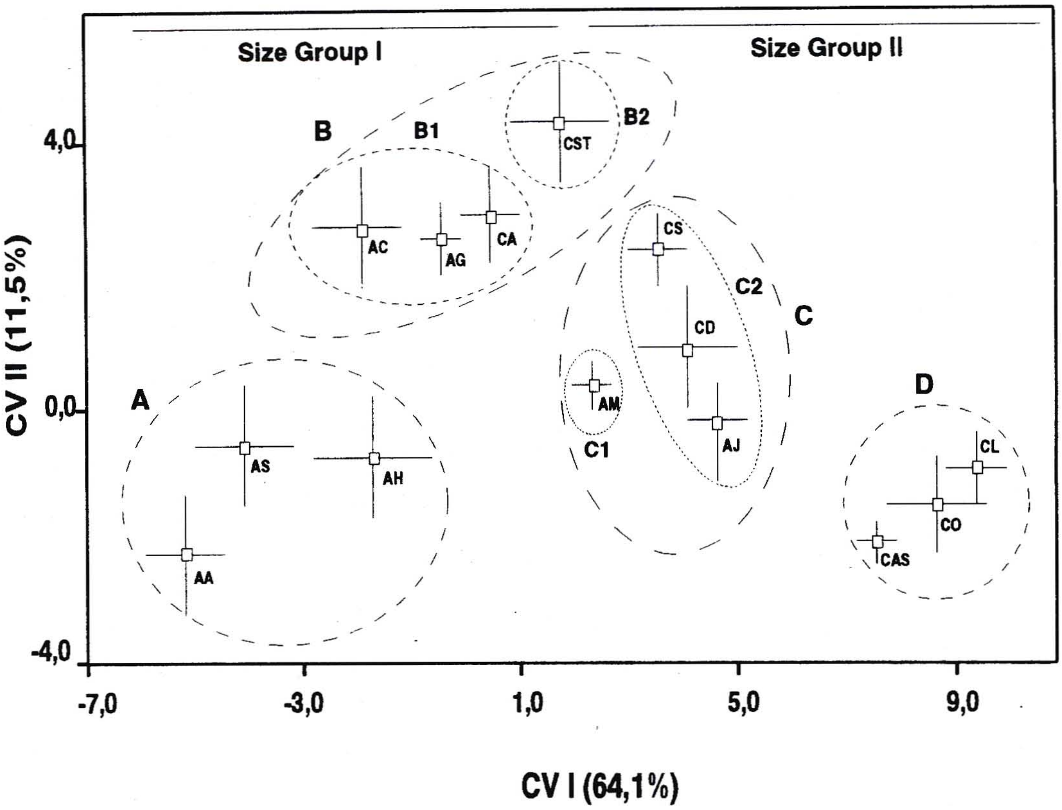
Phenon A, which plotted to the left along CV I, included the larger-sized *Amblysomus* species (*A. hottentotus* [AH], *A. septentrionalis* [AS], *Amblysomus Species A* [AA]). Phenon B, which was well separated from Phenon A along CV II, included the medium-sized species (*A. corriae* [AC], *A. gunningi* [AG]), *C. stuhlmanni* [CST] and *C. arendsi* [CA]). Within this phenon, *C. stuhlmanni* [CST] tended to plot apart from the other OTUs along both CV I and CV II (subphenon B2). Phenon C comprised four smaller-sized OTUs which separated into two subphena: subphenon C1 (only *A. marleyi* [AM]), which plotted to the left of others along CV I; and subphenon C2, (*A. julianae* [AJ], *C. sclateri* [CS] and *C. duthieae* [CD]), which tended to plot apart along CV II. Phenon D, which plotted well to the right of others, included three OTUs (*C. asiatica* [CAS], *C. obtusirostris* [CO] and *C. leucorhina* [CL]) that were generally smallest in overall size (Table 9.6). Multivariate analysis of variance indicated that differences between the group centroids of these OTUs were highly significant ($F_{(196,2418)} = 14,76$; $p < 0,001$).

Pairwise comparison of the first and third canonical variate axes in males revealed a similar pattern of separation, whereby Phena A, B, and the two subphena within Phenon C were discriminated along both axes. However, *A. corriae* [AC] grouped with Phenon A rather than Phenon B, and the OTUs in Phenon D separated into three subphena (D1-3) along CV III.

Scatterplots comparing the first three canonical variate axes in females (Fig. 9.4) were very similar to those of males, and multivariate analysis confirmed that differences between group centroids were highly significant ($F_{(182,1972)} = 15,39$; $p < 0,001$). But, while *A. corriae* [AC] associated with Phenon B along CV II in males, in females this OTU grouped in Phenon A in both scatterplots. Another

Figure 9.2. Pairwise comparison of the first and second (a), and first and third (b), canonical variate axes from a multiple discriminant functions analysis of male specimens representing 14 chrysochlorid species. See Table 9.1 for an explanation of OTU codes. OTU means are indicated by open rectangles, while bars indicate one standard error (±1*se*) of specimen scores along each axis. Dotted lines delimit the phena and subphena recognized, and boldfaced letters (A-D) the codes by which phena are referred to in the text.

a)


Size Group I
Size Group II
B
B1
B2
CST
AC
AG
CA
CS
C2
C
CD
AM
C1
AJ
A
AS
AH
AA
D
CL
CO
CAS
4,0
0,0
-4,0
-7,0
-3,0
1,0
5,0
9,0
CV II (11,5%)
CV I (64,1%)

b)

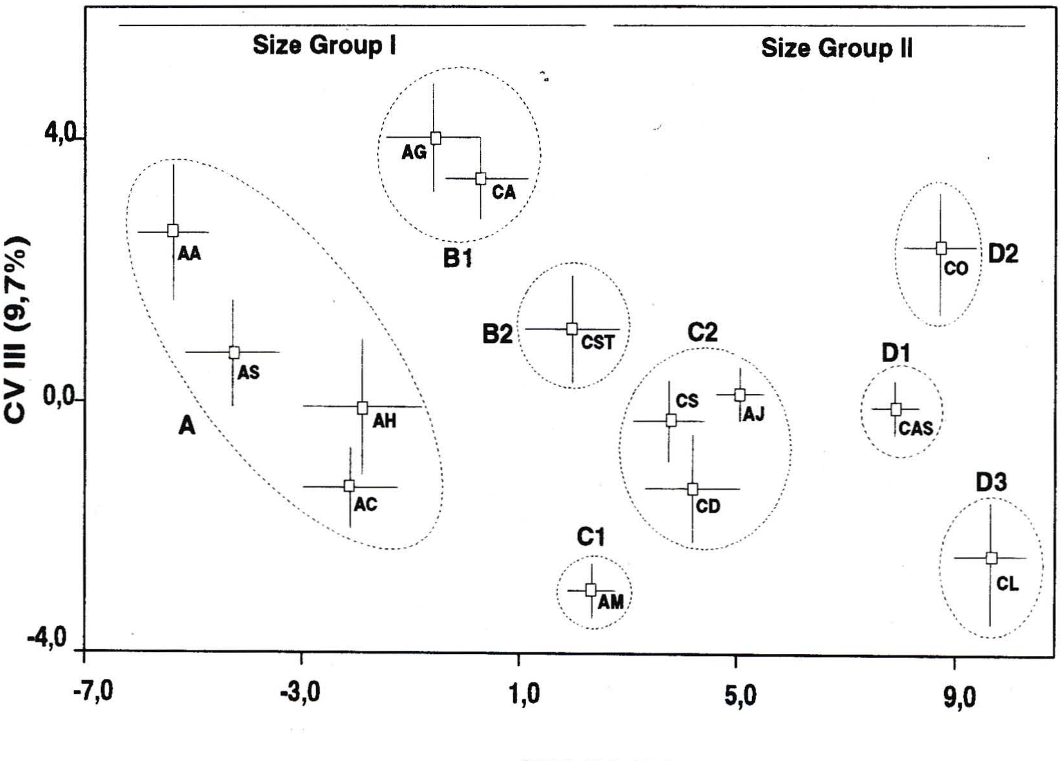
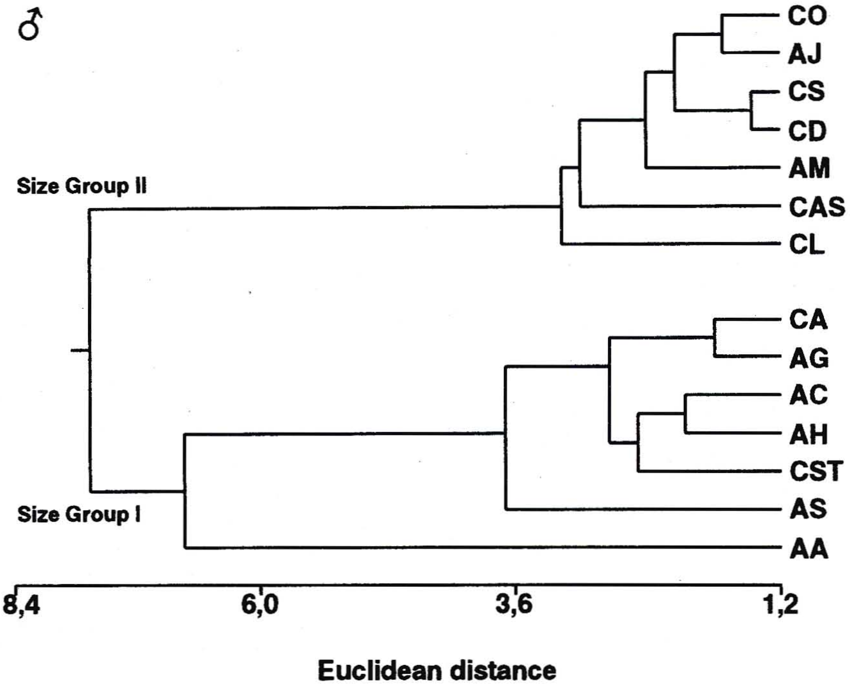

Size Group I
Size Group II
AG
CA
B1
AA
AS
AH
AC
A
B2
CST
C2
CS
AJ
CD
C1
AM
CO
D2
D1
CAS
D3
CL
4,0
0,0
-4,0
-7,0
-3,0
1,0
5,0
9,0
CV III (9,7%)
CV I (64,1%)

Figure 9.3. Phenograms based on UPGMA clustering of euclidean distances between OTU centroids from a discriminant functions analyses of craniometric data for male (co-phenetic correlation = 0,799) and female (co-phenetic correlation = 0,848) specimens representing 14 chrysochlorid species. See Table 9.1 for an explanation of OTU codes.


♂
Size Group II
Size Group I
CO
AJ
CS
CD
AM
CAS
CL
CA
AG
AC
AH
CST
AS
AA
8,4
6,0
3,6
1,2
Euclidean distance

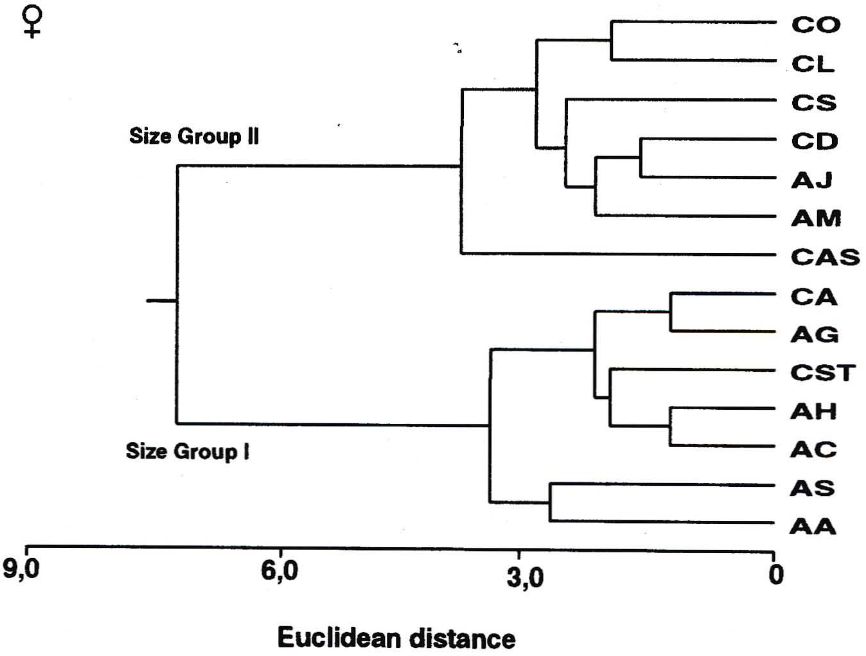
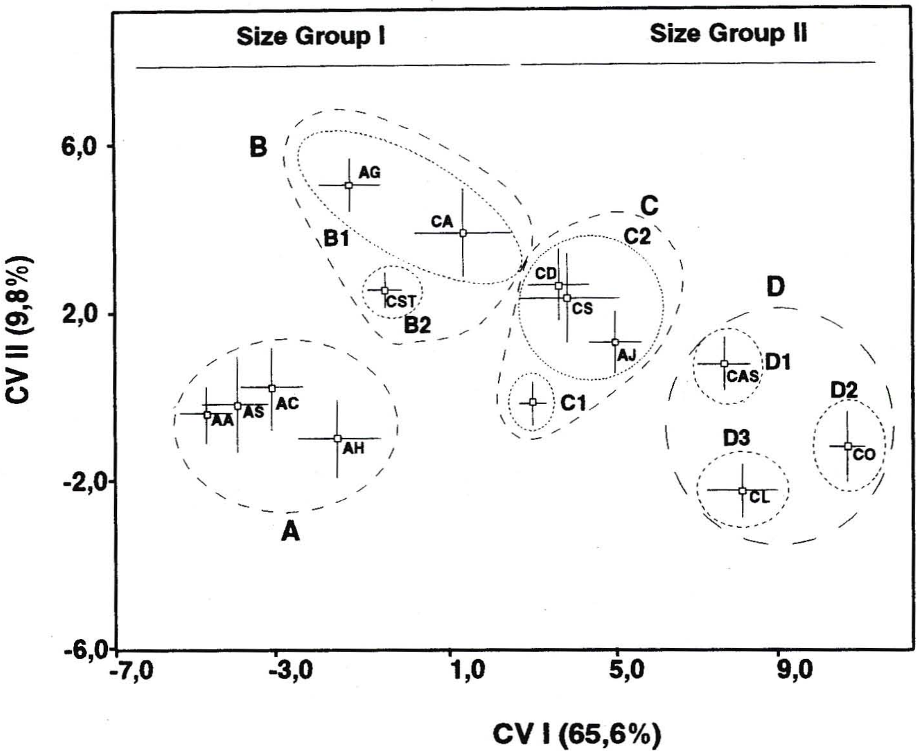
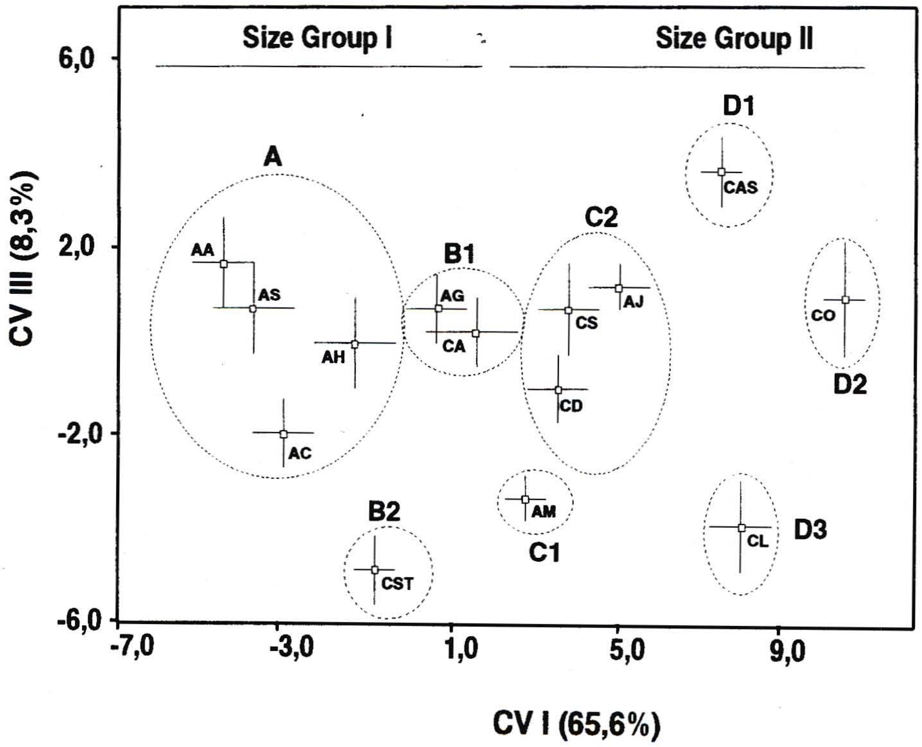

♀
Size Group II
Size Group I
CO
CL
CS
CD
AJ
AM
CAS
CA
AG
CST
AH
AC
AS
AA
9,0
6,0
3,0
0
Euclidean distance

Figure 9.4. Pairwise comparison of the first and second (a), and first and third (b), canonical variate axes from a multiple discriminant functions analysis of female specimens representing 14 chrysochlorid species. See Table 9.1 for an explanation of OTU codes. OTU means are indicated by open rectangles, while bars indicate one standard error (±1*se*) of specimen scores along each axis. Dotted lines delimit the phena and subphena recognized, and boldfaced letters (A-D) the codes by which phena are referred to in the text.

a)


Size Group I
Size Group II
6,0
2,0
-2,0
-6,0
-7,0
-3,0
1,0
5,0
9,0
CV II (9,8%)
CV I (65,6%)
B
B1
B2
AG
CA
CST
C
C2
C1
CD
CS
AJ
D
D1
D2
D3
CAS
CO
CL
A
AA
AS
AC
AH

b)


Size Group I
Size Group II
6,0
2,0
-2,0
-6,0
-7,0
-3,0
1,0
5,0
9,0
CV III (8,3%)
CV I (65,6%)
A
AA
AS
AH
AC
B1
AG
CA
B2
CST
C2
CS
AJ
CD
C1
AM
D1
CAS
D2
CO
D3
CL

difference involved *C. asiatica* [CAS], which plotted between subphena D2 and D3 along CV III in males, but well above these groups in females.

The minor differences between the scatterplots of males and females can be attributed to slightly divergent patterns of variable participation in the first three canonical variate axes (Table 9.9), particularly with respect to CV II and CV III. Basal claw width (BCW) and anterior rostral breadth (ARB) influenced CV II and CV III strongly in both sexes, but in females palatal length (PAL) also loaded highly. In males the latter variable participated only weakly in the respective axes, and coronoid process length (CPL) instead loaded strongly along CV III.

The first axis in these analyses was dominated by five measurements (GSL, GSH, PAL, ZMB and ARB) in both sexes, as well as basal claw width (BCW) in males. Greatest skull length (GSL), palate length (PAL) and greatest skull height (GSH) generally decreased from left to right along CV I (Table 9.10), reflecting a general decrease in overall size. Separation of the OTUs was not, however, based purely on size divergence, since zygomatic breadth (ZMB) was noticeably greater in Phenon D than C. In relative terms (ZMB:GSL ratio), zygomatic width tended to increase from left to right along CV I, indicating that the OTUs in size group II had comparatively wider skulls than those in size group I. This applied particularly to *C. asiatica* [CAS], *C. leucorhina* [CL] and *C. obtusirostris* [CO], which had significantly broader skulls (ZMB:GSL > 70%) than other OTUs of similar size.

Canonical variate axis II was influenced strongly by anterior rostral breadth (ARB) in both sexes, and to a lesser extent by basal claw width (BCW) - variables that loaded highly also along CV I. BCW generally decreased from left to right along CV I, and thus followed the pattern of overall size discrimination suggested by other measurements. However, BCW was significantly smaller in *C. stuhlmanni* [CST] than in the other phena (A and B1) in size group I (Table 9.6 and 9.7), despite the resemblance of these OTUs in overall size. Similarly, BCW was significantly smaller in *C. obtusirostris* ([CO] = subphenon D2) and *C. leucorhina* ([CL] = subphenon D3) than in the other subphena of size group II. In relative terms (BCW:GSL), claw width was markedly narrower (BCW:GSL < 15%) in *C. stuhlmanni* [CST], *C. obtusirostris* [CO] and *C. leucorhina* [CL], and comparatively wider (BCW:GSL > 19%) in Phenon

Table 9.9

Variable loadings for the first three canonical variate axes, from discriminant functions analyses of males and females representing 14 OTUs. Boldfaced loadings indicate variables that influence each axis strongly.

VARIABLE	CV I		CV II		CV III	
	♂	♀	♂	♀	♂	♀
BCW	**-1,893**	-0,637	**-1,667**	**0,834**	**-1,180**	**-2,269**
ARB	**2,629**	**3,161**	**-1,539**	**2,430**	**-1,104**	**1,278**
MIO	-0,468	**-1,139**	**-1,067**	**1,357**	-0,135	0,013
ZMB	**1,026**	**1,554**	-0,781	0,144	0,751	-1,102
IOW	0,093	**-0,921**	**1,125**	**-1,301**	-0,171	-0,201
GSL	**-0,907**	**-1,253**	**1,333**	-0,472	0,195	**1,754**
GSH	**-1,126**	**-1,463**	0,014	-0,446	0,606	-0,832
P@P	0,160	0,901	-0,837	0,167	**2,451**	**-1,638**
PAL	**0,921**	**0,940**	0,521	**-2,267**	0,306	**-1,576**
PPL	-0,086	-0,389	0,127	0,317	-0,123	0,798
BBW	0,062	-0,446	-0,151	-0,429	-0,730	0,661
CPL	0,601	0,454	-0,774	0,727	**-1,590**	0,051
APW	-0,100	-0,682	0,484	**1,217**	-0,722	1,086
MDL	-0,868	-0,260	-0,249	0,694	1,040	-0,360
% Trace	64,1	65,6	11,5	9,7	9,7	8,3

Table 9.10

Selected variables (VAR) and ratios (expressed as percentages ± one standard error) in eight groups of OTUs (Phena A - D3) discriminated by pairwise comparisons of the first three canonical variate axes in Fig. 9.2.

SEX\		SIZE GROUP I			SIZE GROUP II				
AXIS	VAR	A	B1	B2	C1	C2	D1	D2	D3
♂									
I	GSL	29,0±1,8	27,8±0,6	26,9±1,3	23,9±0,3	23,4±0,3	23,2±1,2	22,8±1,0	21,8±0,6
I	GSH	13,3±0,8	12,9±0,4	12,2±0,7	11,6±0,3	11,4±0,2	11,4±0,3	11,0±0,2	10,6±0,3
I	PAL	14,6±1,0	14,3±0,6	13,6±0,9	11,8±0,5	12,0±0,3	12,5±0,9	11,9±0,6	10,7±0,5
I	ZMB	18,1±1,2	16,6±0,8	16,2±0,9	15,3±0,5	15,3±0,5	17,3±1,1	16,1±0,5	15,8±0,3
I	ZMB:GSL	62,4±0,4	61,3±0,1	60,9±1,3	63,9±1,0	63,9±0,9	75,2±1,2	71,0±2,2	72,2±1,0
I,II,III	BCW:GSL	20,5±0,8	17,5±1,6	13,3±1,6	17,3±1,2	15,6±1,3	16,6±0,9	13,4±0,9	12,8±0,5
I,II,III	ARB:GSL	18,2±0,5	17,4±0,3	17,9±0,4	18,6±1,4	18,3±2,0	20,8±0,8	22,2±1,0	23,3±1,0
III	P@P:GSL	26,7±0,9	28,8±0,5	26,8±0,9	27,9±1,1	30,0±0,9	32,1±1,6	35,9±1,1	30,1±1,2
♀									
I	GSL	27,6±0,9	27,4±0,3	25,9±1,4	23,5±0,8	23,2±0,7	23,2±1,2	21,4±1,0	22,2±0,9
I	GSH	13,2±0,4	12,9±0,1	11,7±0,8	11,3±0,3	11,3±0,4	11,6±0,6	10,6±0,4	10,4±0,4
I	PAL	13,8±0,5	14,3±0,1	13,1±0,9	11,5±0,5	11,9±0,6	12,5±0,9	11,2±0,7	10,9±0,5
I	ZMB	16,7±0,8	16,7±0,1	15,8±0,8	14,5±0,5	15,1±0,7	17,3±1,9	15,3±0,7	16,0±0,6
I	ZMB:GSL	61,1±0,5	60,8±0,6	60,2±1,3	63,2±1,4	64,9±3,0	74,4±2,1	71,6±2,6	72,6±0,6
III	BCW:GSL	19,6±0,7	16,2±0,3	12,3±1,1	16,7±0,3	16,2±0,8	16,5±0,8	13,5±0,8	12,9±0,5
I,II,III	ARB:GSL	17,9±0,5	17,7±0,6	18,2±0,7	18,3±0,7	19,0±0,5	20,7±0,7	22,9±0,6	23,5±1,0
III	P@P:GSL	27,1±0,6	26,7±1,8	26,8±0,9	27,8±1,2	30,3±1,2	30,1±0,7	35,9±1,3	30,3±1,3

A, than in the other phena. Opposite trends were thus evident within the two size groups with respect to the separation of OTUs along CV II, basal claw width tending to increase from bottom to top in size group I, but to decrease in size group II.

Anterior rostral breadth (ARB) showed a similar pattern of variation to that indicated by zygomatic breadth (ZMB), in tending to increase from left to right along CV I (ARB:GSL in Table 9.10), but to decrease from bottom to top of the phenograms in Phena A, B and C. The same trend was evident in Phenon D of females, but in males ARB:GSL tended to increase from bottom to top along CV II. These differences notwithstanding, separation of the three subphena in Phenon D reflected a tendency for *C. asiatica* [CAS] to have a markedly broader skull but narrower rostrum than either *C. leucorhina* [CL] or *C. obtusirostris* [CO].

Canonical variate axis III in both sexes was dominated by BCW and palatal width (P@P). Separation of the OTUs along this axis reflected, in part, a tendency for P@P to become relatively broader from bottom to top of the phenogram in both size groups (P@P:GSL in Table 9.10), particularly in Phenon D.

Patterns of variable participation in the first three canonical variate axes, although complex, thus allowed the discrimination of eight distinct phena among the 14 OTUs analysed, as follows.

1) Phenon A: size larger (GSL > 25 mm), with relatively narrower skulls (ZMB:GSL < 63%) and robust claws (BCW:GSL > 19%) - *A. hottentotus*, *A. corriae*, *A. septentrionalis* and *Amblysomus Species A*;

2) Phenon B1: size larger (GSL > 25 mm), but with markedly narrow skulls (ZMB:GSL < 61%) and well-developed claws (BCW:GSL = 16 - 17%) - *C. arendsi* and *A. gunningi*;

3) Phenon B2: size larger (GSL > 25 mm), with a narrow skull (ZMB:GSL < 61%) and gracile claws (BCW:GSL < 15%) - *C. stuhlmanni*;

4) Phenon C1: size smaller (GSL < 25 mm), with a comparatively wide skull (ZMB:GSL > 63%) but relatively narrow palate (P@P:GSL < 29%), and well-developed claws (BCW:GSL > 16,5%) - *A. marleyi*;

5) Phenon C2: size smaller (GSL < 25 mm), with comparatively wide skulls (ZMB:GSL > 63%) but broader palates (P@P:GSL > 30%) and more gracile claws (BCW:GSL < 16,5%) - *A. julianae*, *C. sclateri* and *C. duthieae*;

6) Phenon D1: size smaller (GSL < 25 mm), with well-developed claws (BCW:GSL > 15%), an extremely broad skull (ZMB:GSL > 74%) and relatively narrow rostrum (ARB:GSL < 22%) - *C. asiatica.*
7) Phenon D2: size smaller (GSL < 25 mm), with relatively gracile claws (BCW:GSL < 15%), broad skull (ZMB:GSL > 70%), wide rostrum (ARB:GSL > 22%), and extremely wide palate (P@P:GSL > 34%) - *C. obtusirostris*;
8) Phenon D3: size smaller (GSL < 25 mm), with relatively gracile claws (BCW:GSL < 15%), broad skulls (ZMB:GSL > 70%) and wide rostrums (ARB:GSL > 22%), but relatively narrow palates (P@P:GSL < 34%) - *C. leucorhina.*

Separation between specimens of *C. stuhlmanni* and *C. asiatica* was marked in the scatterplots, to the extent that both OTUs showed a 100% *a posteriori* classification, with no overlap of discriminant score ranges along CV I in either sex, along CV II in males, or along CV III in females. This indicated that these taxa have diverged considerably in cranial configuration, with *C. stuhlmanni* having an elongated skull, in contrast to the shorter and conspicuously broad skull of *C. asiatica.*

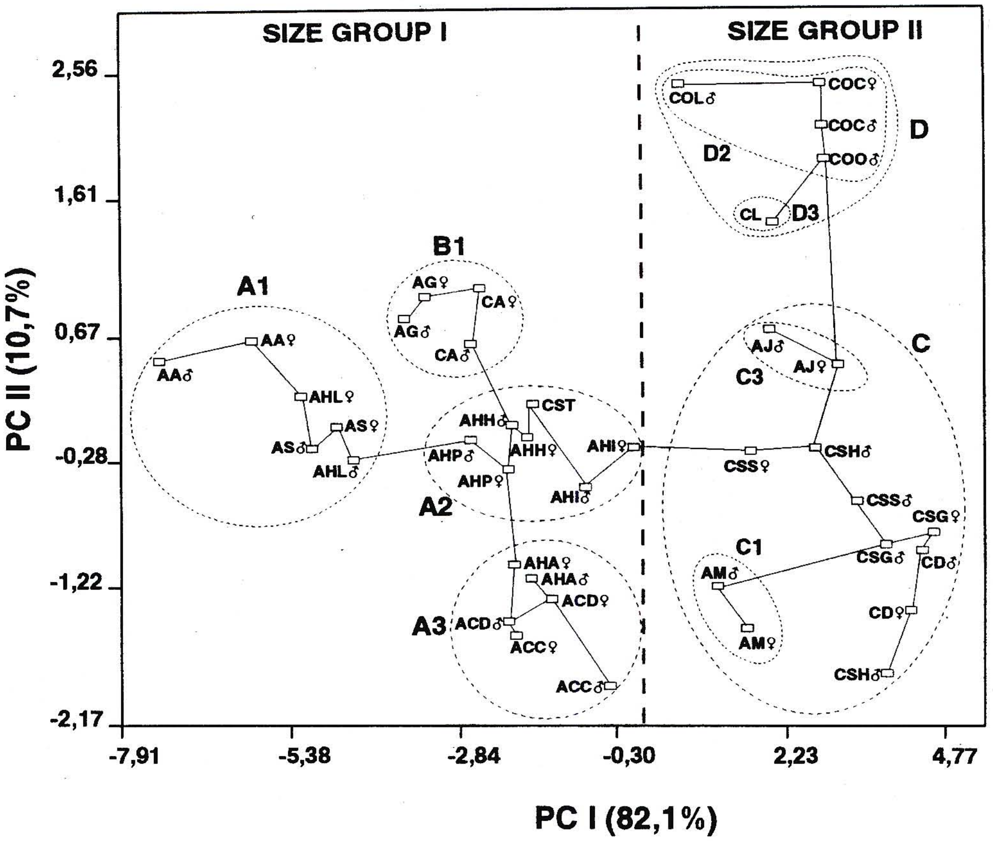
Thorpe (1976) showed that patterns of differentiation among phenetically similar subgroups may be obscured if an extreme or distantly-related taxon is included in ordination analyses. Since *C. stuhlmanni* approaches the *Amblysomus* and *Chlorotalpa* OTUs in cranial configuration, this OTU was included in subsequent phenetic analyses, whereas data for *C. asiatica* were excluded, except for use as an outgroup in cladistic analyses.

9.3.2.2. Principal components analysis

Pairwise comparison of the first two principal component axes, computed using species and subspecies means of males and females following independent standardization by sex, confirmed the existence of two size groups, and eight phena, among the OTUs studied (Fig. 9.5). The first component was a general size vector, as indicated by the high loadings and percentage variance contributions of all variables (Table 9.11). Separation along this axis reflected a decrease in size from left to right,

Figure 9.5. Pairwise comparison of the first and second (a), and first and third (b), principal component axes computed from means of 14 craniometric variables in 40 OTUs representing 13 chrysochlorid species. A minimum spanning tree is superimposed in (a).
The co-phenetic correlation was 0,998. Data for males and females were pooled after independent standardization by sex to correct for size dimorphism. See Table 9.1 for an explanation of of OTU codes. Dotted lines indicated phena delimited, associated with which are the alphanumeric codes by which phena are referred to in the text and other figures.

a)


SIZE GROUP I
SIZE GROUP II
PC II (10,7%)
PC I (82,1%)
2,56
1,61
0,67
-0,28
-1,22
-2,17
-7,91
-5,38
-2,84
-0,30
2,23
4,77
A1
A2
A3
B1
C
C1
C3
D
D2
D3
AA♂
AA♀
AHL♀
AHL♂
AS♀
AS♂
AG♀
AG♂
CA♀
CA♂
AHH♂
AHH♀
CST
AHP♂
AHP♀
AHI♀
AHI♂
AHA♀
AHA♂
ACD♀
ACD♂
ACC♀
ACC♂
COL♂
COC♀
COC♂
COO♂
CL
AJ♂
AJ♀
CSS♀
CSH♂
CSS♂
CSG♀
CSG♂
CD♂
CD♀
AM♂
AM♀
CSH♂

b)

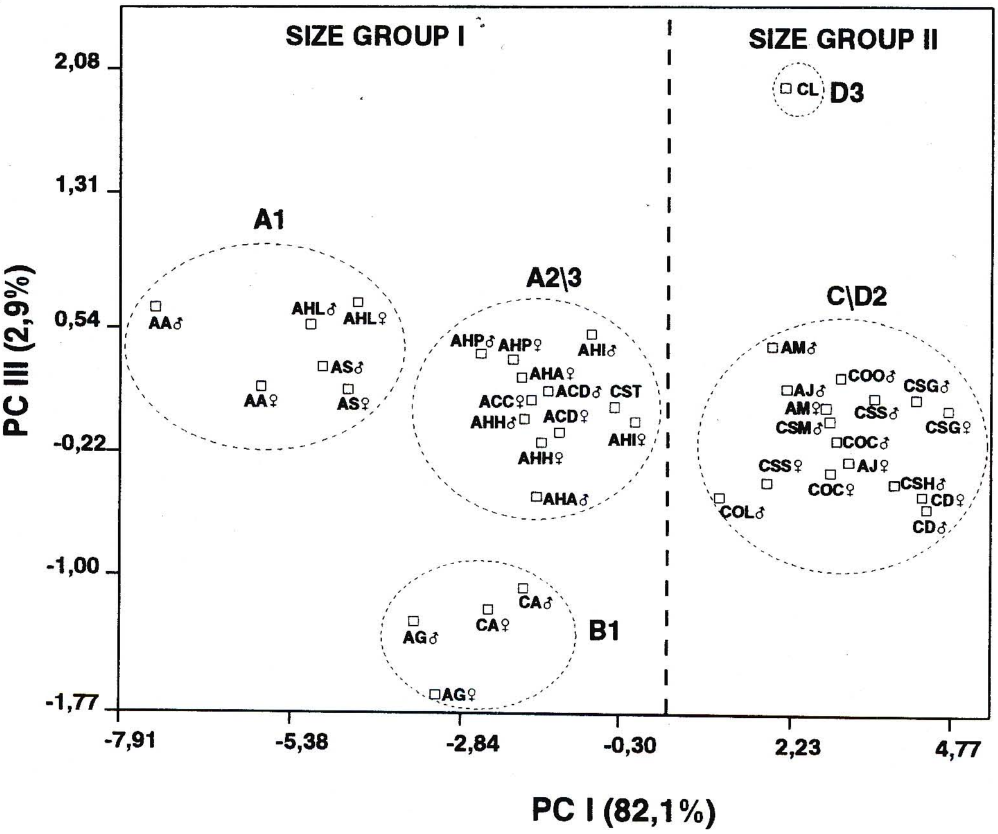

SIZE GROUP I
SIZE GROUP II
PC III (2,9%)
PC I (82,1%)
2,08
1,31
0,54
-0,22
-1,00
-1,77
-7,91
-5,38
-2,84
-0,30
2,23
4,77
A1
A2\3
B1
C\D2
D3
CL
AA♂
AHL♂
AHL♀
AS♂
AA♀
AS♀
AHP♂
AHP♀
AHI♂
AHA♀
ACC♀
ACD♂
CST
AHH♂
ACD♀
AHI♀
AHH♀
AHA♂
CA♂
CA♀
AG♂
AG♀
AM♂
COO♂
AJ♂
CSG♂
AM♀
CSS♂
CSM♂
CSG♀
COC♂
CSS♀
AJ♀
COC♀
CSH♂
CD♀
COL♂
CD♂

Table 9.11

Variable loadings (and the percentage of each variables variance explained) for the first three principal components axes, based on an analysis of 14 cranial measurements in 42 OTUs. Data for males and females were standardized independently to correct for sexual size dimorphism. Boldfaced values indicate strong variable participation in the respective axes.

