INFRASPECIFIC SYSTEMATICS OF THE YELLOW MONGOOSE *CYNICTIS PENICILLATA*

by

Peter John Taylor

Submitted in partial fulfilment of the
requirements for the degree of
Doctor of Philosophy,
in the
Department of Biology,
University of Natal.
1990

Durban
1990

To my wife, Frances

For caring

ABSTRACT

Geographic variation was analysed in morphological (colour, morphometric) and genetic (electrophoretic, chromosomal) characters in the yellow mongoose Cynictis penicillata, a diurnal, colonial, burrow-dwelling viverrid, endemic to and widespread throughout Southern Africa. The causal bases of observed geographic patterns were investigated, and a taxonomic revision of the species was undertaken.

Three physical properties of pelage colour (hue, value and chroma) were measured independently using Munsell colour charts and a tristimulus colorimeter. Hue and chroma varied from yellowish (hue) and bleached (chroma) in the north to a brighter, (chroma) tawny-orange (hue) in the south. A zone of rapid colour change separated northern and southern groups. Specimens from the drier western areas were paler (in value) than specimens from more easterly localities. Colour patterns were interpreted in terms in the principle of metachromism. Environmental correlates of colour were analysed.

Non-geographic (age, sex, individual) and geographic variation was analysed in 14 cranial and two external characters, using multivariate and univariate techniques. The species does not show secondary sexual dimorphism. Multivariate analyses resulted in the description of four

parapatric subspecies, three of which were distinguished on the basis of skull size (which accounted for 93% of geographic variation). Subspecies were separated by continuous zones of craniometric differentiation (transition zones). Craniometric overlap (intergradation) occurred across transition zones. The geographic pattern of craniometric variation in C. penicillata could be explained by either an allopatric or a parapatric mode of speciation. A cladistic analysis of coded cranial characters was used to infer the historical pattern of range expansion in the species.

The population genetical structure, based on electrophoretic analysis of 28 loci in eight populations of yellow mongooses, was characterised by the absence of genetic divergence between morphometrically-defined subspecies, a mean expected heterozygosity of 3.4%, low genetic distances between populations (0.000--0.105 for Nei's genetic distance), and a surprisingly high fixation index (F_{ST}) of 0.585.

The basic karyotype of the yellow mongoose was invariant geographically (2n = 36, NF = 72), although a single, supernumerary microchromosome was detected in four out of the five populations sampled. G- and C-banded karyotypes are presented.

Evolutionary relationships among eight Southern African viverrid species, including the yellow mongoose, were inferred from phenetic and cladistic analyses of allelic variation at 18 protein loci. These data suggested the separate evolution of social and solitary lineages of mongooses.

PREFACE

This study was undertaken at the Department of Biology, University of Natal, Durban, the Mammal Department, Transvaal Museum, Pretoria and the Durban Natural Science Museum, from January 1985 to December 1990, under the joint supervision of Professor J. A. J. Meester and Dr I. L. Rautenbach.

The work presented here, unless specifically indicated to the contrary in the text, is my own, and has not been submitted, in part or in whole, to any other University.

P. J. Taylor

ACKNOWLEDGEMENTS

My sincere thanks go to Professor Meester, for unhesitating support, advice and encouragement, to Dr Rautenbach, for honest criticism and positive encouragement throughout, and to both of them for believing in me.

I am extremely grateful to Dr C. K. Brain, Director of the Transvaal Museum, and to his staff, for allowing me full use of the facilities of the Transvaal Museum during 1986 and 1987, and to Dr Q. B. Hendey, Director of the Durban Natural Science Museum, for giving me full support and free rein to complete this study whilst employed at the Durban Natural Science Museum.

Nico Dippenaar provided invaluable assistance and advice with multivariate statistics and with computer applications. He also provided technical assistance with modifying carnivore traps, as well as much moral support. Thank you, Nico.

I would like to thank Doug Gordon, Glen Campbell, Gian Carlo Contrafatto and Debbie van Dyk for their much-needed and much-appreciated advice and assistance in the laboratory.

Gary Bronner, Johan Eckstein, Hennie Erasmus, John Pallett, Naas Rautenbach, Johan van Heerden, John Visser, Johan

Watson and Sandra Weber helped with collecting viverrid specimens, for which I am extremely grateful.

I am grateful to Elizabeth Herholdt and Professor G. L. Maclean for French and German translations, and to Professor A. Rasa for commenting on part of this work.

Without the financial support of the Foundation for Research Development (FRD) and the University of Natal, the scope of this project would have been considerably restricted.

To my parents, for their pride and belief in me, and their continual support, thank you.

This project would not have been possible without the unwavering support of my wife, Frances, whose belief in me and determination for me to succeed exceeded my own.

Above all, I give thanks to God.