Variable	PC I	PC II	PC III
BCW	**-0,891**(79,4)	**-0,343**(11,8)	0,076(0,6)
ARB	**-0,716**(51,3)	**0,593**(35,2)	**0,306**(9,3)
MIO	**-0,946**(89,6)	0,004(0,0)	**0,242**(5,9)
ZMB	**-0,903**(81,6)	**0,378**(14,3)	0,113(1,3)
IOW	**-0,887**(78,7)	**0,313**(9,8)	-0,034(0,2)
GSL	**-0,963**(92,8)	-0,214(4,6)	-0,131(1,7)
GSH	**-0,973**(94,6)	-0,173(3,0)	-0,052(0,3)
P@P	0,567(32,1)	**0,728**(52,9)	**-0,330**(10,9)
PAL	**-0,923**(85,2)	-0,151(2,3)	**-0,294**(8,6)
PPL	**-0,956**(91,5)	-0,173(3,0)	0,076(0,6)
BBW	**-0,981**(96,2)	0,068(0,5)	-0,022(0,1)
CPL	**-0,961**(92,4)	-0,176(3,1)	0,016(0,1)
APW	**-0,933**(87,1)	-0,284(8,1)	0,076(0,6)
MDL	**-0,984**(96,9)	-0,111(1,2)	-0,091(0,8)

with the OTUs falling into two major size groups (I and II) that were identical in composition to those discerned in univariate and discriminant functions analyses.

The first axis was not, however, influenced only by differences in general size, since palatal width (P@P) loaded positively, and was relatively wider in size group II (P@P:GSL = 30,8±2,7) than in size group I (P@P:GSL = 27,5±1,0). Separation along this axis thus also reflected a trend for palate width to become relatively narrower as overall size increased.

Within each of the major size groups, four subphena distinguished by differences in both size and shape were evident. In size group I, the *C. arendsi* and *A. gunningi* OTUs formed a distinct cluster that plotted above the others along PC II, and corresponded with subphenon B1 evident in canonical variate axis scatterplots. Conversely, the *Amblysomus* species, which grouped together (Phenon A) in canonical variate axis scatterplots, separated into three subphena. Subphenon A1, comprising the *A. h. longiceps*, *A. septentrionalis* and *Amblysomus Species A* samples, plotted well to the left along PC I owing to the larger overall size of these OTUs. The other OTUs, although similar in size, separated into two subgroups along the second axis, with most of the *A. hottentotus* samples plotting together (subphenon A2) above the *A. corriae* and *Amblysomus subspecies A* OTUs (subphenon A3). The single *C. stuhlmanni* OTU plotted within subphenon A2, in contrast to the tendency for this OTU to plot by itself (in subphenon B2) between Phena A and B1 in canonical variate axis scatterplots.

In size group II, the *C. obtusirostris* and *C. leucorhina* OTUs (subphena D2 and D3 in discriminant functions analyses) separated from the *C. sclateri* and *C. duthieae* (subphenon C2) and *A. marleyi* (subphenon C1) OTUs along the second axis. However, the *A. julianae* OTUs, which plotted with subphenon C2 in canonical variate axis scatterplots, mapped out between subphena C2 and D2/3 along PC II, and thus formed the distinct subphenon C3.

The second principal component (PC II) was a shape vector dominated by five variables: four width measurements (P@P, ARB, ZMB and IOW) which loaded high positive; and basal claw width (BCW), which loaded high negative (Table 9.11). Separation of the subphena along this axis reflected a tendency for skull widths in general, and palatal width in particular, to increase (as reflected by the ratio P@P:GSL in Table 9.12) from bottom to top along PC II. Basal claw width (BCW:GSL) showed the opposite pattern of variation, and tended to decrease with increasing scores along PC II, although this is not obvious in size group I because BCW also decreased from left to right along PC I.

Pairwise comparison of the first and third principal component axes (Fig. 9.6) confirmed the phenetic distinctness of the larger-sized *Amblysomus* OTUs (subphenon A1), and the similarity of *C. arendsi* and *A. gunningi* (subphenon B1) in cranial size and shape. The *A. corriae* and *Amblysomus subspecies A* OTUs plotted with the *A. hottentotus* and *C. stuhlmanni* samples along PC III, in contrast to the tendency for these OTUs to separate into two subphena (A2 and A3) along PC II. Similarly, the *C. leucorhina* OTU (subphenon D3) was well differentiated from others along the third axis, but the remaining OTUs in size group II plotted together, rather than separating into four subphena. PC III contrasted rostrum width (ARB) and inter-orbital breadth (MIO) with palate length (PAL) and width (P@P). Increasing scores along this axis thus reflected a relative increase in rostrum width (ARB:GSL in Table 9.12), and a decrease in relative palate length and width (PAL:MIO and P@P:MIO). The *A. gunningi* and *C. arendsi* OTUs plotted below the other OTUs in size group I by virtue of their comparatively longer and broader palates, and more slender rostra (see Section 9.3.1). Similarly, the wide separation of *C. leucorhina* from the other OTUs in size group II, and from *C. obtusirostris* in particular, reflected the markedly shorter palate but wider rostrum of this OTU.

The first principal component accounted for over 80% of the sample variance, indicating that morphometric variation among the OTUs studied was dominated by differences in overall size. If PC I was ignored, to eliminate the effect of size variation, five groups of OTUs distinguished by differences in cranial shape were evident (Fig. 9.6). The *C. obtusirostris* and *C. leucorhina* OTUs (subphena D2 and D3) plotted well to the right of others along PC II owing to their comparatively broader skulls, and relatively gracile claws, but separated from each other along PC III owing to differences in palatal width. The *A. gunningi* and *C. arendsi* OTUs (subphenon B1) also separated from the other OTUs along PC III, this reflecting their relatively longer palates and narrower rostra.

Separation between the remaining OTUs was less marked. However, three subgroups that tended to plot apart along either PC II or PC III were evident. The

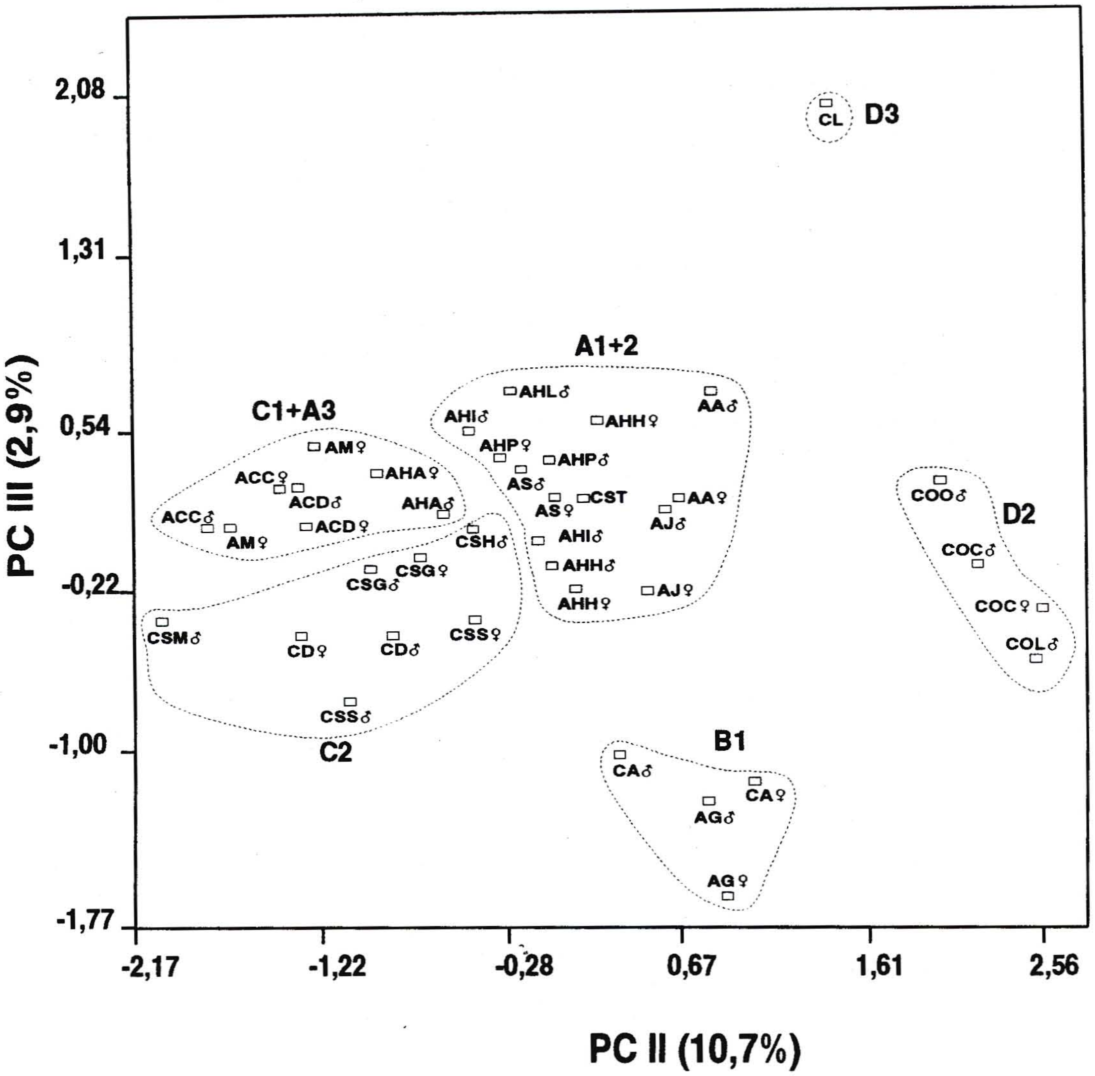


Figure 9.6. Pairwise comparison of the second and third principal component (PC) axes computed from means of 14 craniometric variables in 40 OTUs representing 13 chrysochlorid species. The co-phenetic correlation was 0,998. Data for males and females were pooled after independent standardization by sex to correct for sexual size dimorphism. See Table 9.1 for an explanation of of OTU codes. Dotted lines indicated phena delimited, associated with which are the alphanumeric codes by which phena are referred to in the text and other figures.

Table 9.12

Selected cranial ratios (percentages ± one standard error) for subgroups of OTUs discriminated by pairwise comparisons of the first and second or third principal component axes in Fig. 9.5.

PC	**Size Group**	**Subphenon**	**CRANIAL**	**RATIOS**	
II			BCW:GSL	P@P:GSL	
	II	D2\3	13,2±0,6	33,2±1,5	
		C3	16,4±0,1	31,6±0,3	
		C2	16,4±0,2	29,4±0,1	
		C1	17,2±0,6	28,1±0,3	
	I	B1	16,2±0,4	28,8±0,4	
		A1	20,9±0,6	26,9±0,1	
		A2	19,8±1,0	27,6±0,6	
		A3	18,5±0,5	26,1±0,6	
III			ARB:GSL	P@P:MIO	PAL:MIO
		D3	22,9±0,9	86,4±5,6	139,4±5,7
		A1-3	18,0±0,4	86,6±2,7	162,0±4,3
		C1-3,D2	18,0±0,6	99,1±5,7	164,9±5,9
		B1	17,9±0,4	100,1±1,2	182,7±0,6

Chlorotalpa OTUs (subphenon C2) grouped below the *Amblysomus* and *C. stuhlmanni* samples along PC III, while the latter OTUs fell into two distinct subgroups (subphena A1/2 and A3) separated mainly along PC II. An important difference between this scatterplot, and those including PC I, was that the *A. marleyi* OTUs plotted with subphenon A3, and the *A. julianae* OTUs with subphenon A1/2, rather than with the *Chlorotalpa* samples in subphenon C2. This indicated that, despite their resemblance to the *C. sclateri* and *C. duthieae* in overall size, *A. julianae* and *A. marleyi* differ subtly from these taxa in cranial configuration, and are more similar to other *Amblysomus* in this regard.

9.3.2.3. Cluster analyses

A distance phenogram computed from species and subspecies means, following independent standardization by sex, showed the same pattern of OTU segregation (Fig. 9.7) that was evident in the scatterplot comparing the first two principal component axes. The OTUs clustered into two major size groups, each comprising four subphena. In contrast to discriminant functions analyses, but as in principal component scatterplots, the *A. julianae* OTUs formed a distinct subcluster (subphenon C3), while the larger-sized *Amblysomus* OTUs clustered apart (subphenon A1) from the other samples in size group I.

Cluster analysis based on correlation coefficients revealed a pattern of OTU segregation that differed in several important respects from that evident in distance phenograms and ordination scatterplots. While the OTUs separated into several subphena that corresponded directly with those in ordination analyses, these grouped into two major phena (α and ß) that differed in composition from the size groups recognized in previous analyses. Each of the major clusters contained a combination of smaller- and larger sized OTUs (Fig. 9.8). Thus, the *A. gunningi* and *C. arendsi* OTUs formed a distinct subcluster (subphenon B1), but unlike the pattern in principal component and canonical variate axis scatterplots, this cluster separated from the intermediate and larger-sized *Amblysomus* OTUs (subphenon A1-3), and instead grouped with *C. obtusirostris* (subphenon D2) and *C. leucorhina* (subphenon D3) in Phenon ß. The single sample of *C. stuhlmanni* also plotted in this phenon, in contrast to its association with intermediate-sized *Amblysomus* (subphenon A2) in principal

Figure 9.7. Phenogram based on UPGMA clustering of average taxonomic distances computed from the means of 14 craniometric variables in 40 OTUs representing 13 chrysochlorid species. The co-phenetic correlation was 0,855. Data for males and females were standardized independently by sex, to correct for sexual size dimorphism. See Table 9.1 for an explanation of OTU codes. Alphanumeric codes indicate phena delimited in ordination analyses, and referred to in the text.

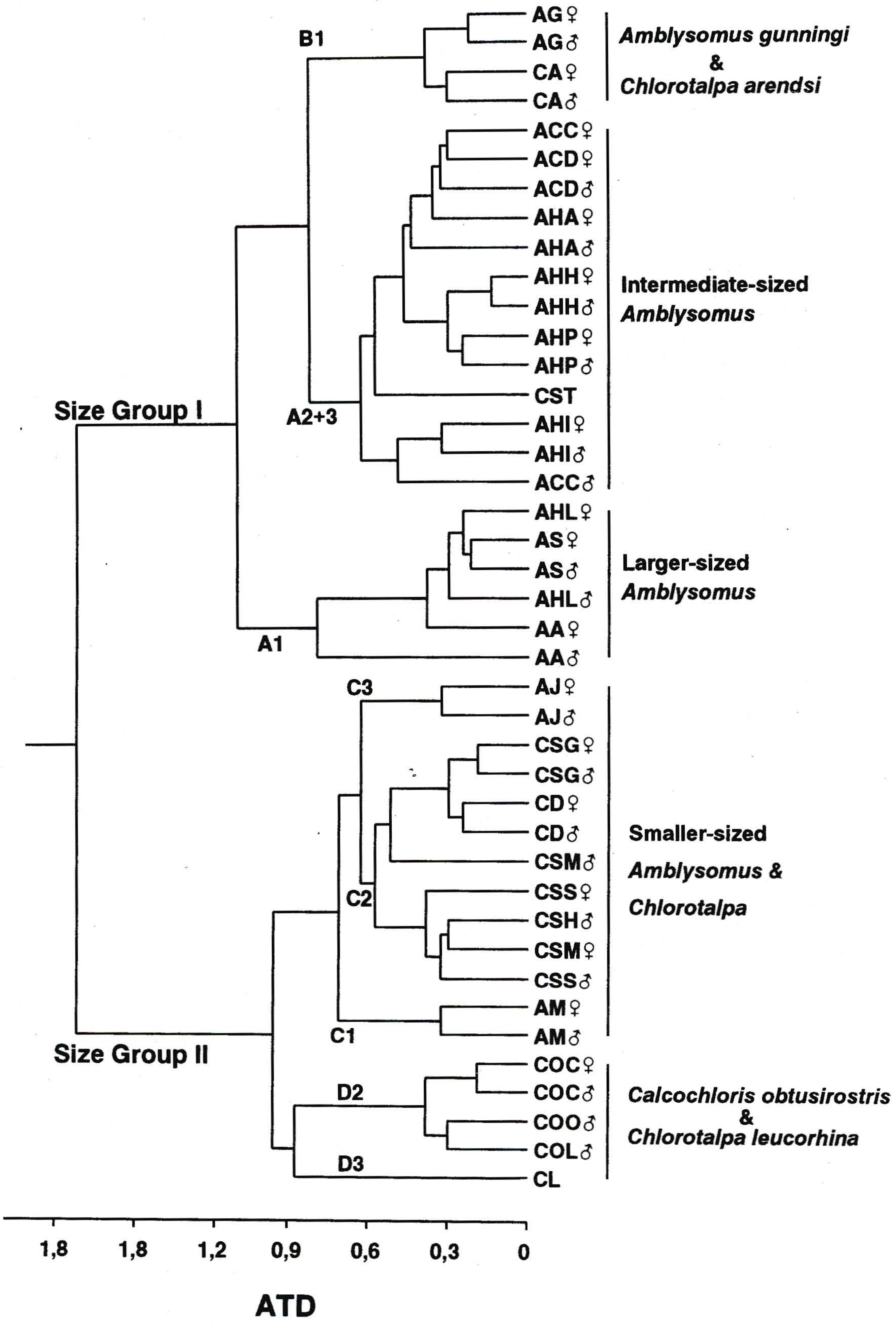
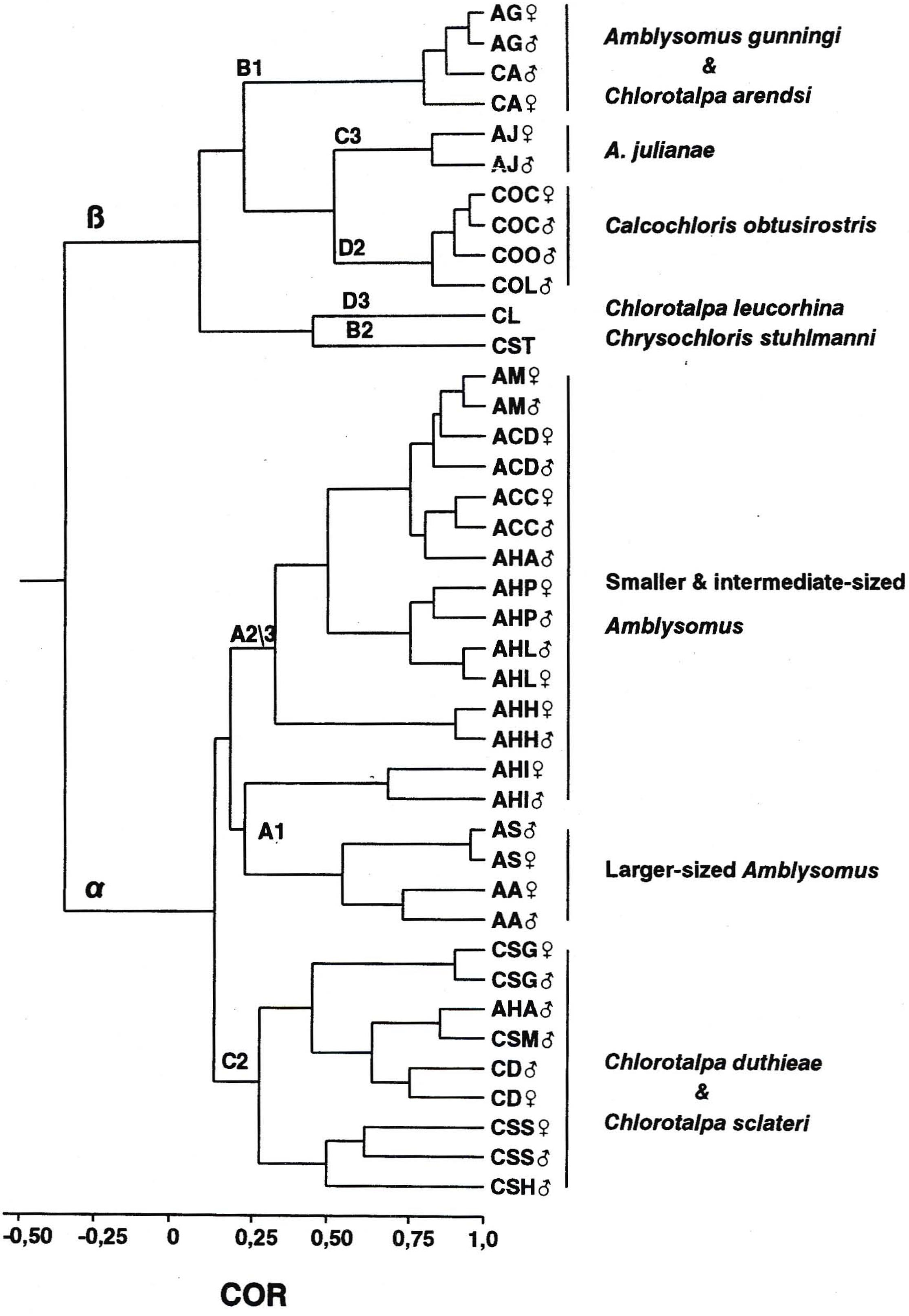

AG♀
AG♂
CA♀
CA♂
Amblysomus gunningi & Chlorotalpa arendsi
ACC♀
ACD♀
ACD♂
AHA♀
AHA♂
AHH♀
AHH♂
AHP♀
AHP♂
CST
AHI♀
AHI♂
ACC♂
Intermediate-sized Amblysomus
AHL♀
AS♀
AS♂
AHL♂
AA♀
AA♂
Larger-sized Amblysomus
AJ♀
AJ♂
CSG♀
CSG♂
CD♀
CD♂
CSM♂
CSS♀
CSH♂
CSM♀
CSS♂
AM♀
AM♂
Smaller-sized Amblysomus & Chlorotalpa
COC♀
COC♂
COO♂
COL♂
CL
Calcochloris obtusirostris & Chlorotalpa leucorhina
B1
A2+3
A1
C3
C2
C1
D2
D3
Size Group I
Size Group II
1,8
1,8
1,2
0,9
0,6
0,3
0
ATD

Figure 9.8. Phenogram based on UPGMA clustering of correlation coefficients computed from the means of 14 craniometric variables in 40 OTUs representing 13 chrysochlorid species. The co-phenetic correlation was 0,787. Data for males and females were standardized independently by sex, to correct for sexual size dimorphism. See Table 9.1 for an explanation of OTU codes. Alphanumeric codes indicate phena delimited in ordination analyses, and referred to in the text.


AG♀
AG♂
CA♂
CA♀
AJ♀
AJ♂
COC♀
COC♂
COO♂
COL♂
CL
CST
AM♀
AM♂
ACD♀
ACD♂
ACC♀
ACC♂
AHA♂
AHP♀
AHP♂
AHL♂
AHL♀
AHH♀
AHH♂
AHI♀
AHI♂
AS♂
AS♀
AA♀
AA♂
CSG♀
CSG♂
AHA♂
CSM♂
CD♂
CD♀
CSS♀
CSS♂
CSH♂
B1
C3
ß
D2
D3
B2
A2\3
A1
α
C2
Amblysomus gunningi & Chlorotalpa arendsi
A. julianae
Calcochloris obtusirostris
Chlorotalpa leucorhina
Chrysochloris stuhlmanni
Smaller & intermediate-sized Amblysomus
Larger-sized Amblysomus
Chlorotalpa duthieae & Chlorotalpa sclateri
-0,50
-0,25
0
0,25
0,50
0,75
1,0
COR

component axis scatterplots. Conversely, the *A. julianae* OTUs fell in a distinct subcluster (subphenon C3) within Phenon ß, with relatively close phenetic affinity to *C. obtusirostris* - a resemblance suggested also by principal component scatterplots.

In Phenon α, the smaller-sized *Chlorotalpa* OTUs [CS,CD] clustered apart from other OTUs, to form a distinct subphenon (C2). Similarly, the *A. marleyi* OTUs fell within the same cluster as *A. corriae* and *Amblysomus subspecies A*, which is consistent with the pattern of phenetic affinity suggested by pairwise comparison of PC II and PC III. As in distance phenograms and ordination scatterplots, the other *Amblysomus* OTUs separated into two subclusters, but the *A. h. longiceps* samples grouped with the *A. hottentotus* OTUs, rather than with *A. septentrionalis* and *Amblysomus Species A* OTUs that they resemble in overall size.

The various subphena evident in correlation phenograms were, therefore, concordant with those apparent in distance phenograms and ordination scatterplots, but phenetic inter-relationships suggested by these analyses were quite different. This may be attributed to the tendency for correlation phenograms to reflect shape variation, rather than overall size (Sneath and Sokal 1973), with the result that the OTUs did not associated into the size groups that are so obvious in other analyses. However, the clustering of *C. arendsi*, *A. gunningi* and *C. stuhlmanni* with *C. obtusirostris* and *C. leucorhina* was incongruous, since these OTUs separated widely along PC II (Fig. 9.5), and associated with the larger-sized *Amblysomus* OTUs in ordination scatterplots, even when the first principal component was excluded to minimize the influence of size.

For mixed-mode analysis, the effect of size was corrected for by eliminating OTU scores along PC I. Cluster analysis was thus based on Gower's coefficients computed from OTU scores along principal component axes II-V (which collectively accounted for 16,1% of craniometric variance), and two qualitative characters (M3 presence/absence; incudomallear ratio) for which a complete data suite was available.

In the resulting phenogram (Fig. 9.9), the OTUs grouped into nine phena that were similar in composition to those evident in analyses based on metric data only, yet with another pattern of phenetic inter-relationship being evident. The *C. leucorhina* OTU separated from all of the others in a distinct subphenon (D3), as in principal components scatterplots, but in conflict with the close association between this OTU

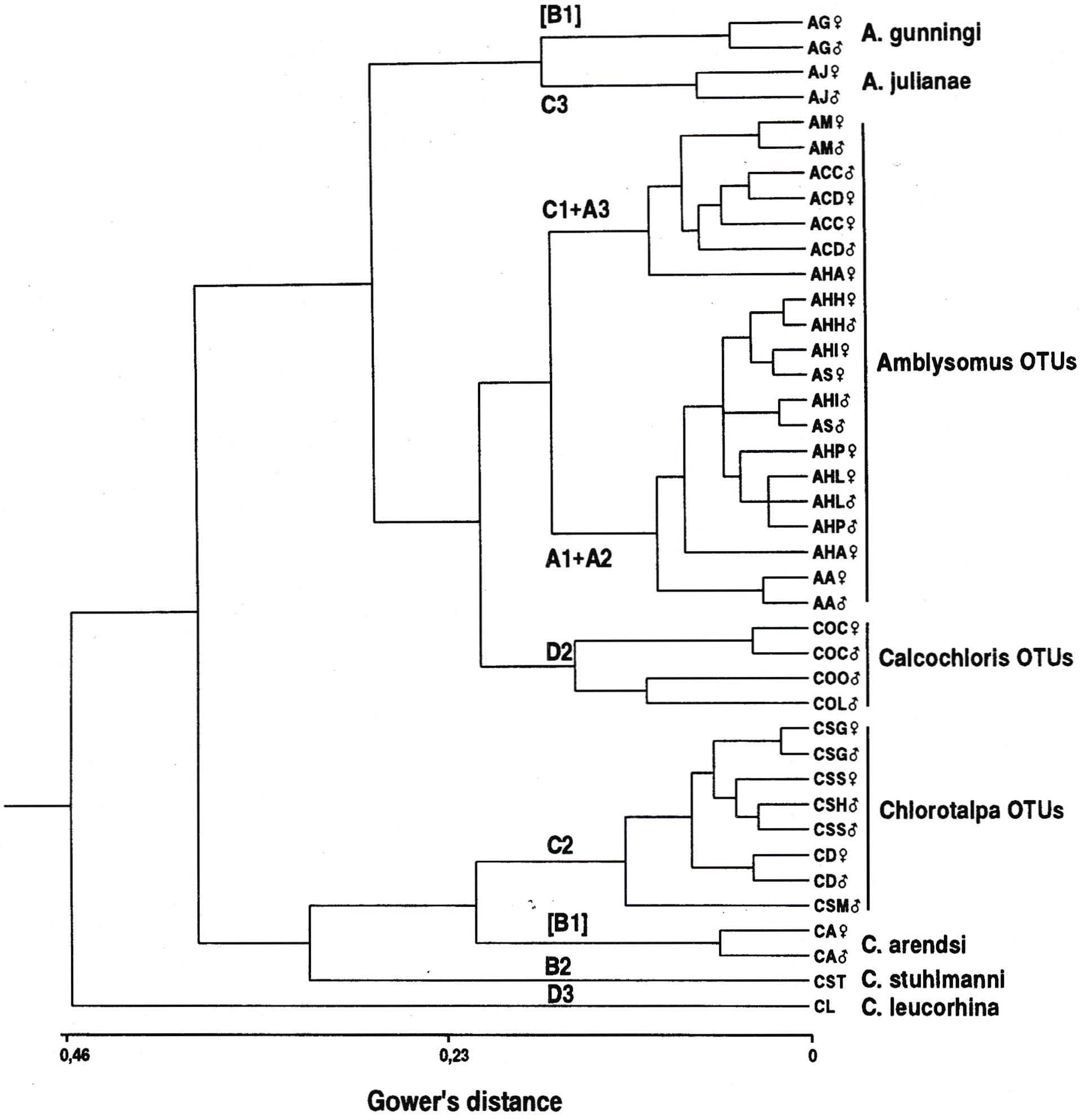


Figure 9.9. Phenogram based on UPGMA clustering of Gower's distance coefficients computed from the means of 14 craniometric variables, and two multistate characters (M3, I:M; see Table 9.2) in 40 OTUs representing 13 chrysochlorid species. The co-phenetic correlation was 0,813. Craniometric data for males and females were standardized independently by sex, to correct for sexual size dimorphism. See Table 9.1 for an explanation of OTU codes. Alphanumeric codes indicate phena that correspond directly or partially ([B1]) with those delimited in ordination analyses.

and *C. obtusirostris* evident in the correlation phenogram. Instead of grouping with either *Amblysomus* OTUs (ordination scatterplots; Fig. 9.5), or with the *C. obtusirostris* OTUs (correlation phenogram; Fig. 9.8), the *C. stuhlmanni* OTU fell in a distinct subcluster (phenon B2) with closer phenetic affinity to the *C. sclateri* and *C. duthieae* OTUs. Similarly, the *C. arendsi* OTUs (phenon B1) grouped with the smaller *Chlorotalpa* OTUs, instead of with the *A. gunningi* samples, the latter showing a closer affinity to the *A. julianae* OTUs than was apparent in analyses based on metric data.

9.3.4. Summary of phenetic relationships

The univariate and multivariate analyses performed showed that morphometric variation among the 14 chrysochlorid OTUs studied was dominated by overall size. If size was taken into account, the OTUs fell into eight phena within two size groups. With the exception of the *C. obtusirostris* OTUs, which formed a distinct phenon (D2) that conforms to Meester's (1974) definition of the genus *Calcochloris*, none of the phena corresponded directly with any of the taxa recognized by previous authors (Meester 1974; Petter 1981; Simonetta 1968). Since overall size makes a relatively small contribution toward taxonomic resemblance, and often obscures systematic relationships (Sneath and Sokal 1973), size variation amongst chrysochlorids is of little significance at higher taxonomic levels.

If the effects of size were controlled for, and only morphometric data were considered, the OTUs grouped into phena that were more concordant with some of the taxa recognized by previous authors. The *C. obtusirostris* and *C. sclateri/C. duthieae* OTUs, for instance, consistently grouped apart from each other, and also from most of the *Amblysomus* samples, which supports Meester's (1974) separation of *Calcochloris* and *Chlorotalpa* from *Amblysomus*. Similarly, the *A. gunningi* OTUs invariably plotted apart from the other *Amblysomus* OTUs, which agrees with Robert's (1924, 1951) allocation of this species to the distinct taxon *Neamblysomus*. The *C. leucorhina* OTU also separated from the other OTUs, and particularly the *Amblysomus* and other *Chlorotalpa* samples, in all of the analyses. Morphometric data therefore indicated that *C. leucorhina* represents a phenetically distinct taxon from either *Chlorotalpa* (Meester 1974) or *Amblysomus* (Petter 1981; Simonetta 1968).

Although the compositions of the phena delimited by the various phenetic analyses were quite similar, the patterns of phenetic inter-relationships suggested by ordination and cluster analyses were often incongruous, and even greater discordance was evident when non-metric characters were also taken into account. For example, greater phenetic affinity was apparent between *C. obtusirostris* and the *Amblysomus* OTUs in the mixed-mode analysis than in those based on metric data only. Conversely, closer affinity of the *C. sclateri/C. duthieae* and *Amblysomus* OTUs was evident in the principal components analysis than in phenograms based on either metric or mixed-mode data.

The most conspicuous differences between the three sets of analyses involved the *A. julianae*, *C. arendsi* and *C. stuhlmanni* OTUs. While the *C. arendsi* OTUs grouped with the *A. gunningi* samples in analyses based on metric data only, they associated with the *C. sclateri* and *C. duthieae* OTUs in mixed-mode analysis. Conversely, a closer phenetic relationship between *C. stuhlmanni* and the *Amblysomus* OTUs was evident in ordination scatterplots than in cluster analyses, regardless of whether only metric or mixed-mode data were used. Even less clear was the affinity of the *A. julianae* OTUs, which grouped with most of the *Amblysomus* samples in the principal components analysis, but clustered with *C. obtusirostris* in a correlation phenogram, and with *A. gunningi* in the mixed-mode analysis.

Phenetic analyses did not, therefore, unequivocally resolve systematic relationships among the chrysochlorid OTUs, and the addition of just two qualitative characters changed the pattern of inferred relationships among taxa markedly. This points to a lack of congruence between craniometric and non-metric malleus and dental characters. Incongruence is the result of differential adaptational patterns and evolutionary rates in character suites (Sneath and Sokal 1973). By affording all characters equal weight, different subsets of characters lead to different similarity estimates, and phenetic analyses will not necessarily yield monophyletic taxa because no distinction is made between true homology and homoplasy (Mickevich 1978; Sokal 1985). One of the greatest practical drawbacks of the phenetic approach is the lack of any theoretical justification of choice among incongruent sets of results from different analyses (Mayr and Ashlock 1991). In the absence of any distinction between similarities due to descent, and those due to homoplasy, it was thus impossible to gauge objectively which set of phenetic results most accurately depicted systematic relationships among the chrysochlorid taxa analysed.

9.3.3. Cladistic analyses

Of the 12 multistate characters analysed, two craniometric ratios (PAL:MIO and APW:ZMB) did not show a linear sequence of transformation. In exploratory analyses (with the multiple parsimonious trees and branch-and-bound options of PAUP engaged), the consistency indices of these two characters were generally between 0,2 - 0,4, which was appreciably lower than those of most other characters (*CI*>0,5). Since the consistency indices of the two craniometric characters were only slightly above those shown by random data (Klassen *et al.* 1991), they were treated as unordered in all cladistic analyses, as recommended by Swofford (1985).

Strict parsimony analyses duplicated with PAUP and Hennig86 yielded trees that were identical in topology and length, with only minor differences in consistency (*CI*) and retention (*RI*) indices. Consequently, only the results of the PAUP analyses are presented below.

Employing the branch-and-bound option with equal weighting of all characters yielded only one most parsimonious tree with a length of 58 steps (Fig. 9.10). The *g1* statistic for this analysis was -0,533, indicating that the distribution of tree lengths was significantly ($p<0{,}01$) more skewed than would be expected from random data. This implies that a strong phylogenetic signal was inherent in the data (Hillis and Huelsenbeck 1992).

The consistency index (*CI*) for the cladogram was 0,638. This was well above the value to be expected from random data (Klassen *et al.* 1991), but pointed to the existence of substantial homoplasy in the tree, as evidenced also by a relatively high homoplasy excess ratio (*HSR* = 0,362). Only four characters - interpterygoid width (IPG:P@P = character F in Fig. 9.10) and the three chromosomal traits (L-M) - were not homoplastic. (The apparent absence of homoplasy among chromosomal characters may, however, have resulted from the lack of data for *C. arendsi*, *C. stuhlmanni* and *C. leucorhina*). The relatively low consistency index for stylohyal morphology (0,667) was an artefact of the coding system used, since the hypothesized changes in this character did not involve any homoplasies. For instance, the changes in stylohyal morphology in *C. obtusirostris* and *C. sclateri*/*C. duthieae* involved a parallel reduction in the size of the bone, but with a proximal shift of the articular surface in the former that is not apparent in the latter. Similarly, the apparent homoplasious development of

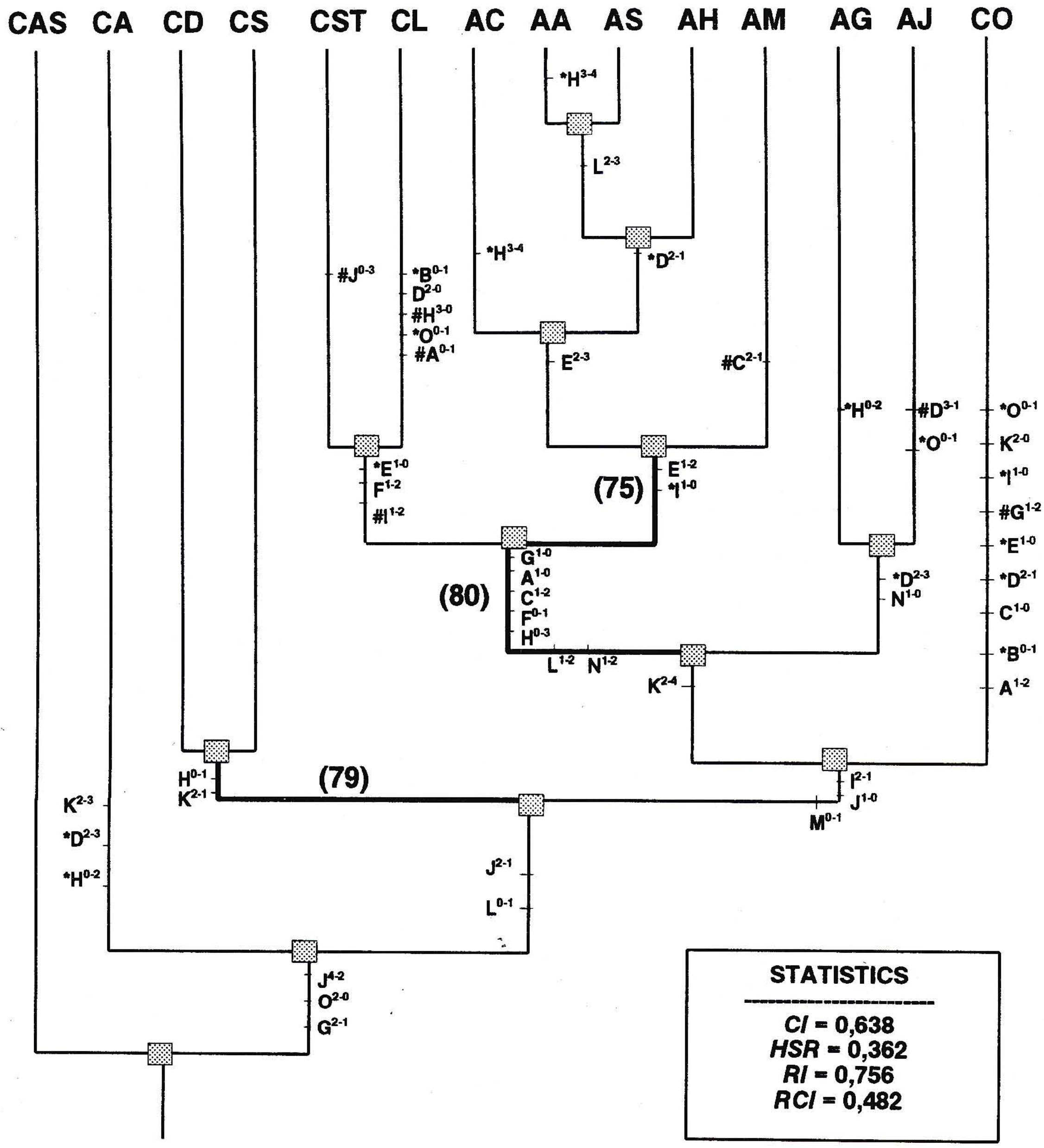


Figure 9.10. Cladogram derived by strict parsimony analysis of 15 characters in 13 chrysochlorid species and the outgroup (*Chrysochloris asiatica*; CAS), with equal weights applied. See Table 9.1 for an explanation of OTU codes, and Table 9.2 for a description of characters and character states. Superscripts indicate hypothesized character state changes. Parallelisms are denoted by asterisks (*), and reversals by a double slash (#). Bold lines indicate internodes that can be considered real on the basis of significant ($p < 0,05$) bootstrap values, which are shown in parentheses.

a high, medial articular surface in *C. stuhlmanni* and the clade leading to the *Amblysomus* species involved an increase in robustness of only the latter.

Consistency indices for the remaining 10 characters ranged between 0,4 and 0,75, with a mean of 0,587±0,11. The distribution of character-states on the cladogram suggested that 17 parallelisms and 7 reversals have occurred during phylogenetic divergence of the 13 HTUs. Of these 24 homoplasies, 20 involved parallelisms or reversals in eight craniometric characters, implying that cranial morphology is relatively plastic among chrysochlorids. This is not unusual among mammals, since cranial size and shape are polygenic traits whose phenotypic expression changes considerably during evolution (Atchley *et al.* 1981).

Of the non-metric characters, only M3 (I) and incudomallear ratio (J) were homoplastic. The parallel loss of M3 in *C. obtusirostris* and the *Amblysomus* lineage seems possible, since it is common for features to be lost independently in different lineages (Mayr and Ashlock 1991). In contrast, the cladogram suggested that the presence of an M3 in *C. stuhlmanni* and *C. leucorhina* is the result of a reversal to a plesiomorphic condition. However, this would entail the loss and subsequent reacquisition of a complex structure, thereby contravening Dollo's rule, for which few if any exceptions have been documented (Mayr and Ashlock 1991).

The transformation series suggested by the cladogram also implied that the hypertrophied, "club-shaped" malleus of *C. stuhlmanni* arose via a reversal toward a plesiomorphous condition. Since *C. stuhlmanni* has a relatively long and elongate skull, this must have occurred after considerable craniometric divergence from the broader and shorter skull present in *C. asiatica*.

That malleus morphology may be homoplastic among chrysochlorids is supported by the apparent existence of parallelisms in the middle ear structure of *Eremitalpa* and *Chrysospalax* (Von Mayer *et al.* 1995). Winge (1941:202) similarly speculated that inflation of the malleus in some fossorial mammals is simply a convergent adaptation to subterranean life. However, these authors did not conclusively demonstrate any lack of homology, and others have argued that middle ear structure is highly conserved among mammals, regardless of differences in size, habit and environment (Fleischer 1978). Furthermore, it is highly improbable that such complex structures would evolve homoplasiously in the same family (Mayr and

Ashlock 1991), especially since this involves considerable modification of the skull (Von Mayer *et al.* 1995). In the absence of any firm evidence to the contrary, the similar malleus morphology of *C. stuhlmanni* and *C. asiatica* must be regarded as phylogenetically significant, and the transformation series suggested by the cladogram invoked yet another contravention of Dollo's rule.

There were, therefore, good reasons to doubt the phylogeny suggested by the cladogram produced with equal character weighting. Since the data matrix contained nine craniometric characters, but only three non-metric skull characters (M3, SH and I:M), the former were afforded three times the collective weight of the latter. This may have forced the cladogram to conform to the pattern of craniometric differentiation among the HTUs, instead of a pattern reflecting divergence across all characters.

This was confirmed by bootstrap analysis, which indicated that only three clades evident on the cladogram could be accepted as real on the basis of bootstrap proportions exceeding 70% (which is equivalent to the 95% confidence level; Hillis and Bull 1993). All three of these internodes were delimited by primarily non-homoplastic craniometric variables.

When there is discordance among characters because of homoplasy, characters should be weighted according to their quality (Mayr and Ashlock 1991). I therefore performed another analysis in which the malleus (IM) and hyoid (SH) characters were afforded four times the weight of the craniometric ratios. This 4:1 weighting regime was justified because the non-metric characters comprise complex features, which are less likely to evolve in a homoplastic fashion (Bock 1977). Moreover, by affording these four times the weight, the collective weights of the craniometric and non-metric skull characters were balanced.

Using branch-and-bound searching with the differential weighting (4:1) regime yielded five equally parsimonious trees, each with a length of 89 steps and a consistency index (*CI*) of 0,685. (The relative increase in tree lengths relative to the equal weighting analysis was the consequence of applying higher weights to non-metric characters). The *g*1 statistic for this analysis was -0,538, which was of the same magnitude as that computed with equal weighting, and indicated that a strong phylogenetic signal was present in the data.

The topologies of the five trees computed differed from each other only in the branching order and sequences among the four larger-sized *Amblysomus* OTUs, with the result that polytomous divergence of these species was indicated in a strict consensus tree (Fig. 9.11). The phylogenetic relationships suggested by this strict consensus tree differed from those of the equal weighting analysis in only the placement of *C. stuhlmanni* and *C. leucorhina.* Instead of grouping in the same clade with close phylogenetic affinity to the *Amblysomus* species, *C. stuhlmanni* diverged from the rest of the ingroup at the base of the tree, and *C. leucorhina* fell in the same clade as *C. obtusirostris*. Otherwise, the branching order and clade compositions were identical.

The bootstrap proportions of only four internodes (I-IV in Fig. 9.11) approximated or exceeded 70%, indicating that they could be accepted as real (p <0,05). The branch separating *C. stuhlmanni* and *C. asiatica* was not consistent, indicating that *C. stuhlmanni* could not confidently be assigned to the ingroup. The other OTUs were, however, delimited as members of the ingroup by Internode I. Internode II defined *C. sclateri* and *C. duthieae* as representatives of a distinct clade, whereas Internode III indicated that the *Amblysomus* OTUs are phylogenetically divergent from the lineage represented by *C. obtusirostris* and *C. leucorhina.* Within the *Amblysomus* clade, Internode IV delimited two phylogenetic lineages: one comprising the larger-sized *Amblysomus* species and *A. marleyi*; and the other represented by *A. gunningi* and *A. julianae.* The cladogram also suggested that *C. arendsi* OTU is distinct from *C. stuhlmanni* (Internode I), but not from *C. leucorhina* and *C. obtusirostris*, since the bootstrap proportions for the branches between these OTUs did not exceed 70%.

The 4:1 weighting analysis therefore defined more phylogenetically significant clades that equal weighting suggested. Moreover, it yielded a higher rescaled consistency index (*RCI* = 0,542) and lower homoplasy excess ratio (*HSR* = 0,315) than the equal weighting test (*RCI* = 0,482; *HSR* = 0,362), indicating a reduction in homoplasy. In contrast to the equal weighting tree, no homoplasy was indicated for malleus morphology (incudomallear ratio). While a parallel loss in M3 was indicated in *C. obtusirostris* and the *Amblysomus* clade, this is more likely to occur than the reacquisition of a complex plesiomorphic structure (Mayr and Ashlock 1991), such as that implied by the equal weighting cladogram.

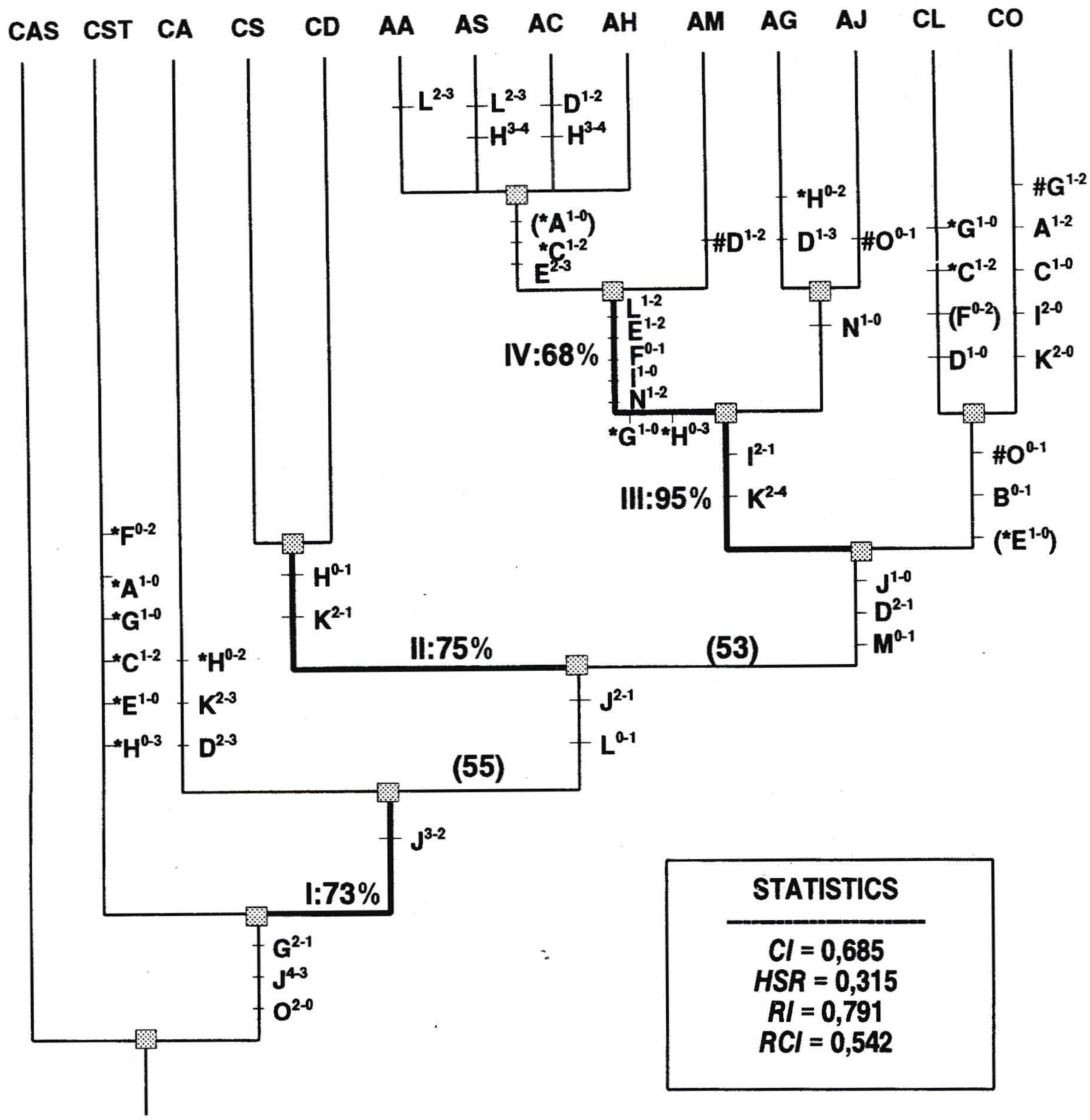


Figure 9.11. A strict consensus tree derived from five equally parsimonious cladograms computed from 15 characters in 13 chrysochlorid species and the outgroup (*Chrysochloris asiatica*; CAS), with differential weights applied. See Table 9.1 for an explanation of OTU codes, and Table 9.2 for a description of characters and character states. Superscripts indicate hypothesized character state changes. Parallelisms are denoted by asterisks (*), and reversals by a double slash (#). Bold lines indicate internodes (I-IV) that can be considered real on the basis of significant ($p < 0,05$) bootstrap values. Values in parentheses indicate non-significant bootsrap proportions. Letters in parentheses denote parallelisms that would not constitute homoplasies if *C. stuhlmanni* is not treated as a member of the ingroup.

The decreased homoplasy of the differential weighting tree was attributable to mainly a reduction in the number of reversals, from seven to four, all of which involved craniometric characters. Two reversals were indicated for ZMB:GSL, suggesting that broader and shorter skulls arose independently in *A. julianae* and the *C. obtusirostris*/*C. leucorhina* clade, by regression toward the plesiomorphous condition in *C. asiatica*. Similarly, the cladogram suggested that the short, broad palates of *C. obtusirostris* (P@P:PPL; character G) and *A. marleyi* (PAL:MIO; character D) arose independently by reversals to an ancestral condition.

Of the 16 parallelisms suggested by the cladogram, all involved craniometric characters. Six of the parallelisms were located on the branch leading to *C. stuhlmanni*, which may underscore the apparent lack of any significant phylogenetic divergence between this OTU and *C. asiatica*. If *C. stuhlmanni* is not considered as member of the ingroup, then the hypothesized changes involving claw size (E^{1-0}) and posterior palate width (F^{1-0}) in the *C. obtusirostris*/*C. leucorhina* lineage, and relative palate width (A^{1-0}) in the *Amblysomus* clade, no longer constitute parallelisms. The remaining parallelisms would thus involve only three characters: MIO:P@P (character C), P@P:PPL (Character G), and APW:ZMB (character H). The cladogram suggested that MIO:P@P increased, and P@P:PPL decreased, independently in *C. leucorhina* and the *Amblysomus* lineage, which could have resulted from a parallel change in only palate width in both clades. Conversely, the hypothesized changes in APW:ZMB must have involved an independent increase in the width of the ascending process in *C. arendsi*, *A. gunningi*, and the *Amblysomus* clade.

The differential weighting (4:1) analysis thus produced a more consilient and less homoplastic cladogram than that yielded by equal weighting. Subsequent exploratory analyses affording non-metric skull characters only double the weight of craniometric traits (*RCI* = 0,486; *HSR* = 0,360), or employing successive weighting (*RCI* = 0,638; *HSR* = 0,250), yielded trees with identical topologies to the 4:1 cladogram, suggesting that this embodies a relatively robust hypothesis of phylogenetic relationships among the chrysochlorid OTUs studied.

Using the technique given by Mayr and Ashlock (1991), and explained in detail by Brothers (1975), a phylogram was derived from the 4:1 cladogram (Fig. 9.12). This indicated that cladogenesis among the *A. gunningi*/*A. julianae*, *C. obtusirostris*/

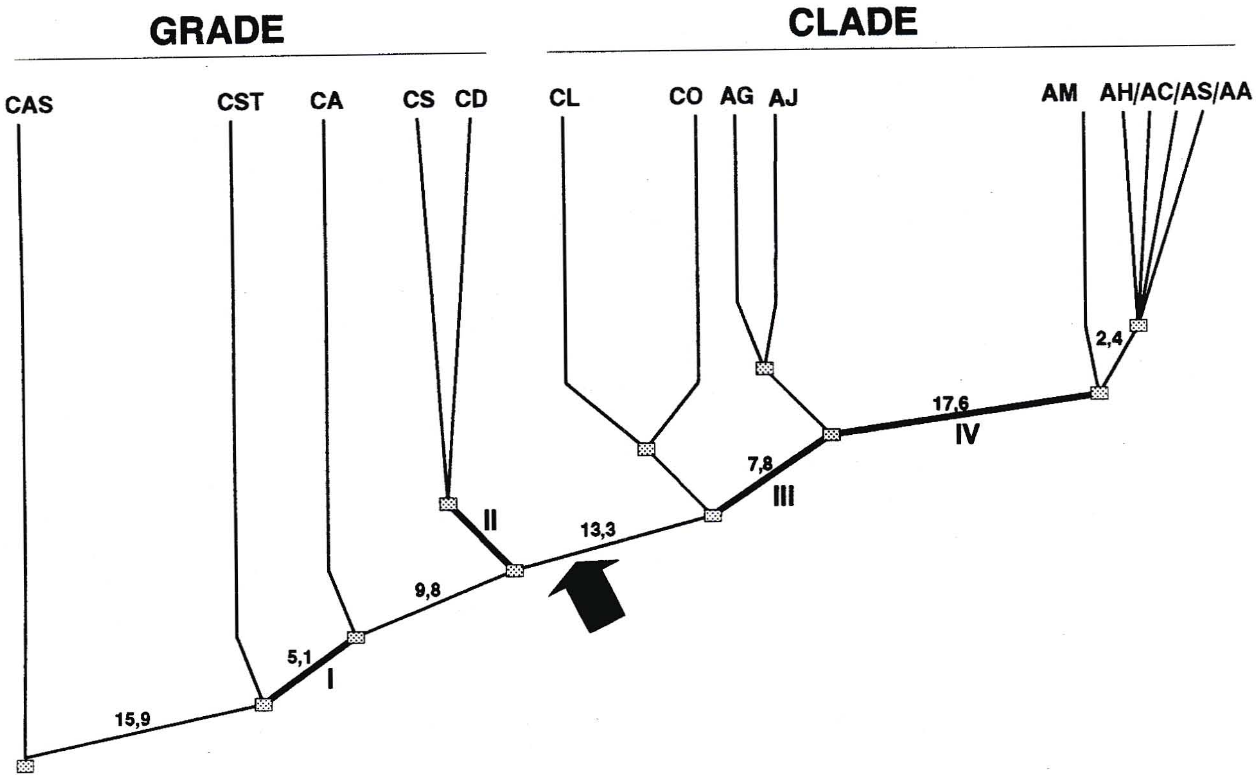


Figure 9.12. A phylogram derived from the 4:1 weighting cladogram (Fig. 9.11) using the technique of Brothers (1975). Patristic distances between OTUs along the horizontal axis are proportional to taxonomic gap values, which are expressed as percentages next to each internode. Internodes (I-IV) that bootstrap analyses showed to be consistent (*p* < 0,05) are indicated by bold lines. The midpoint of anagenetic divergence between the two most dissimilar OTUs is indicated by an arrow, and delimits one clade and one grade of evolution among the 14 species examined.

C. leucorhina and *Amblysomus* clades was accompanied by marked anagenesis. Conversely, the phylogram suggested that marked anagenetic divergence has occurred between *C. stuhlmanni* and *C. asiatica*, in contrast to the lack of any significant phylogenetic differentiation between these OTUs evident in the cladogram. The patristic distance between the *C. obtusirostris/C. leucorhina* and *C. arendsi* OTUs was also quite large, even though the internodes between these taxa were not phylogenetically significant.

If the longest internode (IV) was used to delimit units of anagenetic advance, as suggested by Mayr and Ashlock (1991), the OTUs fell into two assemblages: one clade comprising the *Amblysomus* species excluding *A. gunningi* and *A. julianae*; and one grade, which including the remaining OTUs, and was paraphyletic. This in itself posed no problem, since paraphyletic taxa constitute natural taxa (Ashlock 1971; Charig 1982). But, the grade comprised OTUs that phenetic analyses showed to be quite dissimilar. In contrast, using the midpoint of anagenetic divergence defined one clade and one grade (Fig. 9.12) that concurred with the phena in the Gower's distance phenogram (Figure 9.9), thereby leading to greater consilience.

9.4 TAXONOMIC CONCLUSIONS

9.4.1 Generic boundaries and relationships

The phenetic and cladistic analyses performed showed a fair degree of concordance (Fig. 9.13). In terms of matches between the number of groups (phena/clades) discriminated, the Gower's distance phenogram (Fig. 9.9) and the cladogram (Fig. 9.11) were most similar. Combining largely incongruent craniometric and non-metric characters thus altered patterns of discrimination quite markedly, and resulted in greater concordance than was evident in the phenetic analyses based on craniometric data alone.

Cladistic relationships among *A. hottentotus*, *A. corriae*, *A. septentrionalis*, *Amblysomus Species A* and *A. marleyi* were not resolved by the limited data available. While size varies quite conspicuously in this clade, phenetic analyses showed that differences in cranial shape are not sufficiently marked to warrant the recognition of any discrete supraspecific taxa in this group. Whether or not non-metric characters

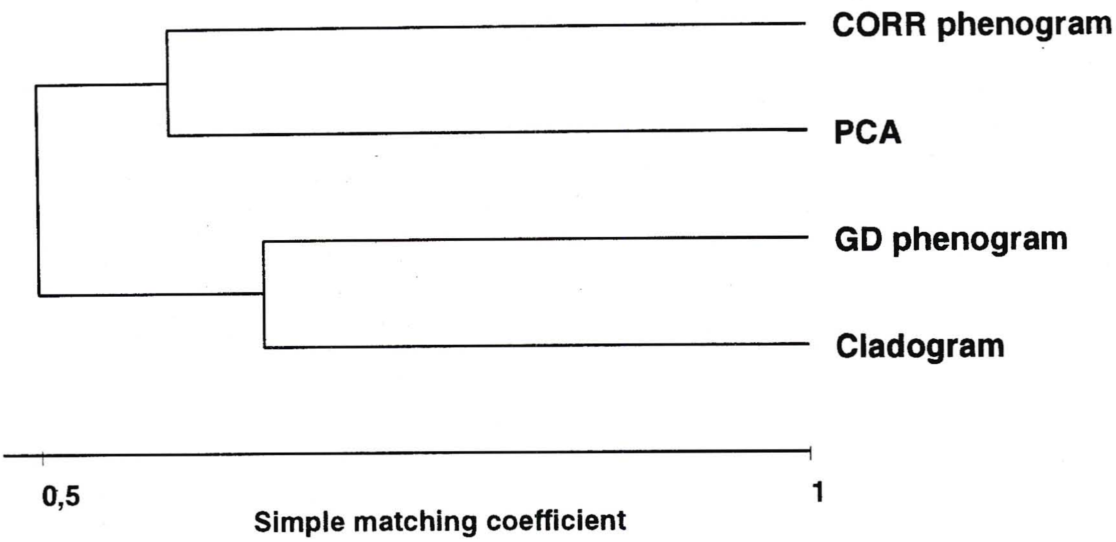


Figure 9.13. Phenogram indicating the degree of concordance between phenetic analyses in which the effect of size was controlled for, and the 4:1 strict consensus tree. Simple matching coefficients were computed from binary data indicating partial or complete correspondece (1), or no agreement (0), between the phena at successive hierachical levels in each analysis. The matrix on which this cluster analysis was performed is shown below.

PHENA (Figure No.)	**CORR** (9.8)	**GD** (9.9)	**PCA** (9.6)	**Cladogram** (9.11)
(CA)	0	1	0	1
(CST)	0	1	0	1
(CL)	0	1	1	0
(CO)	1	1	1	0
(CO+CL)	0	0	0	1
(AG+AJ)	0	1	0	1
(AG+CA)	1	0	0	0
(AJ+CO)	1	0	0	0
(AS+AA)	1	1	1	1
(CD+CS)	1	1	1	1
(CL+CST)	1	0	0	0
(AM+AC+AH)	1	1	1	1
((CD+CS)(CA))	0	1	0	0
((CD+CS)(CA)(CST))	0	1	0	0
((AG+CA)(AJ+CO))	1	0	0	0
((AH+AJ+AA+AS)(CST))	0	0	1	0
((CL+CST)(AJ+CO)(AG+CA))	1	0	0	0
((AM+AC+AH)(AS+AA))	1	1	0	0
((AM+AC+AH)(AS+AA)(CD+CS))	1	0	0	0
((AM+AC+AH)(AS+AA)(CO))	0	1	0	0
((AM+AC+AH)(AS+AA)(CO)(AG+AJ))	0	1	0	0
((AM+AC+AH)(AS+AA)(CO)(CL)(AG+AJ))	0	0	0	1

were included, the various analyses indicated close phenetic and phylogenetic affinity between *C. sclateri* and *C. duthieae*, and also among the *Amblysomus* species (excluding *A. gunningi* and *A. julianae*). Taxonomic recognition of these two groups is thus warranted. Since these two groups are cladistically and phyletically distinct, they cannot legitimately be assigned to the same genus (*Amblysomus sensu* Petter 1981).

The phenetic resemblance of *C. arendsi* and *A. gunningi* suggested by craniometric data was not evident once qualitative characters were taken into account. Since significant phylogenetic and anagenetic divergence has occurred between these OTUs, their similarity in cranial size and shape must be the result of convergence. Conversely, close affinity between *A. gunningi* and *A. julianae* was evident in both the Gower's distance phenogram and the cladogram. This indicated that these OTUs represent a distinct clade in which little anagenetic divergence has occurred, despite their quite marked differences in cranial size. Since the divergence between this clade and the other *Amblysomus* species is phylogenetically significant, their allocation to the same genus by most previous authors (Ellerman *et al.* 1953; Simonetta 1968; Meester 1974; Petter 1981) is not warranted. The relatively wide phyletic gap between these clades instead supports the taxonomic separation of *A. gunningi* and *A. julianae* in a distinct genus, for which the name *Neamblysomus* (Roberts 1924) is available.

That *C. obtusirostris* has a distinct evolutionary tendency from the *Amblysomus* species was evident in not only the cladograms, but also in the correlation phenogram and principal component axes scatterplot. The craniometric divergence of these clades is, therefore, of phylogenetic significance. The tendency for *C. obtusirostris* to group with the *Amblysomus* species in the Gower's distance phenogram may be attributed to the similarity of these OTUs in malleus morphology, and their joint lack of M3. Cladistic analysis showed, however, that the M3 in these groups were probably lost independently. These OTUs therefore share only one synapomorphy. Simonetta's (1968) treatment, which synonymized *Calcochloris* with *Amblysomus* on the basis of this character alone, is therefore not defensible if craniometric properties are also taken into account. The marked phylogenetic and anagenetic divergence between *C. obtusirostris* and the *Amblysomus* OTUs instead supports Meester's (1974) allocation of these taxa to different genera.

The relatively close affinity between *C. obtusirostris* and *C. leucorhina* suggested by the cladogram was evident also in the correlation phenogram, and in the scatterplot comparing the first two principal component axes. These OTUs are, therefore, phenetically and cladistically distinct from the *Amblysomus* and smaller-sized *Chlorotalpa* species with which they were synonymized by some previous authors (Ellerman *et al.* 1953; Petter 1981). From the phylogram, it is however clear that *C. obtusirostris* and *C. leucorhina* have undergone quite marked anagenetic divergence since their origin from a hypothesized common ancestor. Given also the biogeographic differences between these species, which occupy widely separated and quite dissimilar ecotopes (equatorial forests and dry savanna woodland, respectively), their allocation to distinct subgenera seems warranted. *C. leucorhina* should, therefore, be assigned to the subgenus *Huetia* within *Calcochloris*. There is no firm phenetic or phylogenetic evidence in support of Forcart's (1942) hypothesis that this taxon is closely related to *Chrysochloris*.

The apparent similarity of *C. stuhlmanni* and the *Amblysomus* species indicated by phenetic analyses of only craniometric characters was not evident when non-metric characters were included. Since no hyoid or chromosomal data were available for *C. stuhlmanni*, its separation from the *Amblysomus* OTUs in the Gower's distance phenogram and the cladogram was influenced largely by the malleus and dental characters.

Cladistic analyses indicated that *C. stuhlmanni* is phylogenetically distinct from the smaller-sized *Chlorotalpa* OTUs, as argued by Lundholm (1955) and Simonetta (1968). The apparent lack of significant phylogenetic divergence between this *C. stuhlmanni* and *C. asiatica* instead implied that the former should be considered a member of the outgroup, and that its allocation to the genus *Chrysochloris* by Meester (1974) and Petter (1981) is justified. But, discriminant functions analyses showed that *C. stuhlmanni* and *C. asiatica* have diverged markedly in cranial shape. This divergence is correlated with a pronounced difference in malleus size, and consequently also the development of the epitympanic recess (Section 9.2.2.3). The difference in malleus size between *C. stuhlmanni* and *C. asiatica* is similar in magnitude to that between species with enlarged, bulbous mallei (such as *C. arendsi*) and those with with unspecialized mallei (most *Amblysomus*). Since the latter taxa grouped in different clades (Fig. 9.11), and were recognized as different genera by Meester (1974) and Petter (1981), disparity in the size of the malleus between *C. stuhlmanni* and *C. asiatica* must be taxonomically important.

From a biogeographical perspective, it also seems unlikely that these species - which occur at opposite extremes of the range of chrysochlorids - represent the same ontological higher taxon. Even if one assumes that *C. stuhlmanni* and *C. asiatica* are relicts of a formerly widespread lineage, as is suggested by fossil evidence (Butler and Hopwood 1957), the substantial anagenetic divergence evident between these OTUs in the phylogram suggests that they have distinct evolutionary tendencies and fates. Separation of *C. stuhlmanni* in the distinct genus *Kilimatalpa* is thus warranted.

9.4.2 A new classification of chrysochlorids

Classifications derived directly from the cladogram (Fig. 9.11) are shown in Table 9.13. Using the subordination convention, six taxonomic ranks are required to accommodate the 12 ingroup species, and six new higher taxa (two families, two subfamilies and two tribes) need to be described, of which three would be monotypic. While applying the sequencing reduces the number of ranks to four, three new subfamilies and one new subgenus would have to be erected, two being monotypic. In contrast, an evolutionary classification derived using phyletic principles (see Mayr and Ashlock 1981) would also require four categorical levels, but ranking can be adequately achieved using existing higher taxon names, with only one (the genus *Carpitalpa*) being monotypic.

This emphasizes the asymmetrical and excessively monotypic nature of cladistic classifications (Hull 1970). Mayr and Ashlock (1991) have shown that it is erroneous to assume that a classification can be translated into a single cladogram, and *vice versa*, and that sequencing contravenes one of the basic Hennigian tenets. It is thus simplistic and unnecessary to insist that a classification should mirror a cladogram. The evolutionary classification derived above is preferable, not only because it is more parsimonious in a nomenclatural sense, but also because such phylistic classifications provide the most robust, phylogenetically-natural and consilient foundation for studies in biology (Bock 1974; Charig 1982; Michener 1970).