CONTENTS

LIST OF TABLES

FIGURE CAPTIONS

CHAPTER 1

INTRODUCTION

This dissertation is concerned with the infraspecific systematics of the yellow mongoose Cynictis penicillata (Cuvier, 1829). The term 'systematics' implies an understanding of both the evolution and the taxonomy of a particular taxon. The scope of infraspecific systematics therefore includes a knowledge of phylogenetic relationships between populations (as inferred from patterns of geographic variation), as well as the possible description of formal taxa which best summarise the pattern of relationships between populations.

The study of infraspecific variation represents a cornerstone of evolutionary theory. The concept of individual variation and differential reproductive success is central to Darwin's theory of natural selection. The concept of a subspecies as a geographic race is central to the theory of allopatric speciation formulated by Ernst Mayr (Mayr, 1942; 1970). The description of infraspecific (and interspecific) chromosomal variation in a wide variety of invertebrate and vertebrate species has resulted in a diversity of theories of chromosomal speciation, including both allopatric and non-allopatric models (eg. Bickham and Baker, 1979; Capanna et al., 1985; White, 1978).

Infraspecific taxonomy involves the description, naming and synonomising of subspecies. While the subspecific trinomial was first applied in a publication in 1884, and thereafter became adopted in America, it was only after 1912 that its use became entrenched in Europe and elsewhere (Sibley, 1954). During the 'subspecies debate' of the 1950s, there was considerable opposition to the continued use of the trinomial (eg. Wilson and Brown, 1953; Burt, 1954, Gilham, 1956), resulting mainly from the injudicuous naming of subspecies for any and all infraspecific categories, often based on very limited information. Factors such as the existence of character clines, discordance in geographical patterns among different characters, microgeographical races, the phenomenum of polytopy (recurrence of identical character states in geographically distant populations), and the absence of an objective measure of subspecies diagnosis were seen as being antithetical to the formal naming of subspecies. However, many arguments were also put forward defending the restricted and wise use of subspecies, where sufficient information on geographic variation in more than one character was available (Bogert, 1954; Durrant, 1955; Hubbell, 1954; Rogers, 1954; Sibley, 1954). As a result of the subspecies debate, the concept of the subspecies as a unit of evolution, and not as an arbitrary geographic race, has emerged (Bohme, 1978; Endler, 1977; Lidicker, 1962). In the present study the subspecies definition of Lidicker

(1962) was adopted: 'a subspecies is 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 geographical area, is usually at least partially isolated, and may intergrade gradually, although over a fairly narrow zone, with adjacent subspecies'.

The taxonomy of the yellow mongoose echoes in some ways the history of the subspecies debate. During the early 1800s, G. Cuvier and Andrew Smith described three species of yellow mongoose from South Africa. These were later synonymised by Sclater (1900), under Cynictis penicillata. Thomas and Scwann (1904) and Schwann (1906) elevated ogilbyii and lepturus to subspecific rank, and created two further subspecies, pallidior and intensa. A further eight subspecies of C. penicillata were described, most of these by Austin Roberts (Roberts, 1951). Lundholm (1955) provided evidence for clinal variation in colour and size, and therefore regarded the application of subspecies to be invalid. These conclusions were based on very small samples for most of the subspecies, and on univariate methods of analysis.

Since the revision of Lundholm (1955), museum collections of C. penicillata have grown considerably. New techniques, such as multivariate morphometrics, allozyme electrophoresis, and

karyology, are now available for the analysis of geographic variation (see Gould and Johnston, 1972 and Thorpe, 1976, for discussions on the importance and impact of these new techniques in the field of geographic variation). These factors prompted a revision of the infraspecific systematics of the yellow mongoose, based on colorimetric, morphometric, electrophoretic and chromosomal characters.

In revising the taxonomy of the species, the following questions were addressed: 1) what is the extent, pattern (i.e. random or geographically ordered), and nature (continuous or discontinuous) of geographic variation in genetic and morphological characters in the yellow mongoose? 2) based on concordance in geographic trends, and ecological correlates of geographic variation, what is the relationship between the phenotype, the genotype and the environment in the yellow mongoose? 3) what are the probable causes (genetic or environmental, adaptive or non-adaptive, ecological or phylogenetic) of observed patterns of differentiation in the yellow mongoose? 4) what is the pattern and mode (parapatric or allopatric) of subspeciation in the yellow mongoose? 5) on the basis of the above, how many, if any subspecies (or species) of yellow mongooses should be recognised? 6) based on the present study of the yellow mongoose, can the subspecies be regarded as an evolutionary and ontological entity in nature? 7) can subspecies be objectively defined, and described in nature?

8) what is the relationship between character clines and subspecies?