Table 9.13

Schematic representation of subordinated and sequenced cladistic classifications derived from Figure 9.11, and of an evolutionary classification derived using the phylogram in Figure 9.12.

SUBORNINATED CLASSIFICATION	SEQUENCED CLASSIFICATION	EVOLUTIONARY CLASSIFICATION
Family: (New)	**Subfamily**: (New)	**Subfamily**: Chrysochlorinae
Genus: Carpitalpa	**Genus**: Carpitalpa	**Genus**: Carpitalpa
Species: Carpitalpa arendsi	**Species**: Carpitalpa arendsi	**Species**: Carpitalpa arendsi
Family: (New)	**Subfamily**: (New)	
Subfamily: (New)		
Genus: Chlorotalpa	**Genus**: Chlorotalpa	**Genus**: Chlorotalpa
Species: Chlorotalpa duthieae	**Species**: Chlorotalpa duthieae	**Species**: Chlorotalpa duthieae
Species: Chlorotalpa sclateri	**Species**: Chlorotalpa sclateri	**Species**: Chlorotalpa sclateri
Subfamily: Amblysominae		**Subfamily**: Amblysominae
Tribe: (New)	**Subfamily**: (New)	**Genus**: Calcochloris
Genus: Calcochloris	**Genus**: Calcochloris	**Subgenus**: Calcochloris
Species: Calcochloris obtusirostris	**Species**: Calcochloris obtusirostris	**Species**: Calcochloris obtusirostris
Genus: Huetia	**Genus**: Huetia	**Subgenus**: Huetia
Species: Huetia leucorhina	**Species**: Huetia leucorhina	**Species**: Huetia leucorhina
Tribe: (New)	**Subfamily**: Amblysominae	
Genus: Neamblysomus	**Genus**: Neamblysomus	**Genus**: Neamblysomus
Species: Amblysomus gunningi	**Species**: Neamblysomus gunningi	**Species**: Neamblysomus gunningi
Species: Amblysomus julianae	**Species**: Neamblysomus julianae	**Species**: Neamblysomus julianae
Genus: Amblysomus	**Genus**: Amblysomus	
Subgenus: Amblysomus	**Subgenus**: Amblysomus	**Genus**: Amblysomus
Species: Amblysomus hottentotus	**Species**: Amblysomus hottentotus	**Species**: Amblysomus hottentotus
Species: Amblysomus corriae	**Species**: Amblysomus corriae	**Species**: Amblysomus corriae
Species: Amblysomus septentrionalis	**Species**: Amblysomus septentrionalis	**Species**: Amblysomus septentrionalis
Species: Amblysomus Species A	**Species**: Amblysomus Species A	**Species**: Amblysomus Species A
Subgenus: (New)	**Subgenus**: (New)	
Species: Amblysomus marleyi	**Species**: Amblysomus marleyi	**Species**: Amblysomus marleyi

A revised classification of chrysochlorids, derived by integrating the results of this study with the treatment afforded by Meester (1974) to taxa not examined here, is presented in Table 9.14. The clade and grade evident in the phylogram (Fig. 9.12) correspond respectively with the subfamilies Amblysominae and Chrysochlorinae described by Simonetta (1957). These can be regarded as valid, phylogenetically-natural taxa, the Amblysominae being characterized by "normal" mallei, and the Chrysochlorinae by mallei that are enlarged to varying degrees. In contrast, Simonetta's (1957, 1968) allocation of *Eremitalpa* and *Chrysospalax* to the subfamily Eremitalpinae, based on their joint possession of spherical mallei, cannot be accepted because this may be the result of convergence (Von Mayer *et al.* 1995). Also, the malleus morphology of *Eremitalpa* is only intermediate between the "pear" and "pea" shapes (Forster-Cooper 1928), suggesting that these morphologies represent the same line of descent (Broom 1907a). *Eremitalpa* and *Chrysospalax* should, therefore, be regarded as no more than specialized representatives of the subfamily Chrysochlorinae.

My allocation of *C. tytonis* to the subgenus *Huetia* within *Calcochloris* is based on admittedly scanty evidence. This species is known from only a partially-complete type specimen, which was collected in southern Ethiopia, and described as *Amblysomus tytonis* by Simonetta (1968). His measurements of the mandible show that this species approximates the larger *Amblysomus* species in size, but Meester (1974) assigned it to *Chlorotalpa* because of the presence of an M3. The cladistic analyses I performed suggested, however, that the possession of an M3 is a symplesiomorphy, so the allocation of *C. tytonis* to *Chlorotalpa* on this character alone is not warranted. Furthermore, the malleus of *C. tytonis* this species is not inflated like those of the *Chlorotalpa* species, and instead resembles that of *C. leucorhina*, in which an M3 is also present. From the photograph provided by Simonetta (1968), it appears the stylohyal bone of *C. tytonis* is not nearly as robust as that in *Amblysomus* or *Neamblysomus*. Based on the character-state distributions evident in the cladogram, it seems most likely that *C. tytonis* represents a distinct species of the *C. obtusirostris*/ *C. leucorhina* clade, with closer biogeographic affinity to the latter. Until more specimens are available for study, the status of this species should however be regarded as *incertae sedis*.

Table 9.14

A revised classification of the Chrysochloridae. Asterisks indicate type species.

ORDER: Insectivora
SUBORDER: Chrysochloromorpha
FAMILY: Chrysochloridae

SUBFAMILY: Chrysochlorinae
GENUS *Eremitalpa*
SPECIES: *E. granti*
GENUS: *Chrysospalax*
SPECIES: *C. trevelyani**
SPECIES: *C. villosus*
GENUS: *Chrysochloris*
SUBGENUS: *Chrysochloris*
SPECIES: *Chrysochloris asiatica**
SPECIES: *Chrysochloris visagiei incertae sedis*[1]
SUBGENUS: *Kilimatalpa*
SPECIES: *Chrysochloris (K.) stuhlmanni*
GENUS: *Cryptochloris*
SPECIES: *Cryptochloris zyli**
SPECIES: *Cryptochloris wintoni*
GENUS: *Carpitalpa*
SPECIES: *Carpitalpa arendsi**
GENUS: *Chlorotalpa*
SPECIES: *Chlorotalpa duthieae**
SPECIES: *Chlorotalpa sclateri*

SUBFAMILY: Amblysominae
GENUS: *Calcochloris*
SPECIES: *Calcochloris (H.) tytonis incertae sedis*[2]
SUBGENUS: *Calcochloris*
SPECIES: *Calcochloris (C.) obtusirostris**
SUBGENUS: *Huetia*
SPECIES: *Calcochloris (H.) leucorhina*
GENUS: *Amblysomus*
SPECIES: *Amblysomus hottentotus**
SPECIES: *Amblysomus corriae*
SPECIES: *Amblysomus septentrionalis*
SPECIES: *Amblysomus Species A*
SPECIES: *Amblysomus marleyi*
GENUS: *Neamblysomus*
SPECIES: *Neamblysomus gunningi*
SPECIES: *Neamblysomus julianae*

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[1] - known only from the type specimen. Having examined this specimen, I agree with Meester (1974) that it is may simply be an aberrant specimen of *C. asiatica*. More data are, however, needed to confirm that this taxon represents only a subspecies of *C. asiatica*, as maintained by Simonetta (1958).

[2] - known from only the type specimen, which was not examined.

The evolutionary classification of chrysochlorids that I propose represents a scientific hypothesis, since it can be tested by subsequent revisions based on other data suites (Bock 1974; Brothers 1985; Griffiths 1974; Hull 1967; Kitts 1977). Although some authors have argued that classifications are conventions rather than theories (Ruse 1979), the cladogram (Fig. 9.11) on which this classification is essentially based represents a hypothesis that is potentially falsifiable (Mayr and Ashlock 1991). The merits and demerits of this hypothesis need to be established using other data suites, particularly DNA sequence data which allow a more direct and objective assessment of genotypic divergence. Further study of the anatomy and functional role of the middle ear in chrysochlorids is also needed, to confirm that the unusual mallei shown in some species are indeed homologous, and to clarify whether hypertrophied mallei should be considered as plesiomorphic or apomorphic in chrysochlorids. This issue has vexed some previous authors, who argued that the inflated mallei observed in some species are evolutionary innovations (*e.g.* Von Mayer *et al* 1995), but nevertheless considered the *Amblysomus* species having "normal" mallei to be the most advanced of all chrysochlorids (Broom 1907a; Roberts 1951).

CHAPTER 10

KEYS AND SPECIES ACCOUNTS

10.1 KEY TO SUBFAMILIES AND GENERA

1. Malleus enlarged with a spherical or club-like shape; epitympanic recess housing the head of the malleus visible externally as a bony vesicle on the inner side of the zygomatic arch, or as a swelling on the lateral face of the squamosal; if no vesicle is present, an M3 is present **and** well-developed talonids are present on the lower molars (SUBFAMILY CHRYSOCHLORINAE) 2

-. Malleus not expanded, with a typical mammalian shape; M3 absent but molar talonids present and well developed **or** M3 present but molar talonids are absent/feeble (SUBFAMILY AMBLYSOMINAE) 8

SUBFAMILY CHRYSOCHLORINAE

2. Size larger, greatest skull length 32mm or more, zygomatic breadth greater than 20mm; head of malleus housed in a bony vesicle visible externally as a lateral swelling of the squamosal; zygomatic arch produced upwards posteriorly to meet lambdoidal crest at back; fur long and coarse, without a pronounced sheen . . . . *Chrysospalax*

-. Size smaller, greatest skull length less than 30mm, zygomatic breadth 19mm or less; epitympanic recess housing the head of the malleus not visible as a lateral swelling of the squamosal; zygomatic arch not produced upwards posteriorly to meet with lambdoidal crest; fur shorter, softer and invariably glossy 3

3. Head of the malleus housed in a bony vesicle that is clearly visible on the inner side of the zygomatic arch 4

-. Epitympanic recess (housing the malleus) not visible externally on the skull 7

4. Skull extremely broad, width/length index 85-90%; head of malleus spherical and housed in a small vesicle visible as only a slight swelling of the squamous temporal on the inner side of the zygomatic arch; fourth foreclaw well-developed, more than 2,5 mm long . . . . *Eremitalpa*

-. Skull less broad, width/length index less than 80%; head of malleus club-shaped and housed in a bony vesicle clearly visible as a pronounced swelling (bulla) on the inner side of the zygomatic arch; fourth foreclaw not well-developed, less than 2mm long 5

5\. Skull elongate, width/length index less than 65%; talonids usually present on the lower molars . . . . *Kilimatalpa*

-\. Skull broader, width/length index greater than 70%; molar talonids absent.... 6

6\. First claw of forefoot nearly as long as second, with a broad plantar pad at its base; frontal region of skull greatly expanded; temporal bulla (housing the head of the malleus) not prominent . . . . *Cryptochloris*

-\. First claw of forefoot much shorter than second, and without a broad pad at its base; frontal region only moderately expanded; temporal bulla housing the head of the malleus prominent . . . . *Chrysochloris*

7\. Size larger, greatest skull length more than 25 mm; skull elongate, width/length index less than 60%; palate relatively longer, palate length/mid inter-orbital width index greater than 180%; stylohyal bone bulbous . . . . *Carpitalpa*,pg. 273

-\. Size smaller, greatest skull length 21-24.5 mm; skull broader, width/length index greater than 61%; palate relatively broad, palate length/mid inter-orbital width index less than 178%; stylohyal slender, or semi-bulbous only medially . . *Chlorotalpa*, pg.277

SUBFAMILY AMBLYSOMINAE

8\. P1 molariform; rostrum wider, anterior rostral breadth more than 21% of greatest skull length; claws gracile, basal width of the third foreclaw less than 14% of greatest skull length; skull broader, width/length index greater than 70% . . *Calcochloris*, pg. 282

-\. P1 sectorial; rostrum narrow, anterior rostral breadth less than 20% of greatest skull length; claws more robust, basal width of the third foreclaw greater than 16% of greatest skull length; skull narrower, width/length index less than 70% 9

9\. Talonids absent; M3 present variably; palate broader, greatest width across P^2 greater than 29% of greatest skull length, and more than 92% of post-palatal length; nucleolar organizer regions located on the short arms of the twelfth and thirteenth smallest chromosomes . . . . *Neamblysomus*, pg. 289

-\. Talonids present and well developed; M3 usually absent; palate narrower, greatest width across P^2 less than 29% of greatest skull length, and less than 90% of post-palatal length; nucleolar organizer regions located on the short arms of the eigth and eleventh smallest chromosomes . . . . *Amblysomus*,pg. 293

10.2 ACCOUNTS OF SPECIES EXAMINED IN THIS STUDY

The key and accounts below refer to only those species which were included in *Amblysomus*, *Chlorotalpa* and *Calcochloris* by Meester (1974). For keys and notes on the genera (*Chrysospalax*, *Eremitalpa*, *Chrysochloris*, *Cryptochloris* and *Kilimatalpa*) not considered in detail during this study, see Meester (1974) and Hutterer (1995).

In the Specimens Examined section of each species account, the names of localities pooled for analyses of craniometric variation in previous chapters are given in upper case italics. For the South African species, boldfaced district names refer to magisterial districts on the most recent 1:2 500000 map available (Government Printer, 1994). Veld types indicated are those of Acocks (1988), whereas biome names follow Rutherford and Westfall (1986). These updated biomes largely correspond with the biotic zones recognized by Rautenbach (1978), as follows: Fynbos biome = Sout-West Cape biotic zone; Grassland biome = Southern Savanna Grassland biotic zone; Savanna biome = Southern Savanna Woodland biome; Nama-Karoo and Succulent Karoo biomes = South West Arid biotic zone. See the Gazetteer at the end of this chapter for more information about localities, and Chapter 2 for a description of museum number abbreviations.

10.2.1 *Carpitalpa*

Carpitalpa Lundholm, 1955

1955 *Carpitalpa* Lundholm, *Annals of the Transvaal Museum*, 22:285. *Chlorotalpa (Carpitalpa) arendsi* Lundholm.

Simonetta (1968) afforded *Carpitalpa* generic status, to include *Kilimatalpa* (which Lundholm, 1955 described as a new subgenus of *Chlorotalpa* for the species *stuhlmanni*). In contrast, Meester (1974) included *Kilimatalpa* with *Chrysochloris*, and synonymized *Carpitalpa* in *Chlorotalpa*, while Meester *et al.* (1986) commented that differences between the *Chlorotalpa* species do not warrant subgeneric separation. Phylogenetic analyses (Section 9.4) showed, however, that *C. arendsi* has diverged considerably from both *C. stuhlmanni* and the smaller *Chlorotalpa* species in South Africa, implying that it should be allocated to a distinct genus.

Carpitalpa arendsi (Lundholm, 1955) **Arend's golden mole**

1955 *Chlorotalpa (Carpitalpa) arendsi* Lundholm, *Annals of the Transvaal Museum* 22:285. Pungwe Falls, Inyanga, eastern Zimbabwe.

Holotype. TM10512, adult male, TW3, collected at Pungwe Falls (19°05'S; 32°44'E) on the eastern escarpment of Zimbabwe by the Bernard Carp Expedition to Southern Rhodesia, on 26 January 1951. Altitude 2000m. Skin and skull in good condition. Total length 115 mm; hind foot length 15mm; basal claw width 4,19 mm.

Subspecies and Distribution (Fig. 10.1). No subspecies. Restricted to the eastern Zimbabwe escarpment at altitudes of 850 - 2000m a.s.l., from 18° - 20°S, with a marginal intrusion into the Vila Pery district of western Mozambique.

Diagnosis (Table 10.1). A relatively large species, with a total length of 115 - 141 mm, and a mass of 34 - 70g ($\bar{x}$ = 48,1±15,5g, *n* = 13). Males are slightly larger than females, as reflected by their higher mass (♂: $\bar{x}$ = 52,7±11,0, *n* = 7; ♀: $\bar{x}$ 41,6±19,6g, *n* = 5), but sexual dimorphism in cranial morphology is not pronounced. Fur colour is brownish-black (5YR2-3/2) dorsally, and grayish-brown (7,5YR4-5/2-3) ventrally, with a distinct violet or silver sheen. Small, molariform M3 are invariably present, and the first premolars are semi-molariform, although a trigonal/trigonid basin is not formed. Feeble talonids may occur on the lower molars of some young individuals, but are usually absent in adults. *C. arendsi* is easily distinguished from the yellow golden mole (*Calcochloris obtusirostris*) of the nearby Zimbabwe and Mozambique lowlands by its greater size, and the presence of an M3. The head of the malleus is more inflated than in the small South African *Chlorotalpa* species, from which *C. arendsi* is easily differentiated by the lack of well-developed molar talonids, more robust stylohyal bone, and relatively longer palate (palate length/inter-orbital breadth index more than 180%, *cf.* less than 175% in *C. sclateri* and *C. duthieae*).

Habitat. Favours loamy soils in montane grasslands and the fringes of rainforests, but is dependent on areas with less cover (Lundholm 1955), and does not penetrate deep into forests (Smithers and Lobao-Tello 1976; Smithers and Wilson 1979).

Protection status. This species readily exploits cultivated areas, and is adequately protected in the following conservation areas: Inyanga National Park; Mtarazi Falls National Park; Chimanimani National Park; Vumba Botanical Reserve;

Figure 10.1 Map of southern Africa, showing the distribution of *Carpitalpa arendsi*, *Calcochloris obtusirostris* (subspecies *obtusirostris*, *limpopoensis* and *chrysillus*), *Chlorotalpa duthieae*, *Chlorotalpa sclateri* (subspecies *sclateri*, *shortridgei*, *guillarmodi* and *montana*), *Neamblysomus gunningi* and *N. julianae*. Symbols indicate actual distribution records, plotted by quarter degree squares. Lines indicate possible distributional limits for each taxon, which were based largely on biogeographic criteria (see text).

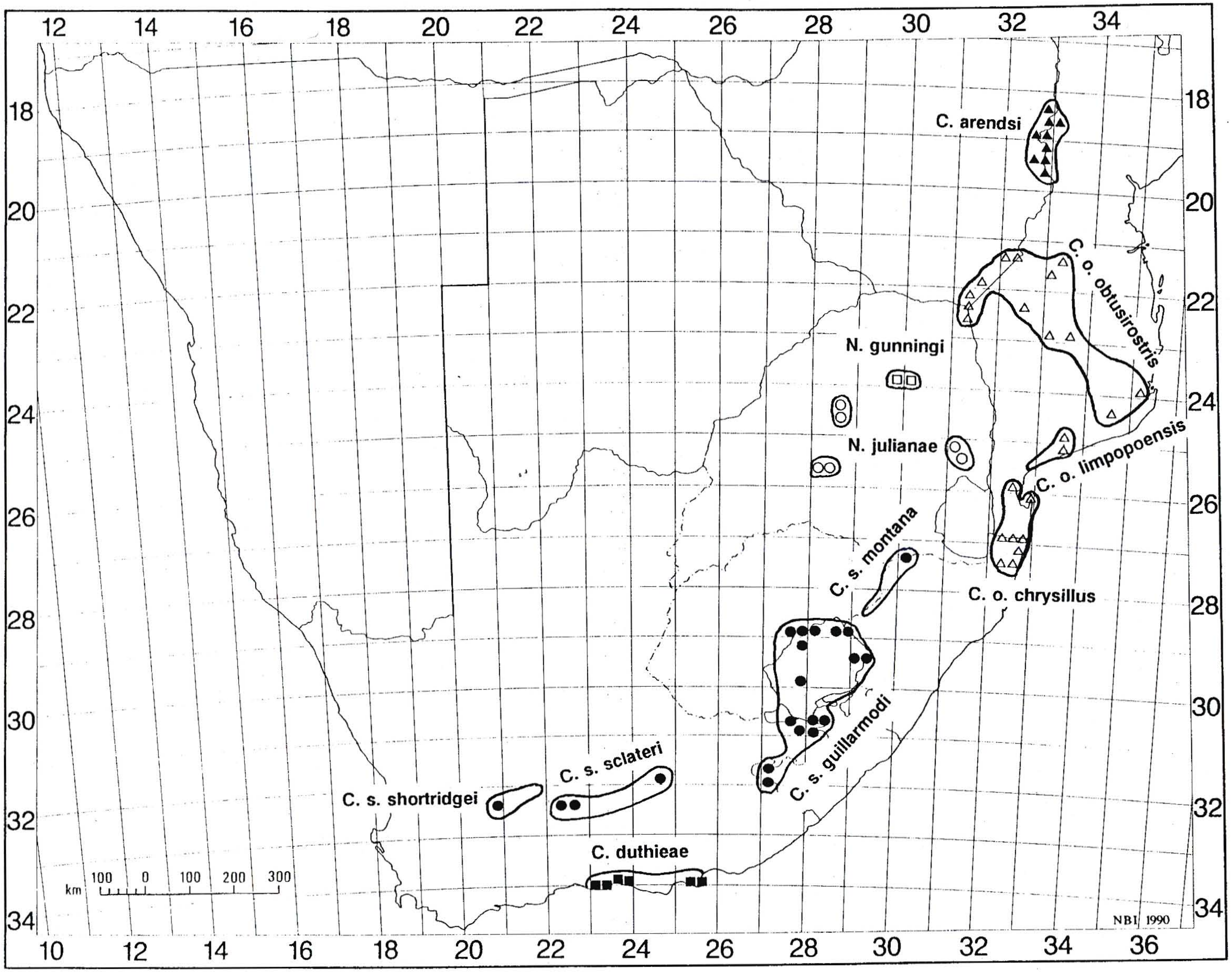
12 14 16 18 20 22 24 26 28 30 32 34
18 20 22 24 26 28 30 32 34
C. arendsi
C. o. obtusirostris
N. gunningi
N. julianae
C. o. limpopoensis
C. s. montana
C. o. chrysillus
C. s. guillarmodi
C. s. sclateri
C. s. shortridgei
C. duthieae
km 100 0 100 200 300
NBI 1990
10 12 14 16 18 20 22 24 26 28 30 32 34 36

Table 10.1

External and cranial measurements (in mm) for *Carpitalpa arendsi* specimens examined. $\bar{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\bar{x}$	*sd*	Range	*n*	$\bar{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	11	123,6	7,8	115-141	11	121,2	7,1	115-139
HF	9	14,2	3,7	14-16	11	13,2	2,7	12-16
BCW	7	4,3	0,1	4,1-4,5	8	4,4	0,4	4,0-4,9
CRANIAL MEASUREMENTS:								
ARB	7	4,9	0,2	4,7-5,2	8	4,9	0,2	4,7-5,1
MIO	7	7,8	0,3	7,5-8,3	8	7,8	0,3	7,4-8,3
ZMB	7	16,8	0,5	16,2-17,5	8	16,6	0,5	15,8-17,2
IOW	7	7,5	0,3	7,2-7,9	8	7,6	0,3	7,1-8,0
GSL	7	27,7	0,7	26,8-29,0	8	27,3	1,2	25,3-28,6
GSH	7	12,8	0,3	12,3-13,1	8	12,9	0,4	12,5-13,4
P@P	7	7,9	0,2	7,6-8,2	8	7,9	0,4	7,4-8,4
PBM	7	4,3	0,1	4,1-4,4	8	4,3	0,4	3,6-4,6
PAL	7	14,4	0,6	13,9-15,6	8	14,3	0,7	13,1-15,2
MTL	7	7,1	0,4	6,5-7,6	8	7,3	0,3	6,9-7,7
IPG	7	2,1	0,1	2,0-2,3	8	2,2	0,1	2,0-2,3
PPL	7	8,4	0,3	7,8-8,6	8	8,4	0,3	7,9-8,8
EAM	7	1,3	0,1	1,2-1,6	7	1,3	0,1	1,1-1,4
BBW	7	11,8	0,5	11,2-12,7	8	11,4	0,2	11,0-11,9
CPL	7	6,9	0,3	6,5-7,4	8	6,9	0,4	6,2-7,3
APW	7	4,2	0,3	3,9-4,7	8	4,1	0,3	3,7-4,6
MDL	7	17,0	0,6	16,4-17,9	8	17,1	0,6	16,0-18,0
FML	5	4,8	0,2	4,5-5,1	9	4,9	0,2	4,7-5,1

and Bunga Forest Reserve. Given its highly restricted geographic distribution, however, it should be considered as Rare according to current IUCN Threatened Species guidelines (Groombridge 1993). Perhaps because it is endemic to the escarpment on the border of Zimbabwe and Mozambique, it is not afforded special protection status in either country at present. This stands testament to the problems associated with defining endemics according to political rather than biological criteria (Gelderblom and Bronner 1995).

Specimens examined (*n* = 25). ZIMBABWE. Inyanga district (*n*= 9): Pungwe Falls - TM10512, 12778; ZM57803; Holdenby - ZM12543; Rhodes Estates - ZM57788, 57796; Trout Research Centre - ZM57793; Pamushana Farm - ZM19992; Mtarazi Falls - ZM57801; Mutare district (*n* = 6): Mutare Town - NM695; Honde Valley - ZM57791-2; Imbeza Valley - ZM57795; Chashammer Pan - ZM57804; Hycroft - ZM57790; Vumba district (*n* = 8): Bunga Forest Botanical Reserve - 57798; Vumba Botanical Reserve -ZM9726; Vumba Mountain - ZM60633; TM12965; Cloudlands Farm - ZM57805; Eagle School - ZM57789; Hermitage - ZM57802; Chinyauwhera - ZM57787; Melsetter district (*n* = 1): Fairview - ZM57797; MOZAMBIQUE. Sofala district (*n* = 1): Vila Gouveia - SI365001.

10.2.2 *Chlorotalpa*

Chlorotalpa Roberts, 1924

1924 *Chlorotalpa* Roberts, *Annals of the Transvaal Museum*, 10:64. *Chrysochloris duthieae* Broom

1. Fur colour uniformly reddish black (10R 2/2) or brownish black (5YR 2/2); stylohyal bone slender, without distinct bulge at the base of the styloid process; X chromosome acrocentric . . . . *C. duthieae*

-. Fur colour reddish brown (5YR 3-5/3-6) dorsally; stylohyal bone more bulbous, with a distinct bulge at the base of the styloid process; X chromsome metacentric . *C. sclateri*

Chlorotalpa duthieae (Broom, 1907) Duthie's golden mole

1907 *Chrysochloris duthieae* Broom, *Transactions of the South African Philosophical Society* 18:292. Knysna, Western Cape Province, South Africa.

Holotype. SAM9790, female, TW3, collected by Miss A. Duthie (after whom this species is named) at Knysna in April, 1907. Skin and skull in good condition, basal claw width 3,70 mm.

Subspecies and Distribution (Fig. 10.1). No subspecies. Ranges narrowly along the southern coast of South Africa, from George (22°E) in the Western Cape to Port Elizabeth (26°E) in the Eastern Cape.

Diagnosis (Table 10.2). A relatively small species, with a total length of 95-130 mm, and a mass of 20-41 g. Sexual size dimorphism is marked, males being slightly heavier ($\bar{x}$ = 33,6±6,1g) than females ($\bar{x}$ = 26,5±4,5), and significantly larger in most cranial measurements. Specimens from Knysna are generally larger than those from further east, but geographic variation is not sufficiently marked to warrant the recognition of any subspecies. The P1 are semi-molariform, and P^1 lack protocones, while well-developed talonids are invariably present on the lower molars. The fur is uniformly reddish-black (10R2/2) or brownish black (5YR2/2), and the stylohyal bone slender, in contrast to the reddish-brown (5YR3-5/3-6) fur and semi-bulbous stylohyal of *C. sclateri*. *C. duthieae* is easily distinguished from *Amblysomus corriae*, with which it coexists in some ares, by the presence of an M3, and its markedly smaller size (GSL < 25mm).

Habitat: Occurs in alluvial sand and sandy loams within coastal forests (Knysna forest, veld type 4) of the Fynbos biome, with a marginal intrusion into the savanna biome near Port Elizabeth. Coexists with *Amblysomus corriae* in parts of its range. Limited trapping data suggest, however, that where these taxa occur together (such as Natures Valley), they select different micro-habitats, *A. c. corriae* apparently favouring false fynbos and the forest fringes, and *C. duthieae* the deeper forest.

Protection status. Although an endemic species with a highly restricted range, the coastal forest habitats favoured by *C. duthieae* are adequately protected by the Tsitsikamma National Park, Wilderness National Park, Keurboomsriver Nature Reserve, as well as numerous forest reserves managed by either the Department of Water Affairs and Forestry, or local authorities. It also thrives in cultivated areas and

Table 10.2

External and cranial measurements (in mm) for *Chlorotalpa duthieae* specimens examined. $\overline{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\overline{x}$	*sd*	Range	*n*	$\overline{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	10	105,7	9,7	95-125	11	101,9	9,5	96-130
HF	9	11,6	1,3	9-14	9	11,6	1,0	9-13
BCW	8	3,7	0,2	3,5-4,0	10	3,5	0,2	3,3-3,7
CRANIAL MEASUREMENTS:								
ARB	8	4,4	0,3	4,0-4,8	10	4,2	0,1	4,0-4,6
MIO	8	7,2	0,3	6,8-7,6	10	6,9	0,3	6,7-7,4
ZMB	8	14,9	0,6	14,4-15,8	10	14,3	0,5	13,7-15,2
IOW	8	7,0	0,3	6,6-7,4	10	6,8	0,3	6,3-7,3
GSL	8	23,8	0,6	22,9-24,5	10	22,8	0,6	22,0-23,9
GSH	8	11,3	0,2	10,9-11,7	10	10,9	0,3	10,6-11,6
P@P	8	6,9	0,3	6,6-7,5	10	6,8	0,3	6,2-7,3
PAL	8	12,4	0,6	11,7-13,4	10	11,8	0,3	11,5-12,5
IPG	8	1,8	0,1	1,6-1,9	10	1,7	0,1	1,5-2,0
PPL	8	7,5	0,3	7,1-8,0	10	7,0	0,3	6,7-7,5
BBW	8	10,6	0,4	10,0-11,0	10	10,0	0,4	9,4-10,6
CPL	8	5,8	0,2	5,5-6,2	10	5,5	0,3	5,2-6,1
APW	8	3,6	0,1	3,3-3,7	10	3,3	0,2	3,1-3,8
MDL	8	14,6	0,4	14,1-15,1	10	13,9	0,4	13,4-14,7

Table 10.3

External and cranial measurements (in mm) for *Chlorotalpa sclateri* specimens examined. $\overline{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\overline{x}$	*sd*	Range	*n*	$\overline{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	16	100,9	11,4	83-135	13	102,2	13,3	82-123
HF	15	12,7	1,3	10-16	13	11,5	1,8	6-13
BCW	15	4,0	0,3	3,6-4,5	12	3,8	0,3	3,3-4,3
CRANIAL MEASUREMENTS:								
ARB	16	4,5	0,3	3,9-5,1	11	4,5	0,4	3,7-5,0
MIO	16	7,4	0,4	6,9-8,5	13	7,3	0,4	6,6-8,2
ZMB	16	15,4	0,9	14,5-17,6	13	15,1	0,8	14,1-16,9
IOW	16	6,9	0,3	6,2-7,8	13	6,9	0,3	6,3-7,4
GSL	16	23,6	1,5	21,8-27,4	13	23,4	1,6	21,2-26,7
GSH	16	11,5	0,6	10,8-13,0	13	11,4	0,7	10,4-12,8
P@P	16	6,9	0,4	6,2-7,9	12	7,0	0,4	6,6-7,7
PAL	17	12,2	0,9	10,6-14,8	12	12,3	0,9	10,8-14,3
IPG	17	1,7	0,1	1,4-2,0	12	1,8	0,1	1,6-2,0
PPL	16	7,4	0,3	6,9-8,2	12	7,4	0,5	6,8-8,3
BBW	14	10,3	0,6	9,7-12,0	12	10,4	0,6	9,5-11,4
CPL	17	5,9	0,4	5,4-7,0	13	5,8	0,4	5,3-6,6
APW	17	3,7	0,3	3,3-4,6	13	3,6	0,3	3,1-4,1
MDL	17	14,4	0,9	13,1-16,9	13	14,3	1,0	13,2-16,3

gardens (particularly in the Walmer district of Port Elizabeth), suggesting that it is not at risk from man's activities. These factors indicate that its Red Data Book status should be changed from Indeterminate (Smithers 1986) to Out of Danger.

Specimens examined (*n* = **34**). WESTERN CAPE. **Knysna district** (*n* = 7): Plettenberg Bay - TM701; Natures Valley - TM 39456,40514,40531-33,40535; POOLED LOCALITIES. *KNYSNA* = **Knysna district** (*n* = 7): Knysna Town and immediate vicinity - BM10962,251281,58101; SAM 9790; TM702,19118-9; *PORT ELIZABETH* = **Port Elizabeth district** (*n* = 20): Baakens Vlei - KM8968; Port Elizabeth city, and Walmer district - KM835-6,8969,18729,24476,PEM1434/61,62,70; SAM13616; SI221420; TM5268,16604,19111-7; ZM57799.

Chlorotalpa sclateri (Broom, 1907) Sclater's golden mole

1907 *Chrysochloris sclateri* Broom, *Annals and Magazine of Natural History* (7)19:263. Beaufort West, Western Cape Province, South Africa.

1924 *Cholotalpa montana* Roberts, *Annals of the Transvaal Museum* 10:64. Kastrol Nek (= Farm Tafelkop), east of Wakkerstroom, Mpumalanga Province, South Africa.

1936 *Chlorotalpa guillarmodi* Roberts, *Annals of the Transvaal Museum* 18:253. Mamathes, north-western Lesotho.

1950 *Chlorotalpa shortridgei* Broom, *Annals of the Transvaal Museum* 21:238. Sutherland, 160km west of Beaufort West, Western Cape Province, South Africa.

Holotype. *C. s. sclateri* - SAM3448, female, TW2, collected at Matjiesvlei near Beaufort West, and named after Mr W. Sclater, a past Director of the South African Museum. Skin and skull in good condition. *C. s. montana* - TM2900, male, TW4, collected by Dr. A. Roberts on 20 January 1922. Skin and skull in good condition, basal claw width = 4,16 mm; *C. s. guillarmodi* - TM7312, female, TW4, collected by Dr. C. Jacot-Guillarmod on 12 December 1933. Skin and skull in good condition, basal claw width 3,19 mm. *C. s. shortridgei* - KM14580, female, TW3. Skin and skull in good condition, basal claw width 4,01 mm.

Subspecies and Distribution (Fig. 10.1). Endemic to mountains in the central and eastern parts of South Africa. Four subspecies were recognized by Meester *et al.*

(1986), and appear to be valid based on the limited craniometric data available. *C. s. shortridgei* is known from only Sutherland in Northern Cape Province, and may range eastwards along the Nuweveldberge toward Beaufort West in the Western Cape, where it is replaced by *C. s. sclateri*. *C. s. sclateri* ranges northeastwards along the Koueveldberge and Sneeuberge to the Graaff-Reinet district. Meester *et al.* (1986) stated that this subspecies ranges also to Herschel and Lesotho, but this seems unlikely owing to the discontinuity of mountain ranges, and the intermediate intrusion of arid-Karoo habitat. *C. s. guillarmodi* occurs in high-altitude grasslands from the Herschel and Lady Grey districts of the Eastern Cape northeastwards through Lesotho (Lynch 1994), with a marginal intrusion into the eastern Free State and KwaZulu-Natal (Taylor *et al.* 1994). *C. s. montana* is known from only Wakkerstroom in Mpumalanga, but may range southwards from there along the Low Berg, to intergrade with *C. s. guillarmodi* in the vicinity of Harrismith and Clarens.

Diagnosis (Table 10.3). Relatively small, with a total length of 95-130 mm, and a mass of 22-54 g (n = 12). Males are slightly larger than females, but sexual dimorphism is not pronounced. P^1 are semi-molariform, and lack protocones, while the lower molars have well-developed talonids.

Cranial size and shape varies quite markedly on a geographical basis. *C. s. shortridgei* is generally larger than the other subspecies, with a broader rostrum ($\overline{x}$ = 4,68±0,1) than *C. s. sclateri* ($\overline{x}$ = 4,51±0,2). *C. s. sclateri* has a relatively longer palate (PAL/GSL: $\overline{x}$ = 53,6±0,3) than *C. s. guillarmodi* ($\overline{x}$ = 51,1±1,5), but the posterior palate is comparatively broader in the latter (IPG/P@P: $\overline{x}$ = 26,0±1,9) than the former ($\overline{x}$ = 23,3±0,4). *C. s. montana* is easily distinguished from *C. s. guillarmodi* by its significantly longer palate ($\overline{x}$ = 12,6±0,4 *cf.* 11,5±0,7, respectively).

Geographic variation in fur colour is negligible. The dorsal fur is reddish-brown (5YR 3-5/3-6), in contrast to the reddish-black fur of *C. duthieae*, from which *C. sclateri* is cranially indistinguishable. Although similar to *A. septentrionalis* in fur colour, *C. sclateri* is easily diagnosed from this species by its smaller overall size, more gracile claws (BCW < 4,5 mm *cf.* greater than 5 mm in *A. septentrionalis*), and also by the presence of an M3.

Habitat. Restricted to montane grasslands, scrub and forested kloofs in the Nama-Karoo and Grassland biomes. *C. s. shortridgei* occurs in Mountain renosterveld (veld type 43), and *C. s. sclateri* in Karooid mountain veld (veld types 42 and 60).

C. s. guillarmodi occurs in mainly *Themeda-Festuca* alpine veld (veld type 58; Lynch 1989), and marginally into transitional Highland Sourveld (veld type 56) of the eastern Free State. *C. s. montana* is known from only North-eastern Sandy highveld (veld type 57) near Wakkerstroom, where it favours forested kloofs over nearby grassland, in which *Amblysomus septentrionalis* instead predominates.

Protection status. Indeterminate. Recorded from the Garden Castle Nature Reserve (KwaZulu-Natal), Karoo National Park (Western Cape) and Golden Gate National Park (Free State). Probably occurs also in other natures reserves along the Drakensberg in KwaZulu-Natal. Where present, this species is locally common, and readily exploits gardens and cultivated areas, suggesting that it is not at any risk from man's activities.

Specimens examined (*n* = 40). LESOTHO. Leribe (*n* = 2) - TM4880,16582; Mamathes (*n* = 1) - TM7312; SOUTH AFRICA. WESTERN CAPE PROVINCE. **Sutherland district** (*n* = 5): Sutherland Town - KM14577-8,14580-2; **Beaufort West district** (*n* = 5): Matjiesvlei - SAM3448; Karoo National Park - TM39439, 39442, 39445,39447; EASTERN CAPE PROVINCE. **Graaf-Reinet district** (*n* = 1): Nieu-Bethesda - BM182182; **Lady Grey district** (*n* = 1): Helvellyn - NMB4358; **Barkly East district** (*n* = 3): Rhodes - KM24794-6; FREE STATE. **Ficksburg district** (*n* = 18): Ficksburg Town - KM19420,19854,19856-8; NMB6866,6868; TM41570-1, 41578,41591,41594-7; Gumtree, Kirklinton - KM18551,18704; **Clocolan district** (*n* = 2):Clocolan Town - TM4845,8766; MPUMALANGA. **Wakkerstroom district** (*n* = 2): Farm Tafelkop (= Kastrol Nek) - TM2900-1.

10.2.3 *Calcochloris*

Calcochloris Mivart, 1867

1867 *Calcochloris* Mivart, *Journal of Anatomy and Physiology, London*, 2(= ser.2, vol. 1):133. *Chrysochloris obtusirostris* Peters.

1907 *Chrysotricha* Broom, *Transactions of the South African Philosophical Society*, Cape Town, 18:303. *Chrysochloris obtusirostris* Peters. As a subgenus of *Chrysochloris*; raised to generic rank by Roberts, *Annals of the Transvaal Museum* 10:63, 1924.

1942 *Huetia* Forcart, *Revue Suisse de Zoologie* 49:2. *Chrysochloris leucorhina* Huet. As a subgenus of *Chrysochloris*.

1. Width of ascending ramus of mandible more than 5 mm . . . *C. tytonis incertae sedis*
-. Width of ascending ramus of mandible less than 4 mm 2

2. M3 present; palate elongated, greatest width across P^2 less than 90% of post-palatal length and smaller than mid inter-orbital width; posterior palate wide, interpterygoid/palate width index more than 30% (Subgenus *Huetia*) . . . . *C. (H.) leucorhina*

-. M3 absent; palate broad, greatest width across P^2 more than post-palatal length or mid inter-orbital breadth; posterior palate narrow, interpterygoid/palate width index less than 25% (Subgenus *Calcochloris*) . . . . *C. (C.) obtusirostris*

Calcochloris tytonis incertae sedis — Somali golden mole

1968 *Amblysomus tytonis* Simonetta, *Monitore Zoologica Italiano* 2(Supplemental):31. Giohar Village (=Villagio Duca degli Abruzzi), southern Somalia.

Holotype: Not traced. In the original description, Simonetta (1968) gave the number of this partially-complete (owl-pellet) specimen as "M.F. c. 4181", suggesting that it is housed in the Museo Zoologico at the Università di Firenze, where he was then based. Repeated enquiries to this university yielded no response, so it is possible that the holotype is missing. This illustrates aptly the problems associated with retaining voucher specimens in University collections (Meester 1990).

Subspecies and Distribution. Known only from the type specimens collected at 2°26'N and 45°30'E.

Notes. Simonetta (1968) showed that this species is considerably larger than either *C. leucorhina* or *C. stuhlmanni*, and that it approximates the larger-sized *Amblysomus* species, which it resembles also in malleus morphology. But, Meester (1974) assigned this species to *Chlorotalpa* based on the presence of an M3, which I have shown is a symplesiomorphic character among chrysochlorids. Although the few characters available for this species suggest that it may be closely related to *C. leucorhina* (Section 9.4), it should nevertheless be regarded as *incertae sedis* until more specimens are available.

Calcochloris (Calcochloris) obtusirostris (Peters, 1851)

Yellow golden mole

1851 *Chrysochloris obtusirostris* Peters, *Monatsberichte der Königlichen Preussichen Akademie der Wissenschaften zu Berlin*:467. Inhambane, coastal Mozambique.

1905 *Amblysomus chrysillus* Thomas and Schwann, *Proceedings of the Zoological Society, London* I:261. Maputo (= Delagoa Bay), coastal Mozambique.
1946 *Chrysotricha obtusirostris limpopoensis* Roberts, *Annals of the Transvaal Museum* 20:311. Masiene, north of the mouth of the Limpopo River, Mozambique.

Holotypes. *C. o. obtusirostris* - not examined, housed in the Berlin Museum. *C. o. chrysillus* - BM84.8.30.2, female, TW2, skin in good condition, skull badly damaged. *C. o. limpopoensis* - TM4110, male, TW4, collected by Mr G. van Dam at Masiene on 27 August 1924. Skin and skull in good condition, basal claw width 3,01 mm.

Subspecies and Distribution (Fig. 10.1). The distribution of *C. obtusirostris* closely follows the limits of the Mozambique sands. Three subspecies are recognized. *C. o. obtusirostris* (Peters, 1851) ranges throughout Inhambane and Gaza in Mozambique, with a marginal intrusion into the south-eastern lowlands of Zimbabwe and the Nyada sandveld of Northern Province (South Africa), via the Changane and Save river systems. In the Masiene district of Mozambique, *C. o. obtusirostris* is replaced by *C. o. limpopoensis* (Roberts, 1946), which intergrades with *C. o. chrysillus* (Thomas and Schwann, 1905b) in the vicinity of Maputo. *C. o. chrysillus* ranges southwards to the Ingwavuma and Ubombo districts of Maputaland in northern KwaZulu-Natal.

Diagnosis (Table 10.4). Amongst the smallest of the southern African species, with a total length of 82-110 mm, and a mass of 15-37g. Sexual size dimorphism is pronounced, with males being slightly heavier ($\bar{x}$ = 26,3±4,8 g) than females ($\bar{x}$ = 23,3±6,1g), and significantly larger in most cranial measurements. *C. o. limpopoensis* is significantly larger than the other subspecies (GSL > 22,5 mm). The rostrum is significantly wider (ARB > 7,2 mm) than in *C. chrysillus* (ARB < 7,1mm), while the claws are more gracile (BCW/GSL = 12,9±1,0%) than in

Table 10.4

External and cranial measurements (in mm) for *Calcochloris (Calcochloris) obtusirostris* specimens examined. $\bar{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\bar{x}$	*sd*	Range	*n*	$\bar{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	17	100,3	5,7	88-110	15	99,3	7,5	82-110
HF	17	11,3	1,2	10-13	13	11,6	1,3	9-14
BCW	20	3,0	0,2	2,6-3,5	17	2,9	0,2	2,5-3,2
CRANIAL MEASUREMENTS:								
ARB	23	5,1	0,2	4,7-5,4	19	4,9	0,3	4,5-5,3
MIO	23	7,2	0,3	6,8-7,7	18	7,1	0,3	6,2-7,6
ZMB	23	16,1	0,5	15,4-16,8	18	15,5	0,7	13,8-16,8
IOW	23	7,1	0,3	6,7-7,8	19	6,8	0,4	5,9-7,3
GSL	21	22,6	1,1	20,8-24,2	17	21,5	1,0	19,0-23,6
GSH	22	10,9	0,3	10,4-11,3	18	10,6	0,4	9,6-11,3
P@P	22	8,1	0,3	7,5-8,9	19	7,6	0,5	6,6-8,4
PAL	22	11,8	0,8	10,1-12,9	18	11,2	0,7	9,7-12,6
IPG	23	2,0	0,4	1,7-2,9	18	1,8	0,1	1,5-2,1
PPL	21	7,3	0,4	6,7-8,2	18	6,9	0,3	6,5-7,6
BBW	23	10,7	0,6	9,9-11,9	15	10,2	0,5	9,4-11,1
CPL	23	6,1	0,3	5,5-6,6	19	5,7	0,4	4,7-6,5
APW	23	3,5	0,3	3,1-3,9	19	3,1	0,3	2,7-3,8
MDL	23	14,5	0,8	13,1-15,8	19	13,7	0,8	11,8-15,0

Table 10.5

Canial measurements (in mm) for *Calcochloris (Huetia) leucorhina* specimens examined. $\bar{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\bar{x}$	*sd*	Range	*n*	$\bar{x}$	*sd*	Range
ARB	3	4,8	0,8	3,9-5,3	4	4,9	0,2	4,6-5,1
MIO	4	7,8	0,7	6,8-8,4	5	7,6	0,3	7,2-8,1
ZMB	4	15,7	1,3	13,8-16,9	5	15,4	1,5	12,9-16,7
IOW	4	7,3	0,6	6,5-7,8	5	7,1	0,4	6,6-7,6
GSL	4	21,7	1,4	19,5-22,8	4	22,2	0,9	21,0-23,1
GSH	4	10,3	0,8	9,3-11,2	5	10,4	0,4	9,9-10,7
P@P	4	7,0	0,3	6,7-7,3	5	6,5	0,6	5,6-7,2
PAL	4	10,6	0,9	9,5-11,3	4	10,9	0,5	10,3-11,4
IPG	4	2,3	0,3	2,1-2,6	5	2,0	0,2	1,7-2,2
PPL	4	7,9	0,4	7,4-8,3	4	7,9	0,2	7,7-8,0
BBW	4	10,2	0,5	9,4-10,5	5	10,5	1,0	8,9-11,5
CPL	3	5,9	0,2	5,8-6,1	5	5,7	0,5	5,0-6,2
APW	3	3,5	0,4	3,1-3,9	5	3,3	0,6	2,6-4,1
MDL	3	14,0	0,8	13,1-14,7	5	13,7	1,0	12,1-14,4

C. o. obtusirostris (BCW/GSL = 13,8±0,1%). Distinguishing between these three subspecies can, however, be problematical since they intergrade in size.

Perhaps the most distinctive feature of *C. obtusirostris* is the yellow-orange underfur, which is greyish in all other chrysochlorids. Dorsal fur colour ranges considerably, from light yellow orange (7,5YR8/4) through orange (7,5YR6/6), bright reddish-brown (7,5YR5/6) to dull brown (7,5YR5/4) and dark brown (7,5-10YR3-4/3-4), owing to a progressive increase in the extent of grizzled-brown tips to the hairs. Ventral fur colour is less variable, and ranges from yellow-orange (7,5YR7/4) through orange (7,5YR6-7/6-8) to bright brown (7,5YR5/8) or reddish brown (5YR4/6). Roberts (1951) and Thomas and Schwann (1905b) stated that the variability in fur colour in *C. obtusirostris* is correlated with subspecific differences. The basis of the variation I observed, however, seems to be the time between moults. Two of the *C. o. chrysillus* specimens examined (TM40469-70), and one *C. o. obtusirostris* (TM39470), were clearly in the process of moulting, with orange fur both dorsally and ventrally. One of these specimens also had a light yellow-orange mantle. From this pale orange extreme, fur colour tends to become more grizzled brown owing to increasing pigmentation of the hair tips, perhaps as a result of abrasion during tunnel construction. Such intergradation in colour is apparent even among individuals from the same locality and toothwear class, so it cannot be ascribed to either geographic or age-related variation *per se*.

C. obtusirostris is easily distinguished from the other southern African species by not only its fur, but also by the presence of a completely molariform P1, and a distinctly bicuspid canine. As in *A. hottentotus* and *A. marleyi*, the third lower molar is absent. But, considerable intraspecific variation occurs in other dental characters. Protocones are present on P^1 in more than 30% of the specimens examined, whereas molar talonids occur with an incidence of 6-13%. This variability is shown by all three subspecies, and thus does not have a geographic or taxonomic basis.

Habitat. Endemic to sandy soils of the Mozambique Coastal Plain. In KwaZulu-Natal, *C. o. chrysillus* occurs in sands supporting coastal forest and thornveld (veld type 1), whereas *C. o. limpopoensis* favours miombo savanna of eastern Mozambique. *C. o. obtusirostris* has been recorded from Acacia and Mopani savanna in Mozambique and the adjacent parts of Zimbabwe, and the north-eastern corner of South Africa.

Protection status. *C. o. chrysillus* is adequately protected in KwaZulu-Natal by Ndumu Game Reserve, Tembe Elephant Park, Kosi Bay Nature Reserve, Lake Sibaya

Nature Reserve, and the Maputaland Coastal Forest Reserve. In Mozambique, this subspecies occurs in the Maputo Elephant Reserve. *C. o. obtusirostris* has been recorded from the Kruger National Park in South Africa, and Gonarezhou National Park in Zimbabwe. It may also occur in the Gorongoza National Park of Mozambique. *C. o. limpopoensis* has not, however, been recorded from any conservation area.

Given that *C. obtusirostris* occurs in many conservation areas, and that its cryptic nature allows it to coexist with man, it does not appear to be at risk. Smithers (1986), however, afforded it Rare status owing to its only marginal occurrence in South Africa. Conservation status should not, however, be defined by political criteria (Gelderblom and Bronner 1995), and the Red Data Book status of this species should thus be changed from Rare to Out of Danger.

Specimens examined (*n* = 58). SOUTH AFRICA. KWAZULU-NATAL PROVINCE. **Ubombo district** (*n* = 2): Ubombo district - TM6071; Lake Sibaya - NM126; **Ingwavuma district** (*n* = 20): Amanzengwenya, Lalanek Inspection Quarters - TM40444,40446-8,40450; Kosi Lake - NM127; SI351335; TM40452,40458-9,40462-3,40469-71; Manguzi (= Maputa) - SI351334; TM6069-70,7396-7,7778,16069; Ndumu Game Reserve - DM407; KM18917,19028; NORTHERN PROVINCE. **Soutpansberg district** (*n* = 2): Kruger National Park, Nyadu Sandveld - TM30696,39470. MOZAMBIQUE. Gaza district (*n* = 1) - SI351995; Inhambane (*n* = 4): Coguno - BM611825-7; TM711; Maciene (*n* = 8) - TM4104-10,4112; Maputo (*n* = 4): Maputo City and suburbs - BM84830,848302; TM4771; Inhaca Island - TM8863; Nyaboa (*n* = 1) - ZM82581. ZIMBABWE. Gonarezhou district (*n* = 11): Confluence of Save and Lundi Rivers - SI470211; Fisham - ZM82582; Malugwe Pan - ZM82366-70,82583; Zinave, ZM82578-80.

Calcochloris (Huetia) leucorhina (Huet, 1885) Congo golden mole

1855 *Chrysochloris leucorhina* Huet, *Nouv. Arch. Mus. Hist. Nat. Paris* 8:8. Gulf of Guinea Coast, Congo.

1910 *Chrysochloris congicus* Thomas, *Annals and Magazine of Natural History* 8:84. Lusambo, upper Sankuru River, south-central Congo (Zaire).

1922 *Chrysochloris cahni* Schwarz and Mertens, *Senckenbergiana* 4:151. Molundo, Ja River, southeastern Cameroun.

1942 *Neamblysomus lulanus* Forcart, *Revue Suisse de Zoologie* 49:3. St. Josephs Mission, Luluaborg, Kassai district, Belgian Congo (Zaire).

Holotypes. *C. leucorhina* - not examined, housed in the Museum National d'Histoire Naturelle, Paris. *C. congicus* - BM9.12.10.2, female, TW2, skin in alcohol, rostrum of skull damaged. *C. cahni* - SKM6546, no sex, TW3. Skin and skull in good condition, basal claw width 2,63 mm. *N. lulanus* - not examined. Skin No. 3828 and Skull No. 7715, housed in the Basle Museum of Natural History, Switzerland.

Subspecies and Distribution. Following Meester (1974), *congicus* and *lulanus* are considered synonyms of *leucorhina*. There are thus two subspecies: *C. l. leucorhina*, which ranges from Zaire southwards to northern Angola, and *C. l. cahni* which is known from Cameroon and the Central African Republic. The validity of these subspecies is, however, far from certain owing to the few specimens available for study.

Diagnosis (Table 10.5). Similar in size to *C. obtusirostris*, with a total length of 65-126 mm. Fur colour dark brown to slate or mouse-grey (Hill and Carter 1941; Thomas 1910), the underside being slightly paler. A creamy-white mask occurs on the face, extending laterally almost to the ear. Although the fur of some *C. l. cahni* specimens appears somewhat lighter than of *C. l. leucorhina*, one of the Cameroun specimens shows a darker colouration, suggesting that there are no clearcut colour differences between the subspecies. Based on the few specimens available, there are also no distinct differences in cranial size between these taxa. M3 are invariably present, and the first premolars are completely molariform, but narrower than in *C. obtusirostris*. The lower premolars have well-developed talonids in *C. l. leucorhina*, but in *C. l. cahni* the talonids are feeble on P_{1-2}, and absent on P_3.

C. leucorhina is readily diagnosed from *C. stuhlmanni* by its smaller size (GSL < 23,5 mm *cf.* > 24 mm in the latter), and also by the shape of its skull, which is much broader (width/length index greater than 70%), than in *C. stuhlmanni* (width/length index less than 65%). The malleus of *C. leucorhina* is not inflated, so that there is no distinct sub-temporal bulla, as in *C. stuhlmanni*.

Habitat. Restricted to lowland equatorial forests of western Africa, and montane forests of central Africa.

Protection status. Indeterminate.

Specimens examined (n = 18). ANGOLA (n = 1). Poste de Canzar - BM631012; CAMEROUN (n = 3). Metet - CM4644; Pama-Quelle - SKM5826; Molundu (SK6546); CONGO (n = 4). Bolopo, Ndive - KMT15407,20838; Kunungu - KMT14157; Kwamouth - KMT6647; CENTRAL AFRICAN REPUBLIC (n = 1). Nsankulu-Betu - KMT81050; ZAIRE (n = 9). Bokungu - KMT19597-8; Kisangani - KMT280; Lusambo - BM912102; KMT8018; Luluaborg - BM277615; KMT35298; Ubangi, Duma - SM6608-9.

10.2.4 *Neamblysomus*

Neamblysomus Roberts, 1924

1924 *Neamblysomus* Roberts, *Annals of the Transvaal Museum* 10:64. *Chrysochloris gunningi* Broom.

1. Size larger, greatest skull length more than 27 mm; skull elongated, width/length index less than 63%; palate narrow, width/length index less than 58% . . . . *N. gunningi*
-. Size smaller, greatest skull length less than 24 mm; skull broad, width/length index greater than 67%; palate wide, width/length index more than 60% . . . . *N. julianae*

Neamblysomus gunningi (Broom, 1908) Gunning's golden mole

1908 *Chrysochloris gunningi* Broom, *Annals of the Transvaal Museum* 1:14. Woodbush Hill, Soutpansberg district, Northern Province, South Africa.

Holotype. TM703, female, TW3, collected in ploughed lands on Woodbush Hill on 7 December 1907. Skin in good condition, basal claw width 3,93 mm. Skull broken, mandible with stylohyal bone attached.

Subspecies and Distribution (Fig. 10.1). *N. gunningi* is known from only the far northern Drakensberg escarpment, between Haenertsburg, New Agatha and Tzaneen. No subspecies are recognized.

Diagnosis (Table 10.6). A relatively large species, with a total length of 111-132 mm, and a mass of 39-70 g. Males are slightly larger than females, as reflected by

Table 10.6

External and cranial measurements (in mm) for *Neamblysomus gunningi* specimens examined. $\bar{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\bar{x}$	*sd*	Range	*n*	$\bar{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	9	125,4	4,3	121-132	8	120,4	5,1	111-128
HF	9	15,3	1,3	14-18	8	14,0	3,2	14-17
BCW	10	4,7	0,1	4,5-4,9	6	4,5	0,2	4,3-4,8
CRANIAL MEASUREMENTS:								
ARB	11	5,0	0,2	4,7-5,3	6	4,7	0,1	4,6-4,9
MIO	11	8,1	0,4	7,6-8,7	6	7,8	0,1	7,6-8,0
ZMB	11	17,3	0,7	16,1-18,2	6	16,6	0,4	15,9-16,9
IOW	11	7,9	0,3	7,6-8,3	6	7,6	0,1	7,4-7,7
GSL	11	28,4	0,7	27,1-29,3	6	27,5	0,4	27,0-27,8
GSH	11	13,2	0,4	12,8-13,8	6	12,9	0,3	12,6-13,3
P@P	10	8,3	0,3	7,8-8,7	5	8,0	0,2	7,7-8,3
PAL	11	15,0	0,5	14,0-15,6	6	14,4	0,3	14,0-14,8
IPG	11	2,1	0,2	1,7-2,4	6	2,2	0,2	1,9-2,3
PPL	11	8,9	0,3	8,4-9,3	6	8,7	0,2	8,5-8,9
BBW	11	12,2	0,5	11,4-13,2	6	11,9	0,3	11,7-12,5
CPL	11	7,4	0,4	6,9-8,1	6	7,0	0,3	6,7-7,3
APW	11	4,5	0,2	4,2-4,8	6	4,1	0,1	4,0-4,4
MDL	11	17,7	0,6	16,7-18,6	6	17,1	0,3	16,8-17,5

Table 10.7

External and cranial measurements (in mm) for *Neamblysomus julianae* specimens examined. $\bar{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\bar{x}$	*sd*	Range	*n*	$\bar{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	7	100,5	6,0	94-111	6	99,2	6,6	92-111
HF	7	13,4	1,0	12-14	6	12,0	2,0	9-14
BCW	7	3,8	0,2	3,6-4,1	7	3,8	0,3	3,6-4,3
CRANIAL MEASUREMENTS:								
ARB	6	4,7	0,1	4,5-4,8	8	4,4	0,2	4,1-4,6
MIO	7	7,4	0,3	7,1-7,8	8	7,0	0,4	6,4-7,6
ZMB	7	16,0	0,5	15,4-16,7	8	15,4	0,5	14,7-16,2
IOW	6	7,5	0,2	7,2-7,6	8	7,1	0,2	6,8-7,5
GSL	7	23,2	0,4	22,4-23,6	8	22,5	0,6	21,8-23,5
GSH	7	11,5	0,1	11,4-11,7	8	11,2	0,2	10,8-11,5
P@P	7	7,3	0,2	7,0-7,6	8	7,2	0,1	7,0-7,3
PAL	5	11,7	0,3	11,4-12,1	8	11,2	0,3	10,6-11,7
IPG	7	1,9	0,1	1,8-2,1	8	1,9	0,1	1,8-2,0
PPL	7	7,5	0,2	7,3-7,8	8	7,3	0,3	7,0-7,7
BBW	7	10,6	0,5	10,1-11,2	8	10,5	0,2	10,1-10,8
CPL	7	6,0	0,2	5,8-6,2	8	5,8	0,2	5,5-6,0
APW	7	3,4	0,1	3,2-3,6	8	3,2	0,1	3,0-3,4
MDL	7	14,5	0,3	14,1-15,0	8	13,9	0,3	13,5-14,4

their higher mass (♂:64,2±5,2 g; ♀:51,0±7,0 g), but sexual size dimorphism is not pronounced. Molar talonids are usually absent, although traces of feeble talonids may occur on the lower molars of younger individuals. M3 are present variably, both among jaw quadrants and individuals. When present, these have a triconid appearance (similar to the other molars) in younger individuals, and become peg-like with increasing toothwear. Dorsal fur colour is quite variable, from dark brown (7,5YR3/4) to dark reddish-brown (5YR3/4) or very dark reddish brown (5YR2/3), while the underparts are always a dull orange (7,5-10YR6-7/3-4).

In overall size, *N. gunningi* resembles *A. septentrionalis* and *A. hottentotus*. It is easily recognized by its more gracile claws (BCW/GSL < 18% *cf.* more than 19%), the lack of well-developed molar talonids, and often also the presence of M3. *N. gunningi* also has a signficantly broader palate (P@P/GSL < 29%) than these species (P@P/GSL < 28%), and a larger malleus, although this is not apparent externally on the skull.

Habitat. Favours montane forest and adjacent grasslands in North-Eastern Sandy Highveld (veld type 8). Thrives in cultivated lands, and also in young plantations.

Protection status. Protected in the De Hoek, New Agatha and Woodbush Forest Reserves. Since this endemic species has a highly restricted distribution, its Red Data Book status should be upgraded from Indeterminate to Rare (Gelderblom *et al.* 1995). Of the mammal species in the former Transvaal, *N. gunningi* and *N. julianae*, are most in need of urgent conservation attention (Van Jaarsveld, *pers. comm.*[1]).

Specimens examined (*n* = 18). NORTHERN PROVINCE. **Letaba district** (*n* = 17): Woodbush Hill - TM703; Woodbush Forest - BM51299; TM704,3382-4,3387-8,4274; De Hoek Forest Station -TM40766,40772,40778-80,42117-8; New Agatha Forest Station - TM23722; **Lebowa district** (*n* = 1): Haenertzberg - SI381481.

Neamblysomus julianae (Meester, 1972) Juliana's golden mole

1972 *Amblysomus julianae* Meester, *Annals of the Transvaal Museum* 28:35. The Willows, Pretoria, Gauteng Province, South Africa.

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[1] Dr. A. van Jaarsveld, Department of Zoology & Entomology, University of Pretoria, Pretoria, 0002

Holotype. TM16916, female, TW3, collected by I. Hofmeyer on 1 October 1965. Skin and skull in good condition, basal claw width 3,70 mm.

Subspecies and Distribution (Fig. 10.1). Known from only three widely separated populations: the type locality in eastern Pretoria; the Numbi Gate, Pretoriuskop and Matjulwana districts of the Kruger National Park; and the Nyl floodplain in Northern Province (Bronner 1990). Given its cryptic and trap-shy nature, it may be more widespread than current records indicate. Although there are consistent colour and dental differences between the western (Pretoria/Nyl floodplain) and eastern (Kruger National Park) populations, sample sizes are too small for objective assessment of intraspecific variation in this species. Consequently, no subspecies are yet recognized.

Diagnosis (Table 10.7). The smallest of the amblysomine species, with a total length of 92-111 mm, and a mass of 21-46 g. Males are slightly heavier than females (♂:33,0±8,1 g; ♀:26,0±3,0 g), and slightly larger in most cranial measurments. However, sexual size dimorphism is not pronounced. Specimens from Pretoria and the Nyl floodplain are reddish-brown (7,5YR4/6) or brown (7,5YR7/8) dorsally, and orange (7,5YR6/6-8) or yellow-orange (7,5YR7/8) ventrally. The Kruger National Park specimens are dark reddish-brown (2,5YR3/4) dorsally, and dull reddish-brown (5YR5-6/4) ventrally. These colour differences are mirrored by variation in the presence of M3, which are invariably absent in the western populations, and present in the lower toothrows of Kruger National Park specimens.

Neamblysomus julianae is easily distinguished from *A. hottentotus* and *A. septentrionalis* by its markedly smaller size, paler fur, and the absence of well-developed molar talonids. Although similar in size to *A. marleyi*, *N. julianae* has a broader skull (ZMB/GSL > 65%) and wider palate (P@P/GSL > 31%) than the former species (ZMB/GSL < 24%; P@P/GSL < 29%). These species can also be distinguished using upper toothrow length, which is longer relative to palate length in *N. julianae* (104,1-105%) than in *A. marleyi* (88-101%).

Habitat. Endemic to the savanna biome, where it is confined to sandy soils. The Nyl floodplain population occurs in Mixed Bushveld (veld type 19), and the Pretoria deme in a Bankenveld-Bushveld transition zone (Acocks 1988), whereas the Kruger National Park specimens were collected in Lowveld Sour Bushveld (veld type 10; Gertenbach 1983). *N. julianae* does not penetrate into more mesic plateau grasslands of Mpumalanga, where *A. septenrionalis* and *Amblysomus Species A* instead predominate.

Protection status. Recorded from the Kruger National Park and Nylsvley Nature Reserve. The topotypical population ranges marginally into the Faerie Glen Municipal Nature reserve of Pretoria, but is being severely impacted by intensive urbanization, *viz.* partitioning of habitat by security walls, predation by pets, and also direct eradication by man. Given the fragmented, and highly-localized, nature of the known populations, the Red Data Book status of this species should be elevated to at least Rare (Gelderblom *et al.* 1995).

Specimens examined (*n* = 17). GAUTENG. **Pretoria district** (*n* = 12): The Willows - TM15992,16916; Tierpoort - TM25431; Shere - TM19373,39932,40126, 40173,40220-1,40271,40371-2; MPUMALANGA. **White River district** (*n* = 3): Kruger National Park, Pretoriuskop Camp - TM39769-70; Numbi Gate - TM16917. NORTHERN PROVINCE. **Potgietersrust district** (*n* = 2): Naboomspruit, Nylsvley Nature Reserve - TM27407,41422; Nylstroom, 19km ESE, Farm Witkoppie - TM45180 (from *Tyto alba* pellet).

10.2.5 *Amblysomus*

Amblysomus Pomel, 1848

1848 *Amblysomus* Pomel, *Archives des sciences physiques et naturelles, Génève* 9:247.
Chrysochloris hottentotus A. Smith.

1. Size smaller, greatest skull length 24,8 mm or less; mid inter-orbital width less than 7,2 mm, and less than 108% of palate width across P^2; claws gracile, basal claw width less than 18% of skull length . . . . *A. marleyi*

-. Size larger, greatest skull length more than 25 mm; mid inter-orbital width greater than 7,5 mm, and more than 110% of palate width across P^2; claws robust, basal claw width more than 20% of skull length 2

2. Fur colour either unformly reddish-black (10R1,7/1), or reddish-black mid-dorsally becoming reddish brown (5YR4-6/4-6) on the flanks and ventrum; cranium more elongate, skull width/length index less than 59%; palate relatively longer, more than 164% of mid inter-orbital width . . . . *A. corriae*

-. Fur colour dark reddish-brown (5YR2-3/3-4) mid-dorsally, becoming reddish-brown (5YR4-6/4-6) on the flanks, ventrum brown (10YR4/4) to orange (7,5YR6/6); cranium less elongated, skull width/length index more than 61%; palate relatively shorter, less than 163% of mid inter-orbital width 3

3. Diploid chromosome number = 30; fundamental number = 56; nucleolar organizer regions located on the short arms of chromomes 8 and 11 . . . . *A. hottentotus*

-. Diploid chromome number more than 30; nuceolar organizer regions located on the short arms of chromosomes 8, 9 and 11 4

4. Diploid chromosome number = 34; fundamental number = 62; rostrum relatively narrower, anterior rostral width less than 18% of skull length; palate relatively broader, palate width across P^2 more than 85% of post-palatal length; width of ascending process of mandible more than 28% of skull width . . . . *A. septentrionalis*

-. Diploid chromosome number = 36; fundamental number = 68; rostrum relatively wider, anterior rostral width more than 18% of skull length; palate relatively narrow, palate width across P^2 less than 85% of post-palatal length; width of ascending process of mandible less than 28% of skull width . . . . *Amblysomus Species A*

Amblysomus marleyi Roberts, 1931 — Marley's golden mole

1931 *Amblysomus marleyi* Roberts, *Annals of the Transvaal Museum* 14:225. Ubombo, Zululand, KwaZulu-Natal, South Africa.

Holotype. TM5578, male, TW2, collected at Ubombo on 17 December 1928. Skin and skull in good condition, basal claw width 4,67 mm.

Subspecies and Distribution (Fig. 10.2). Known only from the eastern slopes of the Lebombo Mountains in KwaZulu-Natal, between Ubombo and Ingwavuma. No subspecies are recognized.

Diagnosis (Table 10.8). The second smallest amblysomine species, with a total length of 90-120 mm. Males are slightly larger than females, but sexual size dimorphism is not pronounced. Dorsal fur colour is very dark reddish-brown (10R-2,5YR2/2) to dark reddish-brown (2,5YR2-3/2-3), while the ventrum ranges from orange (7,5YR6/6) through dull orange (7,5YR6/4) to dull brown (7,5YR5/4). The muzzle and cheeks are considerably lighter than the rest of the dorsum.

Figure 10.2 Map of southern Africa, showing the distribution of *Amblysomus corriae* (subspecies *corriae* and *devilliersi*), *A. hottentotus* (subspecies *hottentotus*, *pondoliae*, *iris*, *longiceps* and *subspecies A*), *A. Chlorotalpa duthieae*, *A. marleyi*, *A. septentrionalis* and *Amblysomus Species A*. Symbols indicate actual distribution records, plotted by quarter degree squares. Lines indicate possible distributional limits for each taxon, which were based largely on biogeographic criteria (see text).

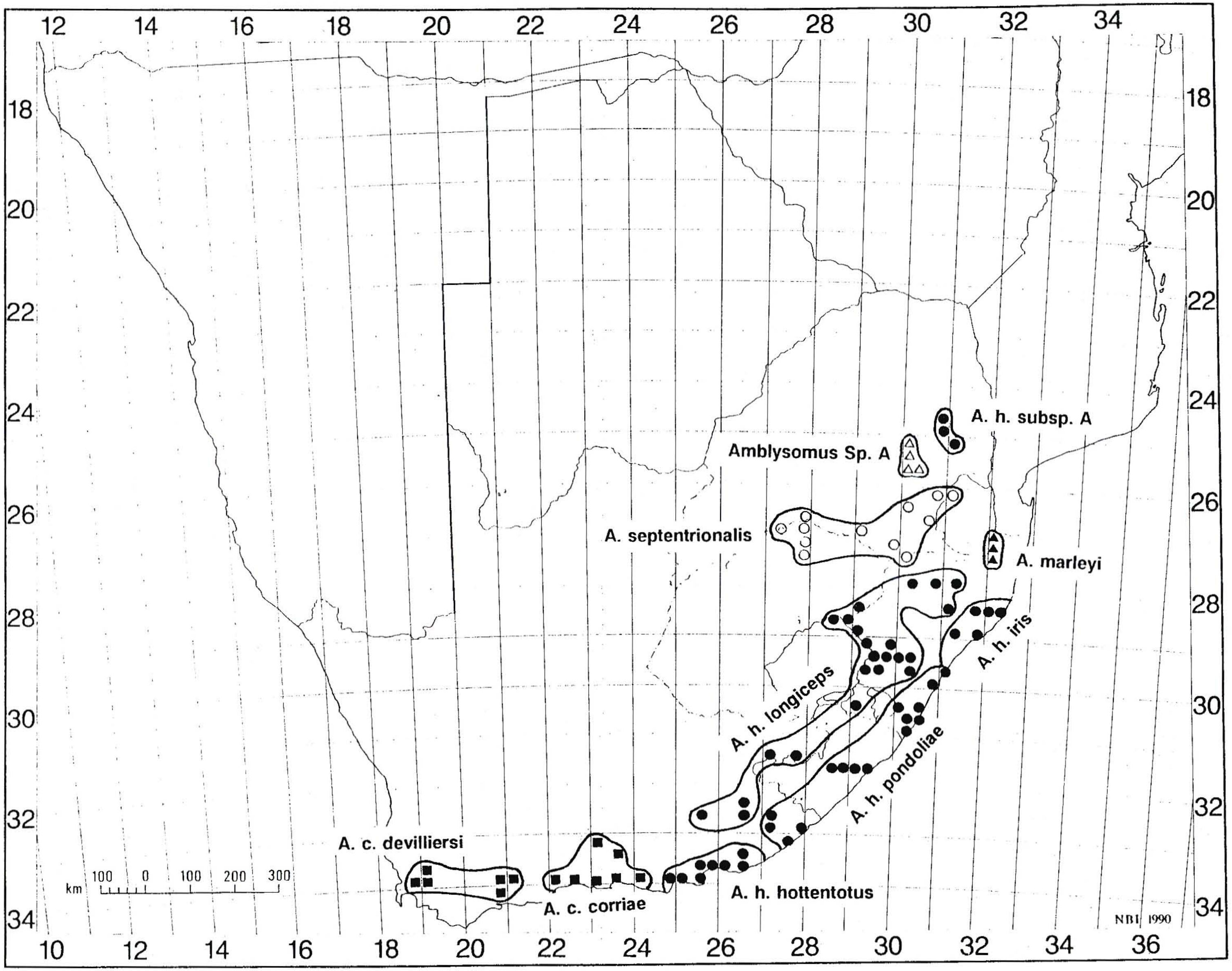

A. h. subsp. A
Amblysomus Sp. A
A. septentrionalis
A. marleyi
A. h. iris
A. h. longiceps
A. h. pondoliae
A. c. devilliersi
A. c. corriae
A. h. hottentotus
km 100 0 100 200 300
NBI 1990
12 14 16 18 20 22 24 26 28 30 32 34
10 12 14 16 18 20 22 24 26 28 30 32 34 36
18 20 22 24 26 28 30 32 34

Table 10.8

External and cranial measurements (in mm) for *Amblysomus marleyi* specimens examined. $\bar{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\bar{x}$	*sd*	Range	*n*	$\bar{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	4	102,0	3,7	96-105	9	100,6	9,3	90-120
HF	4	12,3	0,8	11-13	9	11,4	1,2	10-13
BCW	3	4,3	0,1	4,1-4,4	7	3,9	0,2	3,7-4,2
CRANIAL MEASUREMENTS:								
ARB	4	4,6	0,2	4,4-4,7	8	4,3	0,3	3,9-4,7
MIO	4	7,1	0,1	6,9-7,5	8	6,8	0,3	6,5-7,2
ZMB	4	15,3	0,6	14,8-16,0	8	14,6	0,8	13,9-16,0
IOW	3	6,9	0,2	6,8-7,1	8	6,7	0,4	6,2-7,2
GSL	4	23,9	0,7	23,1-24,6	8	23,5	0,8	22,4-24,7
GSH	4	11,6	0,4	11,3-12,1	8	11,3	0,5	10,7-12,7
P@P	4	6,7	0,3	6,3-6,9	8	6,5	0,4	6,1-7,2
PAL	4	11,8	0,6	11,1-12,4	8	11,6	0,5	10,8-12,3
IPG	4	2,1	0,1	2,0-2,2	7	2,0	0,1	1,9-2,2
PPL	4	7,8	0,3	7,5-8,2	8	7,8	0,3	7,4-8,3
BBW	4	10,8	0,6	10,3-11,6	8	10,7	0,6	10,1-11,6
CPL	4	6,9	0,3	6,5-7,3	8	6,5	0,4	5,8-7,3
APW	4	4,3	0,2	4,1-4,6	8	4,1	0,3	3,6-4,6
MDL	4	15,2	0,6	14,4-15,7	8	14,8	0,6	13,9-15,7

A. marleyi has a more delicate build than either *A. h. iris* or *A. h. pondoliae*, but discriminating between these taxa using external measurements may be problematical because of an overlap in size. However, the skull is markedly smaller in *A. marleyi* (GSL < 24,8 mm) than in the other taxa (GSL > 25 mm). *A. marleyi* also has a significantly narrower skull (MIO < 7,5 mm) than either *A. h. iris* (7,6-8,9 mm) or *A. h. pondoliae* (7,6-9,0 mm).

Habitat. Moist areas, and particularly forests, of the Lebombo Mountains in the savanna biome. Recorded from Zululand Thornveld (veld type 6) and lowveld (veld type 10). Does not occur below the mountains on the Mozambique plain, where *C. obtusirostris* instead predominates.

Protection status. Known to occur in only the Pongola Wilderness Area. Much of its habitat is being degraded, either through overgrazing by cattle, or the destruction of vegetation for firewood by local subsistence communities. Given its restricted distribution, the fragmented nature of populations (Roberts 1951), and the adverse impact of humans on its habitat, *A. marleyi* should be afforded at least Vulnerable status.

Specimens examined (*n* = 16). KWAZULU-NATAL. **Ingwavuma district**: Ingwavuma - TM7160-8; Ubombo - TM5577-84

Amblysomus corriae **Fynbos golden mole**

This species was traditionally included with *A. hottentotus* from the coast of KwaZulu-Natal in the distinct species *A. iris*, and was thus referred to as the "Zulu golden mole". Since *A. corriae* is specifically distinct from *A. h. iris*, this name is no longer suitable. Roberts (1951) referred to *A. corriae* as the "Knysna golden Mole", but Broom (1907a) used this name for *C. duthieae*. Since *A. c. corriae* also occurs far from Knysna, this name is not suitable, and should be replaced with one that more accurately reflects its biogeographic affinity.

Amblysomus corriae corriae Thomas, 1905

1905 *Amblysomus corriae* Thomas, Abstracts, *Proceedings of the Zoological Society, London* 20:5; *Proceedings of the Zoological Society, London* 2:57. Knysna, Western Cape Province.

Holotype. BM5.5.5.5, male, TW5, collected by Colonel C.H.B. Grant at an altitude of 420 m a.s.l. near Knysna. Skin and skull in good condition, basal claw width 4,97mm.

Distribution (Fig. 10.2). Restricted to the coastal plain below the Outeniqua, Kouga and Baviaanskloof mountain ranges. Ranges from the vicinity of George (Western Cape), westwards to Humansdorp (Eastern Cape), where it is replaced by *A. h. hottentotus*. Geographical continuity between *A. c. corriae* and *A. c. devilliersi* seems unlikely, owing to the barrier posed by the dry Gouritz River Valley between George and Riversdale.

Diagnosis (Table 10.9). Body size varies, with a total length of 108-130 mm, and a mass of 41-64 g. Males are usually heavier than females (♂: 55,6±4,9; ♀: 49,5±6,4), but the sexes do not appear to differ markedly in cranial size (Table). Individuals from George and Knysna are generally smaller (GSL: ♂ = 26,5±0,8; ♀ = 26,9±0,5) than those from the Humansdorp district (GSL: ♂ = 27,8±1,0; ♀ = 27,3±1,0). The anterior inter-orbital region is significantly narrower (IOW/ZMB = 44,3±0,7%) than in *A. c. devilliersi* (45,7±0,5%), and the palate more elongate (P@P/ZMB = 43,9±0,8%) than in either *A. c. devilliersi* (45,7±1,4%) or *A. h. hottentotus* (46,5±0,5%). Conversely, the interpterygoid region (IPG/P@P = 30,1±1,6%) and rostrum (ARB/IOW = 67,9±2,6%) are slightly wider than in *A. h. hottentotus* (27,3±1,0% and 65,4±1,3%, respectively). The most reliable criterion for diagnosing *A. c. corriae* is fur colour, which is uniformly reddish-black (10R 1,7/1), without the reddish-brown (5YR 4-6/4-6) tinge that is so conspicuous on the flanks and abdomen of either *A. c. devilliersi* or *A. h. hottentotus*.

Habitats. Restricted to Knysna Forest (veld type 4) and adjoining False Fynbos (veld type 70) of the Fynbos biome, but occurs also in well-watered gardens, golf courses, nurseries and livestock paddocks adjoining its preferred forest habitats. It apparently exists in broad sympatry with *Chlorotalpa duthieae* in the Knysna Forest. However, limited trapping data suggest that where these taxa occur together (such as Natures Valley), they select different micro-habitats, with *A. c. corriae* apparently favouring false fynbos and the forest fringes, and *C. duthieae* the deeper forest.

Protection status. Satisfactory. Preserved in the Wilderness National Park, Tsitsikamma National Park, Diepwalle Forest Reserve, Keurboomsrivier Nature Reserve, Kluitjieskraal Nature Reserve, Ruitersbos State Forest, Saasveld State Forest,

Table 10.9

External and cranial measurements for *A. c. corriae* specimens examined, and craniometric ratios diagnosing this taxon from *A. c. devilliersi* and *A. h. hottentotus*. $\bar{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\bar{x}$	*sd*	Range	*n*	$\bar{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	19	119,7	6,8	108-130	24	115,4	6,5	109-130
HF	19	14,7	1,1	12-16	24	13,9	1,2	12-15
BCW	18	4,9	0,3	4,5-5,6	25	4,8	0,5	4,2-5,9
CRANIAL MEASUREMENTS:								
ARB	19	4,7	0,2	4,5-5,3	24	4,5	0,3	4,1-5,1
MIO	20	8,2	0,2	7,8-8,6	22	8,2	0,4	7,5-8,8
ZMB	20	15,9	0,4	15,1-16,9	25	15,5	0,5	14,7-16,9
IOW	20	7,1	0,3	6,7-7,5	25	6,8	0,2	6,5-7,2
GSL	20	27,4	0,6	25,4-28,9	25	26,7	0,8	25,3-28,6
GSH	20	12,7	0,3	12,3-13,5	25	12,5	0,5	11,8-13,8
P@P	20	7,0	0,2	6,4-7,4	23	6,9	0,3	6,4-7,5
PBM	15	5,0	0,7	4,3-5,1	23	4,6	0,3	4,2-5,3
PAL	20	13,8	0,4	13,0-14,6	24	13,3	0,5	12,3-14,3
MTL	17	6,3	0,9	5,6-6,8	24	6,2	0,3	5,6-7,0
IPG	20	2,0	0,5	1,7-2,3	18	2,1	0,1	1,8-2,2
PPL	20	8,8	0,3	8,0-9,3	25	8,6	0,3	8,3-9,1
EAM	15	1,6	0,2	1,3-2,4	18	1,5	0,1	1,3-1,9
BBW	18	11,5	0,3	11,0-12,0	22	11,2	0,5	10,6-12,5
CPL	20	7,4	0,5	6,9-7,9	25	7,1	0,3	6,6-7,8
APW	20	4,6	0,2	4,4-4,9	25	4,3	0,2	3,9-4,8
MDL	20	16,8	0,5	16,0-18,0	25	16,4	0,8	15,2-18,0
FML	15	4,6	0,2	4,4-4,7	18	4,5	0,3	4,2-4,8

RATIOS:	$\bar{x}\pm 1se$
IOWX100/ZMB	
A. c. corriae	44,3±0,7
A. h. hottentotus	45,7±0,5
A. c. devilliersi	46,1±0,6
P@PX100/ZMB	
A. c. corriae	43,9±0,8
A. c. devilliersi	45,7±1,4
A. h. hottentotus	46,5±0,5
IPGX100/P@P	
A. h. hottentotus	27,3±1,0
A. c. devilliersi	29,7±1,2
A. c. corriae	30,1±1,6
ARBX100/IOW	
A. h. hottentotus	65,4±1,3
A. c. devilliersi	66,3±2,5
A. c. corriae	67,9±2,6

and the Bergplaas Nature Reserve. Probably occurs also in various other areas set aside for forest conservation.

Specimens examined (*n* = 54). WESTERN CAPE PROVINCE. **George district** (*n* = 3): Jonkersberg - TM8992-4; POOLED LOCALITIES. *KNYSNA* = **Knysna district** (*n* = 23): Plettenberg Bay - KM3655; Nature's Valley - CM94944-5; TM40534, 40536; Knysna Town - BM 5.5.5.1-2, 5.5.5.4-5, 5.5.7.35, NM128, SI141523; Goudveld - SI342424; Rondeveld - SI342426; Diepwalle Forest - TM706, 708-9, 8989-91, 26304, 26346, 29314; **George district** (*n* = 6): George Town - ZM57807; George, Saasveld Forestry Institute - TM29315, 39450-53; EASTERN CAPE PROVINCE: *HUMANSDORP* = **Humansdorp district** (*n* = 21): Humansdorp district - KM25942; Hoffmansbos - TM38862, 38859-61, 39164-70, 39171, 39173-8. Kareedouw (*n* = 1) - KM3655.

***Amblysomus corriae devilliersi* Roberts, 1946**

1946 *Amblysomus hottentotus devilliersi* Roberts, *Annals of the Transvaal Museum* 20:310. Lamotte, Franschoek, Western Cape Province. Listed also from Stellenbosch.

1946 *Amblysomus hottentotus swellendamensis* Roberts, *Annals of the Transvaal Museum* 20:310. Grootvadersbosch, Swellendam district, Western Cape Province.

Holotype. *A. h. devilliersi* - TM8998, adult male, TW3, collected by Dr. A. Roberts on 15 October 1940. Skin and skull in good condition, basal claw width 5,14 mm. *A. h. swellendamensis* - TM8997, male, TW3, collected by Dr. A. Roberts on 29 October 1940. Skin and skull in good condition, basal claw width 5,25 mm.

Distribution (Fig. 10.2). Western Cape Province, from Stellenbosch and Paarl in the west, where this taxon coexists with *Chrysochloris asiatica*, westwards to the coastal plain and slopes of the Langeberg mountains in the Riversdale district. Its range also extends northwards to the Hawequas Forest near Worcester, but not into the Succulent Karoo.

Diagnosis (Table 10.10). Very similar in total length (♂: 105-135 mm; ♀: 105-130 mm) and greatest skull length (♂:26,9-28,8 mm; ♀:25,7-27,3 mm) to *A. corriae*, but with a significantly wider inter-orbital region (IOW/ZMB = 46,1±0,6%) and palate (P@P/ZMB = 45,7±1,4%) than in *A. c. corriae* (44,3±0,7% and 43,9±0,8%,

Table 10.10

External and cranial measurements for *A. c. devilliersi* specimens examined, and craniometric ratios diagnosing this taxon from *A. c. corriae*. $\bar{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\bar{x}$	*sd*	Range	*n*	$\bar{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	7	120,6	10,4	105-135	10	115,9	9,6	105-130
HF	7	13,4	3,5	13-16	10	13,4	3,2	13-16
BCW	3	5,2	0,1	5,0-5,3	9	5,0	0,1	4,7-5,4
CRANIAL MEASUREMENTS:								
ARB	7	4,9	0,1	4,8-5,2	9	4,7	0,2	4,7-5,2
MIO	7	8,0	0,1	7,8-8,3	9	7,9	0,2	7,5-8,2
ZMB	7	16,1	0,1	15,6-16,6	8	15,3	0,2	15,2-15,6
IOW	7	7,4	0,2	7,1-8,0	9	7,2	0,1	6,6-7,6
GSL	7	27,5	0,4	26,9-28,8	9	26,4	0,2	25,7-27,3
GSH	7	12,9	0,1	12,7-13,2	8	12,4	0,2	12,0-12,9
P@P	4	7,1	0,3	6,7-7,4	8	7,2	0,0	6,4-7,9
PBM	3	4,8	0,2	4,5-4,9	8	4,6	0,1	4,3-4,9
PAL	7	14,0	0,1	13,4-14,4	8	13,3	0,1	12,2-14,1
MTL	4	6,3	0,4	5,9-6,6	8	6,2	0,1	5,9-6,6
IPG	7	2,1	0,1	2,0-2,4	9	2,1	0,1	1,9-2,3
PPL	7	8,8	0,2	8,1-9,2	8	8,6	0,1	8,4-9,3
EAM	4	1,4	0,1	1,3-1,5	7	1,4	0,1	1,3-1,6
BBW	6	11,6	0,1	10,8-12,1	8	11,2	0,2	10,9-11,7
CPL	7	7,7	0,3	7,5-8,4	9	7,2	0,1	7,0-7,8
APW	7	5,0	0,2	4,8-5,4	9	4,5	0,1	4,2-5,1
MDL	7	17,4	0,4	17,0-18,0	8	16,5	0,2	16,2-17,3
FML	7	4,7	0,1	4,6-4,8	8	4,6	0,1	4,4-5,0

RATIOS:	$\bar{x} \pm 1se.$
IOWX100/ZMB	
A. c. corriae	44,3±0,7
A. c. devilliersi	46,1±0,6
P@PX100/ZMB	
A. c. corriae	43,9±0,8
A. c. devilliersi	45,7±1,4

respectively). The fur is reddish-black (10R 1,7/1) mid-dorsally, and becomes progressively more reddish-brown (5YR 4-6/4-6) towards the flanks and abdomen, unlike the uniform reddish-black colour of *A. c. corriae*.

This subspecies resembles *A. hottentotus* in having reddish-brown fur on the flanks and abdomen, and also in cranial proportions. Since there are no clearcut univariate differences ($\bar{x} \pm 1sd$) between these taxa in cranial measurements or ratios, differentiating between them may be difficult. There are, however, distinct multivariate differences between these taxa, and an unknown specimen can be diagnosed with 95% certainty using the procedure explained in Tables 10.11-12.

Habitats. Occurs mainly in Coastal Renosterveld (veld type 46) and Fynbos (veld type 69), but also readily exploits habitats modified by humans, such as golf courses, agricultural lands, paddocks and gardens. In the western parts of its range, near Stellenbosch, it coexists with *Chrysochloris asiatica*, but apparently favours richer and wetter soils than the former (Broom 1907a).

Protection status. Indeterminate owing to scant distribution data, but since individuals are cryptic and live in close proximity to man and his habitations it is unlikely that this taxon is threatened. Recorded from the Jonkershoek Conservation Area (Stellenbosch), Hawequas State Forest (Worcester) and the Boosmansbos Wilderness Area (Swellendam), Grootvadersbosch Forest Reserve (Heidelberg) and Garcia State Forest (Riversdale). It probably occurs more widely in other conservation areas proclaimed for the preservation of fynbos.

Specimens examined (*n* = 17). *STELLENBOSCH* = **Stellenbosch district** (*n* = 3): Jonkershoek Conservation Area - TM40556, 40562-3; **Paarl district** (*n* = 6): La Motte - TM8998; Worcester, Hawequas Forest - LRW3030; Stellenbosch - TM5016, 5022, 5025, 5027; *GROOTVADERSBOSCH* = **Heidelberg district** (*n* = 6): Grootvadersbosch Forest Reserve - TM8996-7, 8999, 41694, 41696-7; **Riversdale district** (*n* = 2): Garcia Forest Reserve - KM29404, TM9885.

Amblysomus hottentotus (A. Smith, 1829) Hottentot golden mole.

Amblysomus hottentotus hottentotus (A. Smith, 1829).

1829 *Chrysochloris hottentotus* A. Smith, *Zoological Journal* 4:436. "Interior parts of South Africa" (Grahamstown *fide* Roberts, 1951).

Table 10.11

Statistics and coefficients required to differentiate unequivocally between male *A. corriae* and *A. hottentotus*, using a canonical variate scatterplot (Fig. 10.3). To plot an unknown, measure the specimen and subtract each measurement (*X*) from the overall mean (*Y*). Multiply the difference (*X-Y*, either positive or negative) by the respective standardized canonical vectors (*CVI* and *CVII*), and sum the scores for each axis to determine the unknown's scatterplot co-ordinates.

Variable	**Measurement of unknown** *X*	**Overall mean** *Y*	*X-Y*	**Standardized canonical vector I** *CVI*	*CVI* **score** *(X-Y)xCVI*	**Standardized canonical vector II** *CVII*	*CVII* **score** *(X-Y)xCVII*
BCW		5,15		-0,13		1,18	
ARB		4,90		1,18		-2,35	
MIO		8,26		0,42		-1,51	
ZMB		16,47		-1,18		-0,44	
IOW		7,36		0,09		1,18	
GSL		26,85		3,37		0,92	
GSH		12,83		0,23		2,11	
P@P		7,42		-3,37		0,32	
PBM		4,83		0,02		-1,36	
PAL		13,53		-1,07		-1,24	
MTL		6,53		-0,59		2,64	
IPG		2,21		-1,14		-3,15	
PPL		8,82		-3,32		-2,96	
BBW		11,74		-1,62		0,09	
FML		4,62		1,45		-2,28	
CPL		7,22		-1,27		-0,92	
APW		4,53		1,49		2,31	
MDL		16,86		1,09		0,31	
SCORE FOR PLOTTING					*CVI* (Σ) =		*CVII* (Σ) =

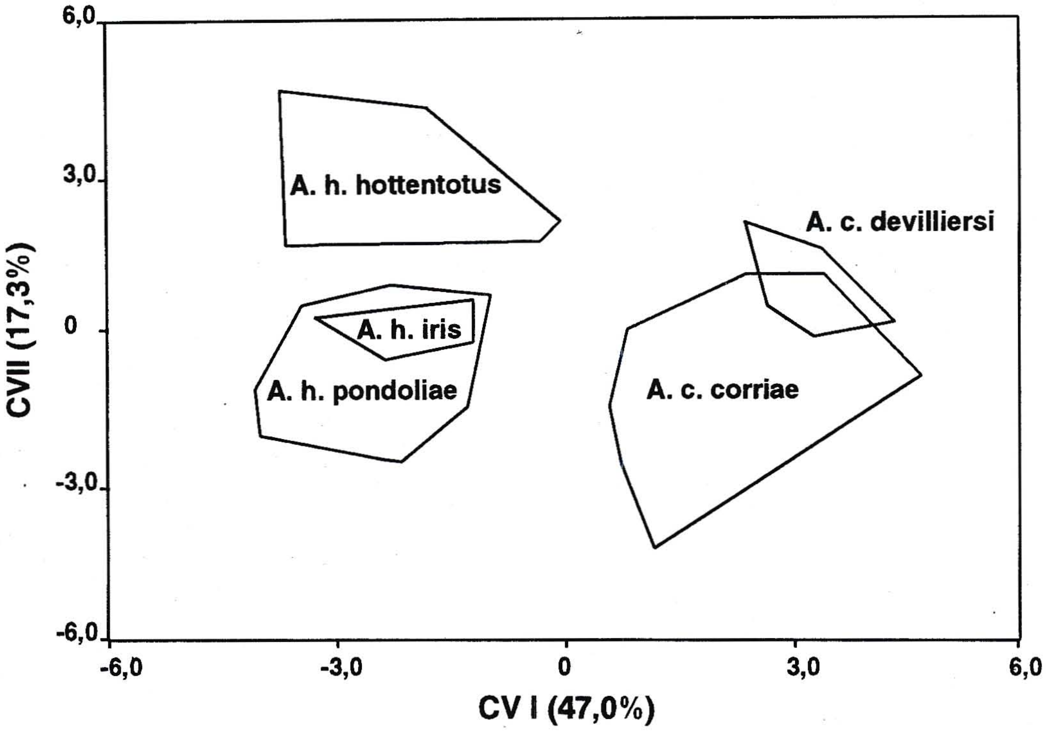
Table 10.12

Statistics and coefficients required to differentiate unequivocally between female *A. corriae* and *A. hottentotus*, using a canonical variate scatterplot (Fig. 10.3). To plot an unknown, measure the specimen and subtract each measurement (*X*) from the overall mean (*Y*). Multiply the difference (*X-Y*, either positive or negative) by the respective standardized canonical vectors (*CVI* and *CVII*), and sum the scores for each axis to determine the unknown's scatterplot co-ordinates.

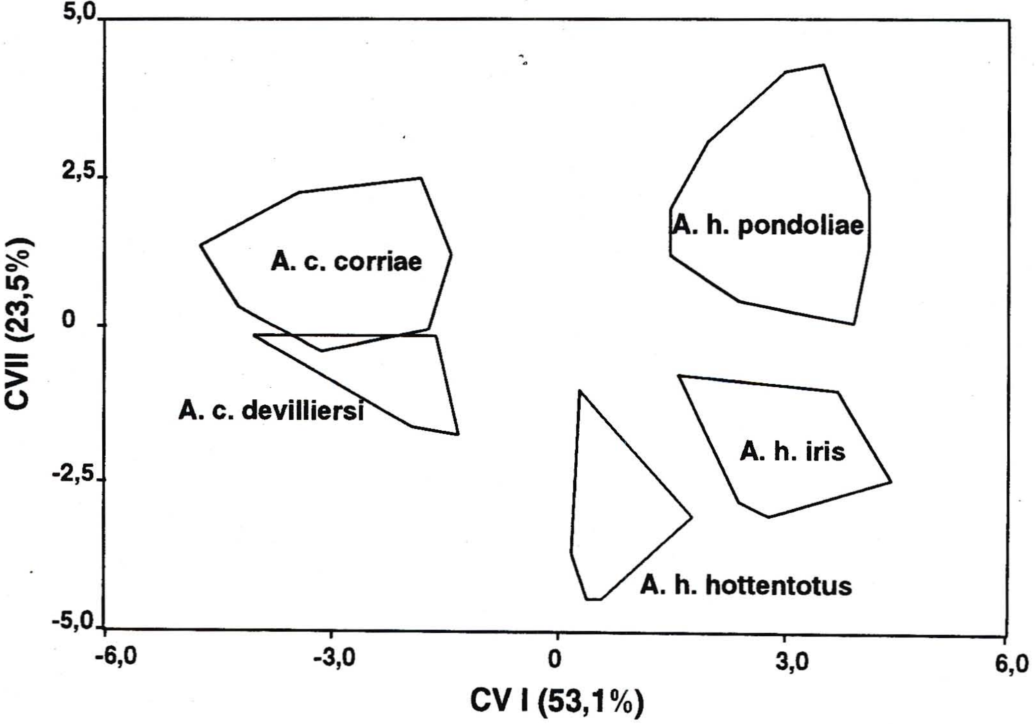
Variable	**Measurement of unknown** *X*	**Overall mean** *Y*	*X-Y*	**Standardized canonical vector I** *CVI*	*CVI* **score** *(X-Y)xCVI*	**Standardized canonical vector II** *CVII*	*CVII* **score** *(X-Y)xCVII*
BCW		4,72		-1,41		-2,19	
ARB		4,69		2,33		-1,85	
MIO		8,13		-0,30		2,12	
ZMB		15,78		1,59		1,02	
IOW		7,11		0,64		-0,76	
GSL		25,99		-3,02		0,04	
GSH		12,37		-0,25		0,03	
P@P		7,22		1,21		0,28	
PBM		4,73		-0,86		-0,54	
PAL		12,94		0,87		1,01	
MTL		6,39		3,82		-0,51	
IPG		2,14		2,98		4,71	
PPL		8,54		1,92		2,06	
BBW		11,28		-0,74		-1,92	
FML		4,53		1,36		2,05	
CPL		6,89		-0,46		3,91	
APW		4,20		-1,91		-3,33	
MDL		16,29		0,94		-0,55	
SCORE FOR PLOTTING					*CVI* (Σ) =		*CVII* (Σ) =

Figure 10.3 Pairwise comparison of the first two canonical variate axes, from discriminant functions analyses of cranial measurements in male and female *A. hottentotus* (subspecies *hottentotus*, *iris* and *pondoliae*) and *A. corriae* (subspecies *corriae* and *devilliersi*). To identify a specimen of unknown affinity, use the procedure explained in Table 10.11

♂


6,0
3,0
0
-3,0
-6,0
CVII (17,3%)
-6,0
-3,0
0
3,0
6,0
CV I (47,0%)
A. h. hottentotus
A. c. devilliersi
A. h. iris
A. h. pondoliae
A. c. corriae

♀


5,0
2,5
0
-2,5
-5,0
CVII (23,5%)
-6,0
-3,0
0
3,0
6,0
CV I (53,1%)
A. h. pondoliae
A. c. corriae
A. c. devilliersi
A. h. iris
A. h. hottentotus

1831 *Chrysochloris holosericea* Lichtenstein, *Darstellung neuer oder wenig bekannter Säugethiere* Plate 41, Fig. 2 and text. Interior of Cape Province on borders of "Kafferland".

1841 *Chrysochloris affinis* Wagner, in Schreber's *Säugthiere Supplementband* 2:123. No locality.

1841 *Chrysochloris albirostris* Wagner, in Schreber's *Säugthiere Supplementband* 2:124. "Kafferland". Based on a young specimen (Roberts, 1951). Possibly a senior synonym of *A. h. pondoliae* (Broom, 1908; Roberts, 1913), and thus considered to be a *nomen dubium.*

1841 *Chrysochloris rutilans* Wagner, in Schreber's *Säugthiere Supplementband* 2:125. "Kafferland".

The epithet *albirostris* (Wagner, 1841) was listed as a senior synonym of *A. h. pondoliae* by Broom (1908) and Roberts (1913). But, Roberts (1951) included it in the synonymies of both *A. h. hottentotus* and *A. h. pondoliae*, while Thomas and Schwann (1905b:261) stated that *albirostris* might prove to be distinct from *A. h. pondoliae*. Since the original description is vague, and designates neither a specific holotype nor precise type locality, diagnosis of this taxon is impossible. The epithet *albirostris* could refer to either *A. h. hottentotus* or *A. h. pondoliae*, and thus is a *nomen dubium.*

Holotype. BM 45.7.3.32, sex unknown, TW3, collected at the "Cape of Good Hope", type locality nominated as Grahamstown (Eastern Cape) by Roberts (1951). Skin in poor condition and skull broken. Although similar to topotypical *A. hottentotus* in size and cranial morphology, the fur of this specimen is abnormally long and dense, and resembles that of *Chrysospalax villosus* (A. Smith, 1833). The first upper premolar lacks a protocone, which is however present on the other cheekteeth.

Distribution (Fig. 10.2). Eastern Cape Province, from Van Staden's River in the south (where coastal savanna gives way to fynbos, and this taxon is replaced by *A. corriae*) to the dry Great Fish River valley in the north. Extends inland as far as the plateau formed by the Elandsberge, Winterhoekberge, Suurberge and Winterberge mountain ranges. Occurs at Uitenhague, Grahamstown, Somerset East and ranges to Bedford, Fort Beaufort and Seymour in the east, where it integrades with *A. h. pondoliae*.

Diagnosis (Table 10.13). An intermediate-sized subspecies, with a total length of 100-135 mm. Males are significantly larger than females in most measurements. The interpterygoid region is narrow in relation to palate width, with IPG/P@P = 27,3±1,0%, as opposed to >29% in either *A. corriae* to the south, and *A. h. pondoliae* to the north. Anterior rostral breadth is also compartively narrower (ARB/IOW = 65,4±1,3%) than in *A. h. pondoliae*, whereas the ascending process to the ramus is significantly wider (APW/MTL = 74,4±2,6%) than *A. corriae* (67,1±1,2). Colour varies considerably, even within populations (Broom 1907a), but is usually brownish-black (5YR2/2) to bright reddish-brown (5YR3-4/3-4) mid-dorsally, becoming more rufous towards the flanks, which are reddish brown (5YR4-5/6-8). The ventrum ranges in colour from bright brown (7,5YR5/6) to dull orange (7,5YR5-6/4-6). Patches of light yellow-orange (7,5YR8/3-6) occur variably on the sides of the muzzle, sometimes extending to above the subdermal eyes.

Habitat. Occurs in Alexandria Forest and False Thornveld (veld type 2), and Valley Bushveld (veld type 23) at the southernmost limit of the savanna biome, with a marginal intrusion into Nama-Karoo further inland, and into False Fynbos (veld type 2) of the Fynbos biome to the south.

Protection status. Lives in close proximity to human habitations, and may be semi-commensal, since individuals thrive in gardens and fields irrigated by man. Adequately protected in the following reserves: Groendal Wilderness Area and Uitenhague Nature Reserve (Uitenhague); Van Stadens Wildflower Reserve and The Island State Forest (Port Elizabeth); Alexandria State Forest; and Andries Vosloo Nature Reserve (Grahamstown).

Specimens examined (*n*=67). EASTERN CAPE PROVINCE. **Somerset East district**: (*n* = 1) - TM9996. POOLED LOCALITIES. *PORT ELIZABETH* = **Port Elizabeth district** (*n* = 14): Perseverance, Coega Station - TM5272; Port Elizabeth, Walmer - TM5271, 16584, 25944, 25952-3; Port Elizabeth district - KM940-3; Van Stadens Wildflower Reserve - TM25944, 38363-4; *ALBANY* = **Albany district** (*n* = 25): Albany district - KM944; Bathurst district - KM21100-4; Grahamstown district - BM45.7.3.32, KM946, 949, 2662, 14573, 26276; SM11513; TM2364, 6671-9, 38456, 40051; Port Alfred Golf Course - TM13513; *ALEXANDRIA* = **Alexandria district** (*n*=15): Alexandria district - TM6680; Alexandria Forest Reserve - KM25381-2, 25517; Farm Groenkop - KM25512-6, 25837; Farm Lidney - KM25384-7; Paterson - KM25621.

Table 10.13

External and cranial measurements for *A. h. hottentotus* specimens examined; and craniometric ratios diagnosing this taxon from the parapatric phena *A. h. devilliersi* and *A. h. pondoliae*. *X* = arithmetic mean; *sd* = standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\bar{x}$	*sd*	Range	*n*	$\bar{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	20	123,6	6,2	114-135	21	118,6	8,5	104-135
HF	21	14,4	2,6	13-19	20	14,3	1,7	12-18
BCW	24	5,4	0,2	4,7-5,8	23	5,0	0,1	4,0-5,5
CRANIAL MEASUREMENTS:								
ARB	21	5,0	0,2	4,5-5,4	24	4,8	0,1	4,2-5,2
MIO	22	8,2	0,2	7,8-8,7	23	8,0	0,1	7,4-8,8
ZMB	22	16,6	0,6	15,3-17,7	24	16,0	0,4	15,1-17,4
IOW	22	7,6	0,2	6,7-8,2	24	7,3	0,1	6,9-8,0
GSL	22	26,5	0,7	25,0-27,7	24	25,9	0,3	24,6-27,7
GSH	22	12,9	0,2	12,2-13,4	24	12,5	0,1	11,6-13,6
P@P	21	7,7	0,3	7,1-8,4	23	7,4	0,2	6,3-8,1
PBM	17	4,7	0,3	4,0-5,5	21	4,7	0,1	4,3-5,6
PAL	22	13,4	0,5	12,1-14,4	23	13,0	0,3	11,9-14,1
MTL	19	6,7	0,3	6,2-7,2	24	6,5	0,2	6,0-7,1
IPG	19	2,1	0,1	1,8-2,3	24	2,1	0,1	1,9-2,4
PPL	22	8,5	0,2	8,0-9,0	24	8,3	0,1	7,6-9,2
EAM	20	1,3	0,0	1,0-1,5	21	1,3	0,1	1,0-1,4
BBW	22	11,9	0,41	10,7-13,0	23	11,5	0,2	10,7-12,7
CPL	22	7,1	0,3	6,5-8,0	24	6,9	0,1	6,3-7,5
APW	21	4,5	0,2	3,8-5,0	24	4,4	0,1	3,9-5,4
MDL	22	16,8	0,6	15,5-18,1	24	16,4	0,2	15,6-18,2
FML	22	4,6	0,0	4,3-5,1	24	4,7	0,1	4,3-5,1

RATIOS:	***$\bar{x}$±1sd.***
IPGX100/P@P	
A. h. hottentotus	27,3±1,0
A. h. pondoliae	29,8±1,2
A. corriae	29,7±1,2
ARBX100/IOW	
A. h. hottentotus	65,4±1,3
A. h. pondoliae	68,9±1,9
A. corriae	66,3±2,5
APWX100/MTL	
A. h. hottentotus	74,4±2,6
A. corriae	67,1±1,2
A. h. pondoliae	70,8±3,2

Amblysomus hottentotus iris **Thomas and Schwann, 1905**

1905 *Amblysomus iris* Thomas and Schwann, *Abstracts, Proceedings of the Zoological Society, London* 18:23; *Proceedings of the Zoological Society of London* I:259. Umfolozi Station, Zululand, KwaZulu-Natal.

1946 *Amblysomus corriae littoralis* Roberts, *Annals of the Transvaal Museum* 20:311. Umdloti River near Verulam, north of Durban, KwaZulu-Natal.

Holotypes. *A. iris* - BM4.12.3.9, adult male, TW3, collected at Umfolozi Station on 16 September 1904 by Colonel C. H. B. Grant. Altitude 50m a.s.l.. Skin and skull in good condition, basal claw width 4,97 mm. *A. c. littoralis* - TM5020, male, TW3, collected by H. W. Bell-Marley. Skin and skull in good condition, basal claw width 4,87 mm.

Distribution (Fig. 10.2). Northern KwaZulu-Natal coastal belt and Zululand, from Umdloti River in the south (where it integrades with *A. h. pondoliae* in the vicinity of Verulam, Mt. Edgecombe and Umhlanga Rocks lagoon) northeastwards to Lake St. Lucia and Cape Vidal (where it is replaced by *Calcochloris obtusirostris*). Its range extends inland to Eshowe, Umfolozi, Hluhluwe, Hlabisa and Ntendeka wilderness near Vryheid. More sampling in this area may reveal transition zones with *A. h. longiceps* in the vicinity of Vryheid and Dundee, and possibly also contact zones with *A. septentrionalis* in southern Mpumalanga.

Diagnosis (Table 10.14). The smallest of the subspecies, with a total length 107-125. Males are larger than females, particularly in greatest skull length (GSL), greatest skull height (GSH) and zygomatic breadth (ZMB). The claws are more gracile (BCW: ♂:4,7-5,9; ♀:4,1-4,8 mm) than in either *A. h. pondoliae* (♂:4,5-6,6 mm; ♀: 4,1-6,6 mm) or *A. h. longiceps* (♂:5,4-6,6 mm; ♀:4,9-6,2 mm). The ascending process of mandibular ramus is comparatively shorter (APW/P@P = 55,5±4,1%) than in *A. h. pondoliae* (62,0±2,4%) and *A. h. longiceps* (65,6±2,6%). Fur colour is extremely variable, and ranges from reddish-black (10R 2/1) through very dark reddish brown (7,5R 2/2) to brownish-black (5YR 3/1) dorsally. A rufous tinge (reddish brown; 5YR 4-5/8) is present variably on the flanks. In specimens lacking any rufous tinge, the ventrum is brownish-black (10YR 2/3) to dark-brown (7,5YR 3/3). Those with a rufous tinge are lighter below, usually dark-brown (10YR 6/4) to orange (7,5YR 6/6), as in *A. h. pondoliae*. This is the result of a progressive increase

Table 10.14

External and cranial measurements for *A. h. iris* specimens examined; and craniometric ratios diagnosing this taxon from the parapatric phena *A. h. pondoliae* and *A. h. longiceps*. $\overline{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\overline{x}$	*sd*	Range	*n*	$\overline{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	5	118,4	4,7	113-125	12	116,8	8,7	104-132
HF	5	14,2	1,64	12-16	11	14,1	1,7	11-16
BCW	9	4,9	0,5	4,3-5,9	10	4,4	0,2	4,1-4,7
CRANIAL MEASUREMENTS:								
ARB	9	4,8	0,4	4,1-5,4	10	4,6	0,2	4,3-4,9
MIO	6	8,5	0,6	7,6-9,3	10	8,0	0,2	7,7-8,4
ZMB	9	16,2	0,9	15,0-17,9	10	15,5	0,4	14,9-16,2
IOW	6	7,2	0,3	7,0-7,8	10	7,0	0,3	6,7-7,5
GSL	9	25,9	1,2	23,4-27,6	10	24,8	0,5	24,0-25,4
GSH	9	12,3	0,6	11,6-13,4	10	11,7	0,3	11,2-12,2
P@P	9	7,3	0,4	6,5-8,0	10	7,3	0,2	6,8-7,6
PBM	6	4,7	0,3	4,3-4,9	6	4,8	0,2	4,5-5,0
PAL	5	12,9	0,6	12,1-13,8	10	12,5	0,4	12,1-13,1
MTL	9	6,5	0,4	5,7-7,0	10	6,4	0,3	6,0-6,8
IPG	6	2,1	0,2	1,8-2,2	10	2,1	0,1	1,9-2,3
PPL	9	8,5	0,5	7,9-9,3	10	8,1	0,2	7,7-8,3
EAM	6	1,3	0,1	1,2-1,5	7	1,3	0,1	1,2-1,4
BBW	9	11,4	0,8	10,0-12,6	7	11,2	0,6	10,7-12,2
CPL	9	6,7	0,5	6,0-7,5	10	6,3	0,3	5,8-6,8
APW	9	4,2	0,4	3,6-4,7	10	3,7	0,2	3,3-4,1
MDL	9	16,2	0,8	15,1-17,6	10	15,4	0,5	14,7-16,1
FML	6	4,4	0,2	4,0-4,7	10	4,3	0,1	4,1-4,5

RATIOS:	$\overline{x}\pm 1sd$.
APWX100/P@P	
A. h. iris	55,5±4,1
A. h. pondoliae	62,0±2,3
A. h. longiceps	65,6±2,6
APWX100/MTL	
A. h. iris	63,1±4,9
A. h. pondoliae	70,9±3,2
A. h. longiceps	70,4±2,7

in the area covered by reddish-brown fur, from the flanks inwards to the middle of the ventrum. Almost complete integradation occurs between these colour extremes.

Habitats. Found in coastal tropical forest veld types, *viz*. Coastal Forest and Thornveld (veld type 1), Zululand Thornveld (veld type 6) and 'Ngonigoni veld (veld type 5) of the savanna biome. Ranges also into grasslands and vleis adjoining forests.

Protection status. Relatively common, especially in mesic habitats. Like most other *Amblysomus*, this subspecies coexists with man, and sometimes is considered a pest owing to the damage it causes to golfing greens and gardens. It is adequately protected in the following reserves: Hazelmere Dam Nature Reserve (Verulam); Umlalazi Nature Reserve (Mtunzini); Greater St. Lucia Wetland Park, Cape Vidal and Eastern Shores Nature reserves (St. Lucia); Hluhluwe-Umfolozi Conservation Complex; and Ntendeka Wilderness Area (Vryheid).

Specimens examined (*n* = 45). KWAZULU-NATAL. **Hlabisa district** (*n* = 32) - KM28109-10; Hluhluwe and Hluhluwe Game Reserve - NM1468; TM40346-7; Mtubatuba, St. Lucia and surrounding districts - TM5016, 6837, 26467-8, 33028, 33043, 37775, 37872-3, 40066-7, 40379, 40392, 40395-6, 40411-3,40423-7, 40438-40; Monzi - TM33040. **Inanda district** (*n* = 4): Verulam, Umhloti River and Hazelmere Dam Nature Reserve - TM5020, 38591, 39933, 39204; **Mtunzini district** (*n* = 4): Mtunzini Town - TM5011-2, 5013; Ngoye Forest - TM5017; **Vryheid district** (*n* = 1): Ngome State Forest - TM39847; **Lower Umfolozi district** (*n* = 4): Umfolozi - BM4.12.3.9; TM5013; Empangeni - TM5019, 33037.

Amblysomus hottentotus longiceps (Broom, 1907)

1907 *Chrysochloris hottentota longiceps* Broom, *Transcations of the South African Philosophical Society* 18:299. "Near 'Maritzburg" (Pietermaritzburg), KwaZulu-Natal.

1907 *Chrysochloris hottentota albifrons* Broom, *Transcations of the South African Philosophical Society* 18:302. Howick, KwaZulu-Natal.

Holotype. NM138, currently housed at the Durban Natural Science Museum, adult female, TW3, collected on 24 October 1904. Broom mentioned that the type was in the "Maritzburg Museum" (= Natal Museum), but did not cite any accession number.

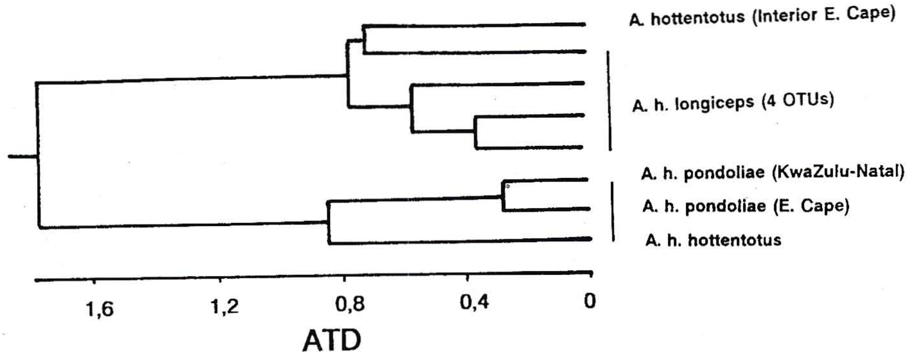
The number NM138 in this collection refers to both a specimen of *Chrysospalax villosus*, and an *A. hottentotus*, collected in Pietermaritzburg. The cranial dimensions of the *A. hottentotus* specimen match those given by Broom almost exactly, and since it is the only specimen of this species accessioned into the collection prior to the publication of Broom's (1907a) paper, it can confidently be assumed to be the holotype. Broom mentioned both a skin and skull for this specimen, but only a skull (in good condition) now exists.

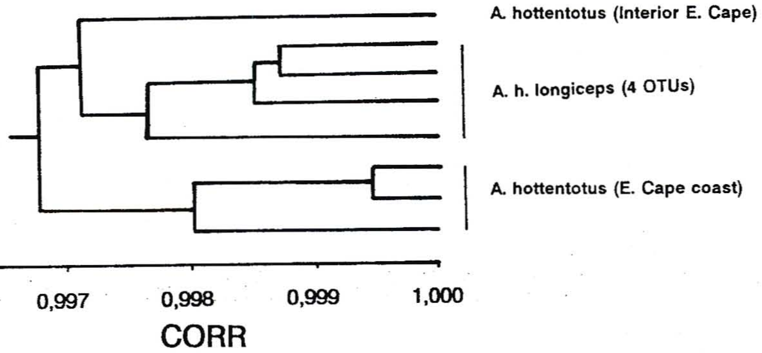
Distribution (Fig. 10.2). Occurs at altitudes above 600 m a.s.l., in the uplands of KwaZulu-Natal, from Underberg in the south to Van Reenen in the north. Its range extends to Pietermaritzburg (where it intergrades with *A. h. pondoliae*), Howick, Nottingham Road and Estcourt in the east, and marginally into the Free State, to Harrismith in the north, and Clarens in the west. The distribution of this subspecies may also extend to the Drakensberg foothills of the Eastern Cape, since principal components and cluster analyses indicated that populations from this region (Elliot, Dordrecht, Ugie and Maclear districts) are more similar in size and cranial shape to this subspecies than to either *A. h. pondoliae* or *A. h. hottentotus* (Fig. 10.4). If these demes are indeed continuous, *A. h. longiceps* may intergrade with *A. h. hottentotus* in the vicinity of Seymour and Stutterheim.

This taxon may also be in geographical contact with *A. septentrionalis* in the vicinity of Volksrust and Wakkerstroom, and with the isolated population of *A. septentrionalis* (from Heilbron) in the vicinity of Reitz (from whence unconfirmed reports of golden moles have been received). There are not, however, any distribution records confirming such geographic continuity.

Diagnosis (Table 10.15). The largest subspecies, with a total length of 120-141 mm in males, and 119-139 mm in females. Sexual size dimorphism is marked, greatest skull length being 27,0-30,1 mm in males, and 26,6-29,9 mm in females. The claws are robust (♂: BCW = 6,1±0,2 mm; ♀ = 5,8±0,1 mm), in contrast to the narrower claws of *A. h. pondoliae* (♂: 5,4±0,3 mm; ♀: 5,2±0,3 mm) and the even more gracile claws of *A. h. iris*. *A. h. longiceps* is characterized by: an more expanded inter-orbital region (MIO/ZMB = 51,1±0,7%) than in *A. h. pondoliae* (49,6±1,2); a relatively wider mandibular ramus (APWX/ZMB = 28,5±0,2%) than in either *A. h. pondoliae* (27,1±0,6%) or *A. h. iris* (25,1±1,2%); and a broader rostral region (ARB/IOW = 68,4±1,2%) than in *A. septentrionalis* (64,7±1,1%). Fur colour is usually reddish-brown (5YR2-4/2-6) mid-dorsally, and

Figure 10.4 Phenetic relationships among male *A. hottentotus* specimens representing *A. h. longiceps* (interior KwaZulu-Natal), *A. h. hottentotus* (Eastern Cape coast), and populations from the Maclear and Dordrecht districts in the Eastern Cape Drakensberg. The phenograms were produced by UPGMA clustering of average taxonomic distance (ATD; co-phenetic correlation = 0,875) and correlation coefficients (CORR; co-phenetic correlation = 0,778). The scatterplot compares the first two principal component axes (co-phenetic correlation = 0,968) computed from single-standardized data.


A. hottentotus (Interior E. Cape)
A. h. longiceps (4 OTUs)
A. h. pondoliae (KwaZulu-Natal)
A. h. pondoliae (E. Cape)
A. h. hottentotus
1,6
1,2
0,8
0,4
0
ATD


A. hottentotus (Interior E. Cape)
A. h. longiceps (4 OTUs)
A. hottentotus (E. Cape coast)
0,997
0,998
0,999
1,000
CORR

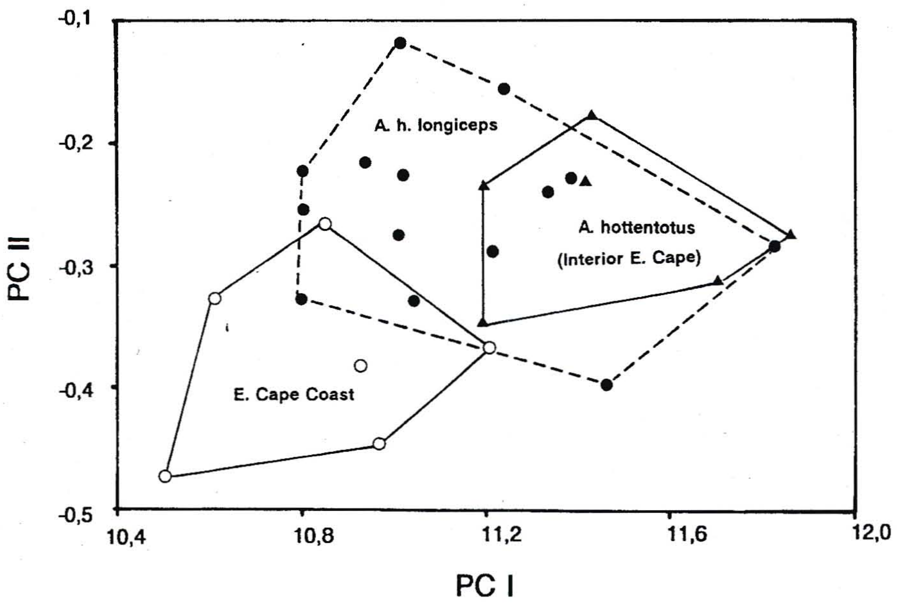

A. h. longiceps
A. hottentotus
(Interior E. Cape)
E. Cape Coast
-0,1
-0,2
-0,3
-0,4
-0,5
10,4
10,8
11,2
11,6
12,0
PC II
PC I

Table 10.15

External and cranial measurements for *A. h. longiceps* specimens examined; and craniometric ratios diagnosing this taxon from the parapatric phena *A. h. pondoliae*, *A. h. hottentotus* and *A. h. iris*. $\overline{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\overline{x}$	*sd*	Range	*n*	$\overline{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	15	131,5	7,1	120-141	19	127,5	7,8	119-139
HF	14	15,9	2,5	14-18	17	15,4	1,5	13-18
BCW	21	6,1	0,2	5,4-6,6	25	5,8	0,1	4,9-6,3
CRANIAL MEASUREMENTS:								
ARB	19	5,4	0,2	4,8-6,0	27	5,2	0,1	4,6-5,7
MIO	19	9,2	0,3	8,2-10,0	27	8,9	0,1	8,1-9,8
ZMB	19	17,9	0,5	16,3-19,4	26	17,2	0,1	16,4-19,1
IOW	19	7,8	0,2	7,0-8,3	27	7,6	0,2	7,1-8,7
GSL	21	29,1	0,7	27,0-30,1	28	28,2	0,1	26,6-29,9
GSH	19	13,9	0,2	13,1-14,8	27	13,6	0,1	12,8-14,6
P@P	13	7,6	0,2	6,5-8,0	26	7,5	0,2	7,0-8,4
PBM	12	5,2	0,2	4,7-5,8	18	5,1	0,1	4,6-5,4
PAL	19	14,6	0,4	13,3-15,3	25	14,1	0,2	12,7-15,3
MTL	15	6,8	0,1	6,4-7,1	24	6,7	0,1	6,1-7,2
IPG	19	2,3	0,1	2,0-2,6	27	2,3	0,1	2,0-2,6
PPL	19	9,2	0,2	8,6-10,0	27	9,1	0,1	8,4-9,7
EAM	15	1,3	0,1	1,2-1,5	21	1,4	0,1	1,1-1,7
BBW	16	12,6	0,4	11,3-13,8	26	12,2	0,2	11,4-13,2
CPL	19	7,8	0,2	7,1-8,6	27	7,6	0,1	6,8-8,1
APW	19	5,2	0,2	4,2-6,0	27	4,8	0,1	4,5-5,4
MDL	19	18,1	0,4	16,5-19,6	26	17,7	0,2	16,5-18,8
FML	19	5,1	0,1	4,9-5,4	27	4,9	0,1	4,6-5,7

RATIOS:	$\overline{x}\pm 1sd$.
APWX100/ZMB	
A. h. longiceps	28,5±0,8
A. h. pondoliae	27,1±0,6
A. h. iris	25,1±1,2
A. h. hottentotus	27,3±0,6
APWX100/MTL	
A. h. longiceps	70,4±2,7
A. h. pondoliae	70,9±3,2
A. h. iris	63,1±4,9
A. h. hottentotus	74,4±2,6
MIOX100/ZMB	
A. h. longiceps	51,1±0,7
A. h. pondoliae	49,6±1,2
A. h. iris	50,2±1,6
A. h. hottentotus	49,6±0,5

becomes lighter towards the flanks and ventrum, which range from bright reddish-brown (5YR5/6) to orange (7,5YR 5-7/6).

Differentiating between *A. h. longiceps*, *A. septentrionalis* and *Amblysomus Species A* is difficult, since there are no clearcut ($\overline{x} \pm 1sd$) univariate differences among them in either cranial measurements or ratios. There are, however, significant multivariate differences between the taxa, which can be used to identify unknown specimens with 95% confidence (see Tables 10.16-17)

Habitat. Mesic, higher-altitude habitats of the grassland biome, where it favours meadows, vleis and montane forests in Highland Sourveld and Dohne Sourveld (veld type 44), Southern Tall Grassland (veld type 65), and North-eastern Sandy Highveld (veld type 57).

Protection status. Satisfactory. Recorded from the the following conservation areas: Karkloof Nature Reserve, Mgeni Vlei Nature Reserve and Midmar Dam Nature Reserve; Loteni Nature Reserve, Kamberg Nature Reserve and Mgeni Vlei Nature Reserve; Giants Castle Nature Reserve and Moore Park Nature Reserve; Royal Natal National Park; Mlilwane Game Reserve (Swaziland); as well as in various municipal and provincial nature reserves in the Pietermaritzburg district.

Specimens examined (*n* = 73). EASTERN CAPE PROVINCE. **Elliot district** (*n* = 1): Ben Voirlich Farm - NMB5242; **Maclear district** (*n* = 3): Ugie, Rocky Park - NMB5330; Maclear - NMB5929-30; **Wodehouse district** (*n* = 1): Dordrecht - KM13987; KWAZULU-NATAL. **Bergville district** (*n* = 1): Royal Natal National Park - NM1754; **Estcourt district**. Giants Castle Nature Reserve (*n* = 4) - DM129,SI344223-4, TM38110; **Mooi River district**. Kamberg Nature Reserve (*n* = 1) - TM40113; Loteni Nature Reserve (*n* = 1) - NM1309; **Polela district** (*n* = 1): Bulwer, Wylde Halme Farm - NM1752; **Underberg district** (*n* = 2): Castle View Farm - NM1111-2; POOLED LOCALITIES. *PIETERMARITZBURG* = **Pietermaritzburg district** (*n* = 15): Pietermaritzburg City - NM138,786,1618,1967; TM33038,33041,33044-5; Sweetwaters - NM1882; Prestbury - NM1883; Ketelfontein - TM40115; Town Bush - NM625,631; Hilton - NM1884;TM38479; *KARKLOOF* = **Lions River district** (*n* = 8): Howick and Curry's Post - TM9985,37165; Dargle - SI380484-5;TM728-30,8920; **New Hanover district** (*n* = 11): Karkloof - TM12505-15; *ESTCOURT* = **Estcourt district** (*n* = 8): Petchange - SI351323-8; Tabamhlope - TM12504; Estcourt, Moore Park Nature Reserve - TM40014; **Mooi River district** (*n* = 8): de Hoek - NM825,1113-7; Rosetta - NM1321; Weston - TM38555; FREE

Table 10.16

Statistics and coefficients required to differentiate unequivocally between male *A. h. longiceps*, *A. septentrionalis* and *Amblysomus Species A*, using a canonical variate scatterplot (Fig. 10.5). To plot an unknown, measure the specimen and subtract each measurement (*X*) from the overall mean (*Y*). Multiply the difference (*X-Y*, either positive or negative) by the respective standardized canonical vectors (*CVI* and *CVII*), and sum the scores for each axis to determine the unknown's scatterplot co-ordinates.

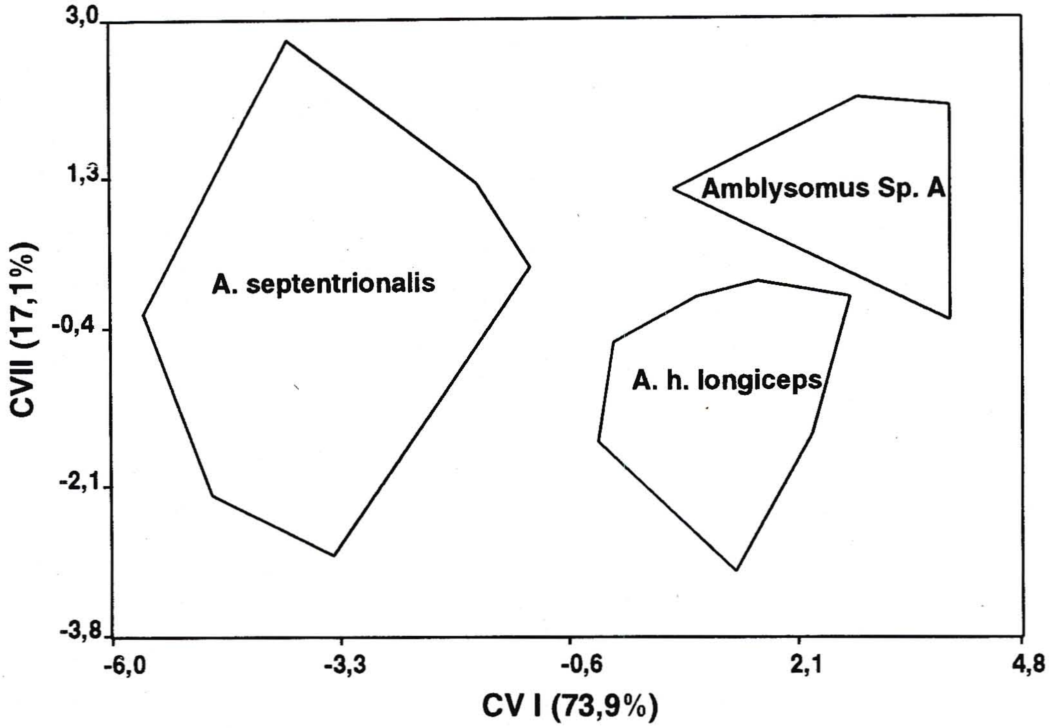
Variable	**Measurement of unknown**	**Overall mean**		**Standardized canonical vector I**	***CVI* score**	**Standardized canonical vector II**	***CVII* score**
	X	*Y*	*X-Y*	*CVI*	*(X-Y)xCVI*	*CVII*	*(X-Y)xCVII*
ARB		5,28		-2,26		2,16	
MIO		8,90		-0,14		0,15	
ZMB		18,02		4,56		-0,08	
IOW		7,91		-2,06		-2,03	
GSL		29,18		-2,42		-0,75	
GSH		14,03		-0,71		0,58	
P@P		7,77		0,63		-1,76	
PAL		14,65		2,06		0,79	
MTL		7,02		1,73		-4,04	
IPG		2,29		-2,35		4,59	
PPL		9,25		3,19		2,57	
BBW		12,65		-0,93		0,16	
FML		5,09		3,47		3,28	
CPL		7,94		-3,17		1,29	
APW		5,22		-3,64		-2,63	
MDL		18,17		3,32		0,78	
SCORE FOR PLOTTING					*CVI (Σ)* =		*CVII (Σ)* =

Table 10.17

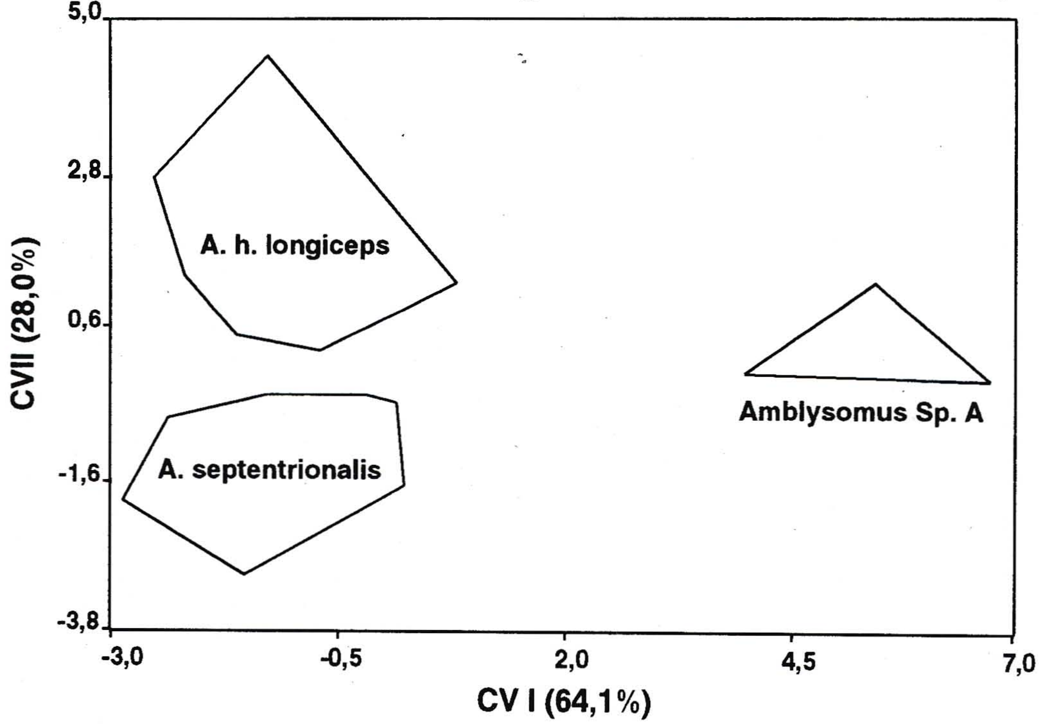
Statistics and coefficients required to differentiate unequivocally between female *A. h longiceps*, *A. septenrionalis* and *Amblysomus Species A*, using a canonical variate scatterplot (Fig. 10.5). To plot an unknown, measure the specimen and subtract each measurement (*X*) from the overall mean (*Y*). Multiply the difference (*X-Y*, either positive or negative) by the respective standardized canonical vectors (*CVI* and *CVII*), and sum the scores for each axis to determine the unknown's scatterplot co-ordinates.

Variable	**Measurement of unknown**	**Overall mean**		**Standardized canonical vector I**	***CVI* score**	**Standardized canonical vector II**	***CVII* score**
	X	*Y*	*X-Y*	*CVI*	*(X-Y)xCVI*	*CVII*	*(X-Y)xCVII*
ARB		5,09		2,46		-4,01	
MIO		9,00		-2,12		-0,04	
ZMB		17,27		-0,58		0,53	
IOW		7,72		2,04		1,15	
GSL		28,36		-0,01		1,41	
GSH		13,57		-1,74		-2,14	
P@P		7,63		-1,68		-0,36	
PAL		14,03		0,28		-0,49	
MTL		6,83		-5,22		0,69	
IPG		2,25		15,51		-1,26	
PPL		9,02		3,23		-1,42	
BBW		12,06		1,23		-0,47	
FML		4,94		1,72		0,64	
CPL		7,55		-0,36		-0,58	
APW		4,86		-6,72		-0,75	
MDL		17,68		3,82		2,09	
SCORE FOR PLOTTING					*CVI (Σ)* =		*CVII (Σ)* =

Figure 10.5 Pairwise comparison of the first two canonical variate axes, from discriminant functions analysis of cranial measurements in male and female *A. h. longiceps* (2n=30), *A. septentrionalis* (2n=34) and *Amblysomus Species A* (2n=36). To identify a specimen of unknown affinity, use the procedure explained in Table 10.15.


♀

3,0
1,3
-0,4
-2,1
-3,8
-6,0
-3,3
-0,6
2,1
4,8
CVII (17,1%)
CV I (73,9%)
A. septentrionalis
Amblysomus Sp. A
A. h. longiceps


♂

5,0
2,8
0,6
-1,6
-3,8
-3,0
-0,5
2,0
4,5
7,0
CVII (28,0%)
CV I (64,1%)
A. h. longiceps
A. septentrionalis
Amblysomus Sp. A

STATE. *GOLDEN GATE* = **Harrismith district** (*n* = 3): Waterfall/Summerslie and Mooihoek Farms - NMB3120,3945,1643; **Bethlehem district** (*n* = 5):Clarens - NMB3344; Golden Gate National Park - TM16621-2, 16646,16749.

Amblysomus hottentotus pondoliae Thomas and Schwann, 1905

1905 *Amblysomus hottentotus pondoliae* Thomas and Schwann, *Proceedings of the Zoological Society, London* I:260. Notinsila, western Pondoland, Transkei, Eastern Cape Province.

1908 *Chrysochloris hottentota albirostris* Broom, *Annals of the Transvaal Museum* 1:15. *Nomen dubium.*

1913 *Amblysomus hottentotus albirostris* Roberts, *Annals of the Transvaal Museum* 4:73. *Nomen dubium.*

1946 *Amblysomus hottentotus natalensis* Roberts, *Annals of the Transvaal Museum* 20:311. Durban, KwaZulu-Natal. Listed also from "the coast of Natal".

Holotypes. *A. hottentotus* - BM 4.6.6.4, adult male, TW2, collected by H. H. Swinny at Notinsila, west Pondoland (Transkei, Eastern Cape) at an altitude of 700m a.s.l. on 10 February 1904. Skin in good condition, skull with damaged braincase, basal claw width 4,87 mm. *A. h. natalensis* - TM6247, male, TW2, collected by R.J. Urqhart on 19 September 1930. Skin and skull in good condition, basal claw width 4,90 mm.

Distribution (Fig. 10.2). The most widespread of the five subspecies, occurring from the Great Fish River valley in the Eastern Cape, where it intergrades with *A. h. hottentotus*, northwards along the coast to the Umdhloti River near Durban. Its range extends inland to the Stutterheim, Hogsback and Seymour districts, and possibly as far as the Drakensberg foothills in the vicinity of Elliot and Maclear, where it is replaced by *A. h. longiceps*. In Transkei and KwaZulu-Natal it is restricted to the coastal plain, and intergrades with *A. h. iris* in Zululand, and with *A. h. longiceps* in the KwaZulu-Natal midlands.

Diagnosis (Table 10.18). The second largest subspecies, with a total length of 105-145 mm. Sexual size dimorphism is prounced, with males being larger than females in most measurements, particularly greatest skull length (GSL - ♂:25,04-29,4 mm; ♀:24,9-28,6 mm). This subspecies is significantly larger than *A. h. iris* to the north,

Table 10.18

External and cranial measurements for *A. h. pondoliae* specimens examined; and craniometric ratios diagnosing this taxon from the parapatric phena *A. h. longiceps*, *A. h. hottentotus* and *A. h. iris*. $\overline{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\overline{x}$	*sd*	Range	*n*	$\overline{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	88	125,2	9,3	107-145	92	122,8	7,1	105-135
HF	78	15,2	1,5	12-18	103	14,4	1,5	11-18
BCW	125	5,4	0,3	4,4-6,6	113	5,2	0,3	4,0-6,6
CRANIAL MEASUREMENTS:								
ARB	116	5,2	0,1	4,3-5,7	109	4,9	0,1	4,3-5,6
MIO	120	8,3	0,2	7,4-9,0	111	8,2	0,1	7,0-8,9
ZMB	121	17,1	0,5	14,6-19,3	112	16,4	0,3	14,6-18,0
IOW	126	7,5	0,1	6,4-8,2	113	7,1	0,2	6,3-8,1
GSL	116	27,2	0,4	25,0-29,4	108	26,4	0,4	24,9-28,6
GSH	121	13,2	0,3	12,1-14,4	113	12,9	0,3	12,0-13,8
P@P	122	7,6	0,1	6,5-8,8	108	7,3	0,1	6,5-8,1
PBM	107	5,0	0,1	4,3-5,7	85	4,9	0,1	4,2-5,4
PAL	118	13,5	0,2	11,8-14,8	107	13,1	0,2	12,0-14,6
MTL	114	6,6	0,1	5,8-7,2	88	6,4	0,1	6,0-7,0
IPG	119	2,2	0,1	1,8-2,7	113	2,2	0,1	1,9-2,6
PPL	119	8,9	0,2	7,8-9,8	112	8,5	0,2	7,8-9,4
EAM	85	1,4	0,1	1,0-1,8	93	1,3	0,1	1,0-2,4
BBW	112	12,2	0,4	10,6-13,9	102	11,7	0,4	10,6-13,2
CPL	120	7,4	0,2	6,4-8,5	112	7,1	0,2	6,5-8,1
APW	121	4,7	0,2	3,0-5,6	108	4,5	0,2	3,8-5,4
MDL	121	17,1	0,3	15,6-18,5	113	16,6	0,3	15,2-18,5
FML	111	4,8	0,1	4,1-5,5	110	4,7	0,1	4,2-5,2

RATIOS:	$\overline{x}\pm$ ***1sd.***
APWX100/ZMB	
A. h. longiceps	28,5±0,8
A. h. pondoliae	27,1±0,6
A. h. iris	25,1±1,2
A. h. hottentotus	27,3±0,6
APWX100/MTL	
A. h. longiceps	70,4±2,7
A. h. pondoliae	70,9±3,2
A. h. iris	63,1±4,9
A. h. hottentotus	74,4±2,6
MIOX100/ZMB	
A. h. longiceps	51,1±0,7
A. h. pondoliae	49,6±1,2
A. h. iris	50,2±1,6
A. h. hottentotus	49,6±0,5

but noticeably smaller than *A. h. longiceps* further inland in KwaZulu-Natal. Size varies clinally in relation to altitude, as in *A. h. longiceps*. The interpterygoid region is wider (IPG/P@P = 29,8±1,2%) than in *A. h. hottentotus* (27,3±1,0%), whereas the inter-orbital region is relatively narrower (MIO/ZMB = 49,6±1,2%) than in *A. h. longiceps* (51,1±0,7%). The mandibular ramus (APW/MTL = 70,8±3,2%) is wider than in *A. h. iris* (63,1±4,9%), and its claws are more robust. Colour is quite variable as in other subspecies, but is usually dark reddish-brown (7,5YR 2/2) mid-dorsally, tending to become more rufous towards the flanks and ventrum, which range from brown (10YR 4/6) through dull yellow-orange (10YR 6/4) to orange (7,5YR 6/6). In parts of Transkei (particularly Port St. Johns), darker specimens with a blackish-brown dorsum predominate, but more reddish specimens also occur (Broom 1907a). A few darker (reddish-black; 10R 2/1) specimens have been collected also at Durban and Umdoni, along with a rare albino specimen in which the fur colour is much paler, approaching the orange colour of *N. julianae*.

Habitats. Restricted to the savanna biome, in coastal tropical forests (Coastal Forest and Thornveld - veld type 1; Pondoland Coastal Plateau Sourveld - veld type 3; Eastern Province Thornveld - veld type 7), but found also in semi-karooid Valley Bushveld (veld type 23) in the south near King Williams Town.

Protection status. Satisfactory. Recorded from the following conservation areas: Pirie Forest, Kabusi Forest, Kalogha Forest (Hogsback/King Williams Town); Nyadu forest (Umtata); Oribi Gorge Nature Reserve (Port Shepstone); Umtavuma Nature Reserve (Port Edward); Vernon Crookes Nature Reserve (Scottburgh); Entumeni Nature Reserve; various reserves in Durban, including Durban Botanic Gardens, University of Natal Shepstone Reserve, Kenneth Stainbank Nature Reserve, Bluff Nature Reserve, Palmiet Nature Reserve and Krantzkloof Nature Reserve.

Specimens examined (*n* = 295). EASTERN CAPE PROVINCE: **Ciskei district:** Seymour (*n* = 11) - KM939, 8930-2, 8995, 24925-30; **Stutterheim district** (*n* = 9): Kabusi State Forest - CM94942-3; Pirie Forest and Trout Hatchery - KM975-7, 18123; SI344221; TM712-3; POOLED LOCALITIES. *KING WILLIAMS TOWN* = **King Williams Town district** (*n* = 108): King Williams Town and surrounding district KM953,983,986-7,989-993,995,998,1003,1005-6,1009-10,1014,1017,1020,1023,1027,10301,1033,1036,1042,1045,1048,1053-4,1057,1060-1,1063-4,1067,1069,1072,1075,1078-9,1082,1086,1088,1090-1,1096-7,1099,1102,1105-7,1118-20,12492,12511,17128,18143,18414,18424,18530,18550,18756,18841,18860,18943-5,18950,18960, 19031,19036,19088,19101,19109-10,19112,19127-8,19147,19175-6,19224,19252, 19324,19364,19998,20662,24158,24160-70;TM39457; Ciskei, Berlin - KM19329; *EAST LONDON* = **East London district** (*n* = 33): East London City and district - KM957,959-60,962,965,968,19631,20124,20129,20131,20134,20137-42,20147-51, 20155-6,20158; Thorneycroft - TM6033; Gonubie - KM24156; Kidds Beach - TM41674-77,41689,41698; *UMTATA* = **Transkei district** (*n* = 10): Umtata City and surrounding districts - KM2609-101; *PORT ST. JOHNS* (*n* = 21): Port St. Johns - BM4.6.6.4; DM126; TM716-8,720-1,724-7,1312,5627,12384,12386-91; KWAZULU-NATAL. *ORIBI GORGE* = **Port Shepstone district** (*n* = 12): Oribi Gorge - TM1506-8,1510,1523,1525,1530,1532-3,1564; Port Edward, Umtavuma Nature Reserve - TM14740; Hibberdene - TM36298; **Transkei district** (*n* = 1): Bizana - KM26091; *UMDONI* = **Umzinto district** (*n* = 14): Scottburgh - DM405; Umdoni Park Golf Course - NM1764-5; TM33027,33029-32,33034-6,33039; Vernon Crookes Nature Reserve - TM38115,38430; *DURBAN* = **Durban district** (*n* = 82): Durban City and suburbs - DM133; TM5008,5010,5274,6247,12516-8,33042,38324,38325, 39200-3,39205-6,39240,39246-8,39296-7,39329,39422-3,39928,40000,40023,40097-8, 40782,40848,40850-65,40867-71,40873-75,41126-44; **Pinetown district** (*n* = 5) - DM615; TM9884,33046; Kloof - DM677; Gilletts - TM5836; **Inanda district** (*n* = 1): Verulam, Hazelmere Dam - TM39260.

Amblysomus hottentotus subspecies A (provisional name)

There is no name available for this taxon, which is in the process of being formally described. The designation above is, therefore, provisional.

Distribution. Known from the Graskop and Mariepskop districts of the northern Drakensberg escarpment, possibly ranging southwards to the White River district, where a single specimen has been collected.

Diagnosis (Table 10.19). Similar in size to *A. h. pondoliae*. Too few specimens are available to assess if sexual dimorphism is pronounced, as in the other *A. hottentotus* subspecies. Differs from *A. h. pondoliae*, *A. septentrionalis* and *Amblysomus Species A* in having a reddish-black (10R2/1) band of fur mid-dorsally. Unlike the latter species, molar talonids are weak or absent, whereas P1 tend to be more molariform, but these differences are not clearcut owing to intraspecific

Table 10.19

External and cranial measurements (in mm) for *Amblysomus hottentotus subspecies A* specimens from Mpumalanga. $\overline{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

Variable	*n*	$\overline{x}$	*sd*	**Range**
EXTERNAL MEASUREMENTS:				
TL	5	113,4	7,3	105-122
HF	5	15,2	1,1	14-17
BCW	5	5,2	0,2	4,9-5,4
CRANIAL MEASUREMENTS:				
ARB	5	4,7	0,1	4,5-4,8
MIO	5	7,9	0,1	7,8-8,0
ZMB	5	16,0	0,5	15,3-16,6
IOW	5	7,3	0,1	7,2-7,4
GSL	5	27,5	0,8	26,6-28,5
GSH	5	12,6	0,2	12,2-12,8
P@P	5	7,5	0,3	7,1-7,7
PAL	5	14,1	0,7	13,0-14,8
MTL	5	6,6	0,2	6,3-6,8
IPG	5	2,2	0,1	2,0-2,3
PPL	5	8,4	0,2	8,3-8,7
BBW	5	11,4	0,4	10,8-11,9
CPL	5	7,3	0,3	6,7-7,7
APW	5	4,7	0,3	4,3-5,1
MDL	5	17,0	0,5	16,4-17,4

variability. The skull of *Amblysomus hottentotus subspecies A* is significantly smaller (GSL = 27,5±0,8 mm) than in *Amblysomus Species A* (GSL = 29,5±1,2 mm), whereas the claws are more gracile (BCW = 5,2±0,2 mm) than in either *A. septentrionalis* (BCW = 5,9±0,4 mm) or *Amblysomus Species A* (BCW = 6,2±0,5 mm). These taxa also show clearcut differences in chromosome number (Section 4.3).

Habitat. Mesic montane grasslands and indigenous forests, at the junction of the savanna and grassland biomes. Recorded from Mountain Sourveld (veld type 8) in the vicinity of Graskop, and Lowveld Sour Bushveld (veld type 9) near White River.

Protection status. Indeterminate owing to the few specimens available. Recorded only from the Blyde River Canyon Nature Reserve.

Specimens examined (*n* = 8). MPUMALANGA. **Pilgrims Rest district** (*n* = 7): Bylde River Canyon Nature Reserve - TM44177; Graskop Town - TM40781,40789-90,42132; Mariepskop - 12748-50. **White River district** (*n* = 1): Farm De Gama - TM42392.

Amblysomus septentrionalis Roberts, 1913 Highveld golden mole

1913 *Amblysomus corriae septentrionalis* Roberts, *Annals of the Transvaal Museum* 4:73. Wakkerstroom, Mpumalanga Province, South Africa.

1917 *Amblysomus hottentotus garneri* Roberts, *Annals of the Transvaal Museum* 5:278. Commisioner's Residence, Piggs Peak, Swaziland.

1946 *Amblysomus hottentotus drakensbergensis* Roberts, *Annals of the Transvaal Museum* 20:310. Wakkerstroom, Mpumalanga Province, South Africa.

1946 *Amblysomus hottentotus orangensis* Roberts, 1946, *Annals of the Transvaal Museum* 20:310. Wakkerstroom, Mpumalanga Province, South Africa.

Holotypes. *A. c. septentrionalis* - TM710, female, TW2, collected by Dr. A. Roberts on 14 November 1909. Skin and skull in good condition, basal claw width 6,02 mm; *A. h. garneri* - TM1995, male, TW3, collected by Dr. A. Roberts on 22 May 1916. Skin and skull in good condition, basal claw width 5,78 mm; *A. h. drakensbergensis* - TM2903, male, TW5, collected by Dr. A. Roberts on 12 January 1921. Skin and skull in good condition, basal claw width 6,45 mm; *A. h. orangensis* - TM3654, male, TW2, collected by W. Chivers on 11 July 1923. Skin and skull in good condition, basal claw width 5,70 mm.

Subspecies and Distribution (Fig. 10.2). Known from two, widely-separated areas: Heilbron and Parys, in the north-eastern Free State (Lynch 1983); and the south-eastern Mpumalanga highveld, from Wakkerstroom northwards to Ermelo and Barberton, with a marginal intrusion in the Piggs Peak and Mbabane districts of Swaziland. Two specimens are available from localities (Standerton, Bethal) between these areas, which suggests that that these populations may be in geographic contact.

Diagnosis (Table 10.20). A large species, with a total length of 105-145 mm, and a mass of 52-86 g. Sexual size dimorphism is very pronounced, with males being larger than females. In size and fur colour, it is indistinguishable from *Amblysomus Species A*, although these species do differ in chromosome number.

A. septentrionalis is easily distinguished from *Chlorotalpa sclateri*, with which it coexists at Wakkerstoom, by the absence of an M3, and its much greater size. But, there are no clearcut ($\bar{x} \pm 1sd$) univariate differences between *A. septentrionalis*, *A. h. longiceps* or *Amblysomus Species A*, in either cranial measurements or ratios. There are, however, significant multivariate differences between the taxa, which can be used to identify unknown specimens with 95% confidence (see Tables 10.16-17)

Although there are some consistent cranial differences between the Free State and Mpumalanga populations, sample sizes are too small to allow a thorough analysis of geographic variation in *A. septentrionalis*, and no subspecies are recognized.

Habitat. Montane grasslands and vleis of the grassland biome above the Great Escarpment. Recorded from Near-Highland Sourveld (veld type 57b), which is common in the south-eastern Mpumalanga Highveld, and in drier *Cymbopogin-Themeda* veld (veld type 48) along the Vaal River in the north-eastern Free State.

Protection status. Indeterminate owing to the few locality records available. Not recorded from any provincial or national nature reserves. Gelderblom *et al.* (1995) identified the south-eastern Mpumalanga highveld as a hotspot of chrysochlorid endemicity, and recommended that urgent action be taken to augment the national protected areas network in this region.

Specimens examined (*n* = 58). FREE STATE. **Parys district** (*n* = 5). Parys, Roseberry Plain - TM3515-6; Viljoensdrift, Farm Zandfontein - 3650-1,3655; **Heilbron district** (*n* = 6): Heilbron, farm Vaalbank - TM3652-5,3657-8; MPUMALANGA. **Amersfoort district** (*n* = 1): Begin der Lyn - TM4962; **Bethal district** (*n* = 3): Bethal - TM1571,4572; Farm Vlakfontein - TM1793; **Barberton district** (*n* = 2): Barberton - TM3365; Devils Knuckles - TM1373; **Carolina district**

Table 10.20

External and cranial measurements (in mm) for *Amblysomus septentrionalis* specimens examined. $\bar{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\bar{x}$	*sd*	Range	*n*	$\bar{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	12	128,6	8,4	114-135	25	125,3	7,8	105-145
HF	11	15,3	2,1	13-20	21	14,7	2,7	12-17
BCW	16	6,1	0,4	5,5-6,6	25	5,3	0,1	5,1-5,4
CRANIAL MEASUREMENTS:								
ARB	16	5,2	0,3	4,8-5,6	25	5,0	0,2	4,6-5,4
MIO	16	9,2	0,4	8,5-9,7	25	9,0	0,3	8,5-9,6
ZMB	16	17,9	0,6	16,8-19,5	25	17,1	0,7	16,1-19,0
IOW	16	7,9	0,3	7,4-8,4	25	7,6	0,3	7,1-8,1
GSL	16	29,0	0,9	27,2-30,5	25	28,2	1,1	26,2-30,0
GSH	16	13,9	0,4	13,0-14,7	25	13,4	0,4	12,8-14,4
P@P	16	7,8	0,4	7,0-8,3	25	7,6	0,3	6,7-8,2
PAL	16	14,6	0,5	13,2-15,6	25	14,1	0,6	12,9-14,9
PPL	16	9,2	0,4	8,4-10,1	25	8,7	0,3	8,1-9,4
BBW	16	12,6	0,6	11,2-13,3	25	12,0	0,6	10,8-12,9
CPL	16	7,9	0,4	6,9-8,5	25	7,5	0,4	6,5-8,3
APW	16	5,3	0,4	4,6-5,9	25	4,8	0,3	4,3-5,4
MDL	16	18,1	0,6	16,8-18,9	25	17,5	0,7	15,9-18,7

Table 10.21

External and cranial measurements (in mm) for *Amblysomus Species A* specimens examined. $\bar{x}$ = arithmetic mean; *sd* = 1 standard deviation; *n* = sample size.

	MALES				FEMALES			
Var.	*n*	$\bar{x}$	*sd*	Range	*n*	$\bar{x}$	*sd*	Range
EXTERNAL MEASUREMENTS:								
TL	6	131,7	7,8	118-143	7	127,7	9,4	109-138
HF	6	18,5	0,5	18-19	7	15,9	2,0	13-18
BCW	6	6,8	0,3	6,5-7,2	14	5,9	0,3	5,3-6,2
CRANIAL MEASUREMENTS:								
ARB	7	5,7	0,2	5,4-5,9	14	5,1	0,2	4,8-5,6
MIO	7	9,8	0,4	9,5-10,6	14	9,2	0,4	8,2-9,6
ZMB	7	19,2	0,6	18,6-20,4	14	17,6	0,6	16,6-18,2
IOW	7	8,3	0,3	8,0-8,7	14	7,9	0,3	7,3-8,3
GSL	7	30,8	0,6	29,9-32,0	14	28,8	0,8	27,2-29,7
GSH	7	14,7	0,4	14,3-15,3	14	13,7	0,3	13,1-14,1
P@P	7	8,2	0,2	7,8-8,5	14	7,8	0,4	7,2-8,3
PAL	7	15,6	0,4	15,1-16,2	14	14,3	0,5	13,0-14,9
IPG	7	2,3	0,1	2,2-2,6	14	2,3	0,1	2,1-2,5
PPL	6	9,8	0,3	9,3-10,1	14	9,2	0,4	8,7-9,6
BBW	7	13,3	0,5	12,8-14,1	14	12,2	0,7	11,0-13,2
CPL	7	8,3	0,2	8,0-8,5	14	7,6	0,2	7,2-8,0
APW	7	5,4	0,3	5,1-5,8	14	4,8	0,2	4,4-5,1
MDL	7	19,3	0,4	18,9-20,0	14	18,1	0,5	17,5-18,9

(n = 1): TM1372; **Ermelo district** (n = 7). Amsterdam, Joshua Moolman Private Nature Reserve - TM20270; Ermelo - KM932-6; Ermelo Municipal Dam - TM42136; **Piet Retief district** (n = 3): Farm Goedgevorde - SI380481-3; **Standerton district** (n = 1): Farm Roodepoort - TM24995; **Wakkerstroom district** (n = 24). Wakkerstroom, Farm Tafelkop (= Kastrol Nek) - TMCR578; TM582,584,710,732-3,734-5,737,1216,1220,2902,2905,4321-2,39861,39871-2,39876,41600,41604,41609, 41613; Farm Langfontein - TM25208; SWAZILAND (n = 5). Piggs Peak - TM1995; Mbabane - TM25693,40909-10,44888.

Amblysomus Species A (provisional name)

Distribution. Known only from the Belfast and Dullstroom districts of the eastern Mpumalanga highveld.

Diagnosis (Table 10.21). The largest of the amblysomine species, with a total length of 109-143 mm, and a mass of 61-98 g. Sexual size dimorphism is pronounced, males being significantly larger than females in most cranial measurements. Very similar to *A. h. longiceps* and *A. septentrionalis* from the south-eastern Mpumalanga highveld in size and fur colour, and also in cranial configuration. However, these three taxa differ in chromosome number, and can be diagnosed statistically (with 95% confidence) using the procedure outlined in Tables 10.16-17.

Habitat. High altitude (< 1800m a.s.l.) grasslands and vleis in the Steenkampsberge. These localities fall in Near-Highland Sourveld (veld type 57b) of the grassland biome.

Protection status. Indeterminate owing to the few locality records available. Recorded from the Verloren-Vallei provincial Nature Reserve.

Specimens examined (n = 20). MPUMALANGA. **Belfast district** (n =20): Belfast - TM738-40,1156,4572,40903; Dullstroom - TM23820,38467-9,39163,39181;Swartkoppies Farm - TM40062; Wemmershuis Farm - TM40063; Palmer Vlei - TM39966; Verloren-Vallei Nature Reserve - TM41659-63,41666.

10.3 Gazetteer

Co-ordinates and quarter-degree square grid references were obtained from a variety of sources, mostly 1:50 000 or 1:250 000 topocadastral maps (available from the Government Printer, Pretoria) and specimen labels, but also from Skead (1973), Smithers and Lobao-Tello (1976) or Smithers and Wilson (1979). An error margin of approximately 5' should be allowed for co-ordinate data. Localities for which co-ordinates could not be established (owing to poor specimen documentation) are listed by quarter-degree square only.

ANGOLA: Lunda district, Poste de Canzar (07°37'S; 21°34'DA).

CAMEROON: Metet (32°30'N; 11°43'E); Molundu (02°03'N;15°13'E); Pama-Quelle (04°58'N;17°44'E).

CENTRAL AFRICAN REPUBLIC: Kanenga, Nsankulu Betu (05°54'S; 22°25'E).

CONGO: Kunungu (02°06'S; 16°26'E); Kwamouth (03°11'S; 16°16'E); Ndive, Bolopo (02°09'S; 16°14'E); Ruwenzori West (00°20'N; 29°48'E); Yambuya (01°17'N;24°34'E).

LESOTHO: Mamathes (29°08'S; 27°50'E); Leribe (28°53'S; 28°03'E).

KENYA: Kaimosi Forest (00°11'N; 34°56'E).

MOZAMBIQUE: Gaza district, Chigubo Administration Post (22°50'S; 33°31'E); Maputo City (25°38'S; 32°30'E); Inhaca Island (26°00'S; 32°55'E); Rikatla (25°46'S; 32°37'E); Inhambane, Coguno (24°16'S; 34°40'E); Masiene (25°03'S; 33°48'E); Nyaboa (2033BC); Sofala district, Vila Gouveia (18°03'S; 33°11'E).

REPUBLIC OF SOUTH AFRICA: WESTERN CAPE PROVINCE: George District: Jonkersberg - (33°55'S; 22°14'E). **Heidelberg District**: Grootvadersbosch - (33°50'S; 20°53'E); Grootvadersbosch Forest (34°01'S; 20°47'E). **Knysna District**: Knysna Town (34°02'S; 23°03'E); Goudveld, Harkerville and Rondeveld (34°02'S; 23°03'E); Diepwalle Forest (33°57'S; 23°10'E; and 32°03'S; 23°03'E); Plettenberg Bay town (33°57'S; 23°44'E) and district (34°03'S; 23°23'E); Nature's Valley Town (33°59'S; 23°34'E). **Paarl District:** Paarl, La Motte Estate (33°53'S; 19°05'E). **Riversdale District**: Garcia (33°57'S; 21°13'E); Garcia Forest Reserve (34°00'S; 21°13'E). **Somerset West District**: Witmoss (32°43'S; 25°35'E). **Stellenbosch District**: Stellenbosch Town (33°56'S; 18°51'E); Jonkershoek (33°55'S; 32°53'E). **Worcester District**: Haweqwas Forest (33°34'S; 19°08'E). **EASTERN CAPE PROVINCE: Albany District**: Albany district (33°20'S; 26°30'E); Grahamstown City, Atherstone, Caravan Park, Fir Glen, Kleinpoort and Orinway Farm (33°19'S; 26°32'E). **Alexandria District**: Alexandria Town (33°21'S; 25°45'E); Alexandria Forest Reserve, Farms Groenkop and Lidney (33°41'S; 26°00'E); Paterson Farm (33°21'S; 25°45'E). **Barkly East District**: Carlisles Farm (30°44'S; 27°57'E); Rhodes (30°41' S; 28°08'E); Rhodes Farm (30°58'S; 27°37'E). **Bathurst District**: Port Alfred Town (33°34'S; 26°44'E) and golf course (33°36'S; 26°54'E). **Beaufort West District**: Karoo National Park (32°20'S; 22°35'E); Matjiesvlei (32°20'S; 22°35'E). **Ciskei District**: Berlin (32°52'S; 27°34'E); King Williams Town City and surrounding area and Debe Nek (32°52'S; 27°23'E); Kat River Valley, Seymour Farm and Tombookies Vlei (32°29'S; 26°41'E). **East London District**: East London City and surrounding suburbs (33°01'S; 27°55'E); East London Museum, Thorneycroft suburb (32°56'S; 28°02'E); Kidds Beach Caravan Park (33°09'S; 27°42'E); Gonubie Town - (32°56'S; 28°02'E). **Elliot District**: Ben Voirlich Farm (31°20'S; 27°51'E). **George District**: George Town, Garden Route Nursery, Saasveld Forestry Reserve Station (33°58'S; 22°31'E). **Graaf-Reinet District**: Nieu-Bethesda (31°52'S24°33'E). **Humansdorp District**: Hoffmansbos, Bokkeplaas Farm (34°02'S; 24°16'E); Kareedouw (33°59'S; 24°07'E). **Lady Grey District**: Hellvellyn Farm (31°42'S; 27°14'E). **Maclear District**: Ugie, Rocky Park (31°12'S; 28°13'E). **Port Elizabeth District**: Port Elizabeth City and surrounding areas, Baakensvlei and Walmer (33°58'S; 25°38'E); Van Stadens Wildflower Reserve (33°58'S; 25°13'E); Perseverance, Coega Station (33°50'S; 25°31'E). **Transkei District**: Port St. Johns (31°38'S; 29°33'E); Nqeleni (31°40'S; 29°02'E); Bizana, Mzamba River Mouth (31°06'S; 30°10'E); Tsolo (Isolo), St. Cuthberts (31°19'S;28°40'E); Notinsila (31°44'S; 29°11'E); Umtata Town and district (31°35'S; 28°47'E), including Fort Gale suburb, University grounds and Viedgesville (31°43'S; 28°41'E). **Stutterheim District**: Kabusi Forest (32°31'S; 27°15'E); Pirie Forest and Pirie Trout Hatchery (32°43'S; 27°18'E); **Uitenhague District**: Groendal Wilderness (33°43'S; 25°16'E). **Wodehouse District**: Dordrecht (31°22'S; 27°03'E).

FREE STATE PROVINCE: Bethlehem District: Clarens, Boshoek Farm (28°21'S; 28°25'E); Golden Gate National Park (28°33'S; 28°38'E). **Clocolan District**: Clocolan (28°55'S; 27°34'E). **Ficksburg District**: Ficksburg town and caravan park (28°52'S; 27°52'E); Gumtree, Kirklington (28°52'S; 27°43'E). **Harrismith District**: Mooihoek, Summerslie and Waterfall (28°16S; 29°08'E). **Heilbron District**: Heilbron town, district and Vaalbank Farm (27°17'S; 27°58'E). **Parys district**: Parys, Roseberry Plain (26°55'S; 27°27'E); Viljoensdrift, Zandfontein Farm (26°43'S; 27°50'E).

GAUTENG PROVINCE: Pretoria District: Pretoria, Shere, The Willows and Tierpoort Plots (25°43'S; 28°11'E).

KWAZULU-NATAL PROVINCE: Babanango District: Goudhoek Farm (28°23'S; 31°05'E). **Bergville District**: Royal Natal National Park (28°41'S 28°57'E). **Durban District**: Durban City and Beach, Bellair (Sarnia Road), Clairwood, Sydenham, Umbilo and University of Natal (29°52'S; 31°01'E); Bluff Nature Reserve (29°55'S; 30°59'E); Botanic Gardens, Country Club (29°50'S; 31°02'E); Glenwood (29°53'S; 31°00'E); Isipingo Flats (29°52'S; 31°03'E). **Eshowe District**: Eshowe Town (28°54'S;31°28'E), Buxton (29°54'S; 31°28'E). **Estcourt District**: Petchange, Moore Park, Tabamhlope (29°00'S; 29°53'E); Giant's Castle Nature Reserve (29°14'S; 29°30'E). **Hlabisa District**: Charters Creek (28°12'S; 32°25'E); Hluhluwe town (28°02'S; 32°17'E); Hluhluwe Game Reserve (28°05'S; 32°04'E); Mtubatuba town, Mtubatuba Flats, Mtubatuba district and Dukuduku Forest (28°22'S; 32°21'E); Futululu Forest Station (28°22'S; 32°25'E); St. Lucia Forest Station (28°20'S; 32°24'E); Mapelane (28°25'S; 32°25'E); St. Lucia (28°22'S; 32°25'E); Monzi village (28°22'S; 32°25'E). **Impendle District**: Sani Pass, Malchake Store (29°35'S; 29°16'E). **Inanda District**: Verulam district, Umhloti River (29°39'S; 31°08'E); Hazelmere Dam (29°36'S; 31°01'E). **Ingwavuma District**: Ingwavuma (27°08'S; 32°02'E); Kosi Lake and KwaNgwanase district (26°59'S; 32°45'E); Ndumu Game Reserve (26°53'S; 32°16'E); Amanzengwenya, Lalanek (27°13'S; 32°47'E). **Ixopo District**: Cornhill Farm (30°12'S; 30°00'E). **Klipriver District**: Elandslaagte, Spring Grove (28°24'S; 29°58'E). **Lions River District**: Dargle district, Kilgobbin Farm (29°28'S; 30°06'E); Howick town (29°30'S; 30°14'E); Curry's Post (29°29'S; 30°13'E). **Lower Umfolozi District**: Empangeni Town and district (28°46'S; 31°54'E); Umfolozi district (28°21'S; 31°59'E); Umfolozi Station (28°27'S; 32°10'E). **Mooi River District**: Kamberg Nature Reserve (29°24'S; 29°40'E); Loteni Nature Reserve (29°27S; 29°31'E); Mooi River town and De Hoek Farm (29°06'S; 30°01'E); Rosetta town (29°18'S; 29°58'E); Weston (29°12'S; 30°02'E). **Mtunzini District**: Mtunzini town (29°06'S; 31°33'E); Ngoye Forest (28°51'S; 31°41'E). **New Hanover District**: Karkloof Forest (29°24'S: 30°17'E). **Pietermaritzburg District**: Hilton (29°33'S; 30°18'E); Pietermaritzburg district, Town, Hardingdale, Ketelfontein, Prestbury, Sweetwaters and Town Bush (29°36'S; 30°23'E); Hilton (29°33'S; 30°17'E). **Pinetown District**: Gilletts - (29°48'S; 30°48'E); Pinetown (29°50'S; 30°52'E); Kloof (29°48'S; 30°51'E). **Polela District**: Bulwer, Wylde Halme Farm (29°48'S; 29°40'E). **Port Shepstone District**: Oribi Gorge (30°43'S; 30°16'E); Umtamvuna Nature Reserve (31°04'S; 30°12'E). **Ubombo District**: Lake Sibaya (27°21'S; 32°43'E); Ubombo district (27°34'S; 32°02'E). **Umzinto District**: Hibberdene (30°34'S; 30°35'E); Scottburgh, Kingsburgh suburb (30°16'S; 30°45'E); Umdoni Park (30°24'S; 30°41'E); Vernon Crookes Nature Reserve (30°16'S; 30°36'E). **Underberg District**: Castle View Farm (29°48'S; 29°30'E). **Utrecht District**: Klipspruit (27°39'S; 30°19'E). **Vryheid District**: Ngome Forest Reserve (27°52'S; 31°24'E); Vryheid district (27°46'S; 30°48'E).

MPUMALANGA PROVINCE: Amersfoort District: Begin der Lyn (27°01'S; 29°58'E). **Barberton District**: Barberton town and Devils Knuckles (25°47'S; 31°03'E). **Belfast District**: Belfast town (25°42'S; 30°02'E); Palmer Vlei, and Farms Swartkoppies and Wemmershuis (25°31'S; 30°04'E); Dullstroom town and district (25°18'S; 30°07'E); Verloren-Vallei Provincial Nature Reserve (25°13'S; 30°08'E). **Bethal District**: Bethal Town (26°27'S; 29°28'E). **Carolina District**: Carolina town, district and Vlakfontein farm (26°04'S; 30°06'E). **Ermelo District**: Amsterdam, Joshua Moolman Nature Reserve (26°38'S; 30°40'E); Ermelo town and district (26°31'S; 30°00'E); Ermelo Dam (26°28'S; 28°57'E). **Pilgrims Rest District**: Graskop town and district (24°56'S; 30°51'E); Mariepskop (24°35'S; 30°50'E). **Wakkerstroom District**: Goedgevonden Farm (27°16'S;30°29'E); Wakkerstroom town, district and Langfontein Farm (27°21'S; 30°09'E); Tafelkop

Farm = Kastrol Nek (27°17'S; 30°16'E). **White River District**: Kruger National Park, Pretoriuskop Camp (25°11'S; 31°16'E); White River, De Gama Farm (25°08'S; 31°03'E).

NORTHERN CAPE PROVINCE: Sutherland District: Sutherland Town and district (32°23'S; 20°40'E).

NORTHERN PROVINCE: Lebowa District: Haenertzberg (23°57'S; 29°57'E). **Soutpansberg District**: Kruger National Park, Nyadu Sandveld (22°41'S; 31°23'E); Numbi Gate (25°07'S; 31°11'E). **Potgietersrust District**: Naboomspruit, Nylsvley Provincial Nature Reserve (24°29'S; 28°42'E); Nylstroom district, Witkoppie Farm (24°45'S; 28°42'E). **Letaba District**: Tzaneen, De Hoek Forest Station (23°49'S; 30°01'E); New Agatha Forest Station (24°01S; 30°04'E); Woodbush Forest (23°47'S; 30°04'E).

RWANDA: Rugege Forest (02°15S; 29°14'E).

SWAZILAND: Mbabane (26°19'S; 31°08'E); Malolotja Nature Reserve (26°08'S; 31°08'E); Piggs Peak (25°59'S; 31°15'E).

TANZANIA: Rungwe district, Mporotä (09°08'S; 33°40'E).

UGANDA: Djugu (01°55'N; 30°31E); Kigezi district, Kayonza Forest (01°16'S; 29°45'E); Mt. Elgon (01°10'N; 34°32'E); Ruwenzori East (00°22'N; 30°00'E); Nyakahanga, Bakoba (01°37'S; 31°08'E).

ZAIRE: Blukwa (01°44'S; 30°37'E); Bokungu (00°45'S; 22°25'E); Kibumba (02°11'S; 28°48'E); Kisangani (00°33'N; 25°14'E); Kivu, Albert National Park (01°23'S; 30°26'E). Luluaborg, Kasai (05°53'S; 22°26'E); Lusambo (04°50'S; 23°26'E); Mutsora, PNA Station (00°19'N; 29°44'E); Rutschuru (01°11'S; 29°27'E); Ubangi, Duma (03°53'N; 18°42'E).

ZIMBABWE: Gonarezhou district: Fisham (2132AC); Confluence of Save and Lundi Rivers (2132AD); Malugwe Pan (2131DC); Zinave (2132BA). **Holdenby**

district: Lower Pungwe Valley (18°23'S; 32°58'E). **Inyanga district**: Mtarazi Falls (18°27'S; 32°45'E); Pamushana Farm (1832BD); Pungwe Falls (18°25'S; 32°47'E); Rhodes Estate (18°16'S; 32°45'E); Rhodes Experimental Station (18°17'S; 32°45'E); Trout Research Centre (1832BB). **Melsetter district**: Fairview (19°46'S; 32°48'E). **Mutare district**: Chinyuwhera (19°18'S; 32°32'E); Honde Valley, Eastern Highlands Estate (18°31'S; 32°50'E); Imbeza Valley (1932BB); Mutare (18°59'S; 32°41'E). **Vumba district**: Bunga Forest Botanical Reserve (19°07'S; 32°45'E); Vumba Botanical Reserve (19°05'S; 32°52'E); Vumba Mountain (19°05'S; 32°44'E); Cloudlands Farm, Eagle School, Hermitage, Hycroft (1932BB).

CHAPTER 11

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