Chapter 2 is a review of the biology of the yellow mongoose, and provides a background for the following chapters. Chapter 3 analyses colour variation in the species, and attempts to establish environmental correlates of the observed patterns of geographical variation. A novel quantitative method of measuring colour was adopted, using Munsell colour charts and a tristimulus colorimeter, and the statistical technique of trend surface analysis was used to obtain geographic contour maps of colour variation in three quantitative colour variables. Multiple linear regression analysis was used to investigate the relationship between colorimetric and climatic variables. The statistical properties of quantitative colour variables were examined.

Chapter 4, which comprises the bulk of the dissertation, analyses morphometric variation in C. penicillata, including individual, age, sex and geographic sources of variation. In addition to conventional univariate and multivariate techniques, the cladistic approach of Thorpe (1984b) was used to attempt to reconstruct the historical pattern of range expansion in the species. Discriminant analysis was used to estimate the extent of intergradation between recognised phenetic groups. These morphometric analyses, in conjunction with the results of the previous chapter on

Chapter 5 analyses electrophoretically-detectable genetic variation in 28 enzyme and protein loci in C. penicillata. Material was analysed from a sample of 35 animals from eight localities, representing two of the morphometrically-defined subspecies. Data on allelic variation were used to test the hypothesis that reduced gene flow had occurred between morphometrically-defined subspecies. The population genetical structure of the yellow mongoose was analysed from the point of view of the geographic distribution of allelic polymorphisms, inter-population genetic distances, genetic heterozygosity, and Wright's (1965) F statistics.

Chapter 6 involves a comparison of unbanded karyotypes from 12 yellow mongooses collected from five separate localities, and G- and C-banded karyotypes of three animals from two localities. Measurements of centromeric index and relative length were obtained for each of 17 autosome pairs as well as for the X and Y chromosomes, and mean differences between the different localities were analysed statistically.

Chapter 7 involves a phylogenetic analysis of eight viverrid

species, including the yellow mongoose, based on electrophoretic data for 18 enzyme and protein loci. Phenetic and cladistic methods of analysis were used, and the phylogeny and classification of the mongooses was discussed in terms of the present results as well as previous studies involving palaeontological, morphological and behavioral data.

Chapter 8 comprises a theoretical synthesis of the data on morphological and genetic variation in the yellow mongoose.

References

Bickham, J. W. & Baker, R. J. (1979). Canalization model of chromosomal evolution. Bulletin of Carnegie Museum of Natural History 13: 70--84.

Bogert, C. M. (1954). Subspecies and clines: the indication of infraspecific variation. Systematic Zoology 3: 111--112.

Burt, W. H. (1954). The subspecies category in mammals. Systematic Zoology 3: 99--104.

Böhme, W. (1978). Das Kuhnelt'sche Prinzip der regionalen Stenozie und seine Bedeutung für das Subspezies-Problem: ein theoretischer Ansatz. Zeitschrift für zoologische Systematik und Evolutionsforschung 16: 256--266.

Capanna, E., Corti, M., Nascetti, G. & Bullini, L. (1985).

Pre- and post-mating isolating mechanisms in the speciation of the European long-tailed house mouse Mus musculus domesticus. Acta zoologica Fennica 170: 115--120.

Durrant, S. D. (1955). In defense of the subspecies. Systematic Zoology 4: 186--190.

Endler, J. A. (1977). Geographic variation, speciation and clines. Princeton: Princeton University Press.

Gilham, N. W. (1956). Geographic variation and the subspecies concept in butterflies. Systematic Zoology 5: 110--120.

Gould, S. J., & Johnston, R. F. (1972). Geographic variation. Annual Review of Ecology and Systematics 3: 457--498.

Hubbell, T. H. (1954). Subspecies and clines: The naming of geographically varied populations or what is all the shouting about. Systematic Zoology 3: 113--121.

Lidicker, W. Z. (1962). The nature of subspecies boundaries in a desert rodent and its implications for subspecies taxonomy. Systematic Zoology 11: 160--171.

Lundholm, B. G. (1955). A taxonomic study of Cynictis penicillata (G. Cuvier). Annals of the Transvaal Museum 22: 305--319.

Mayr, E. (1942). Systematics and the origin of species. New York: Columbia University Press.

Mayr, E. (1970). Populations, species and evolution. Cambridge, Mass.: Harvard University Press.

Roberts, A. (1951). The mammals of South Africa. Johannesburg: 'The mammals of South Africa' Book Fund.

Rogers, J. S. (1954). Subspecies and clines: summary. Systematic Zoology 3: 131--133.

Schwann, H. (1906). A list of the mammals obtained by Messr. R. B. Woosnam and R. E. Dent in Bechuanaland. Proceedings of the Zoological Society, London, 1: 101--111.

Sclater, W. L. (1900). The mammals of South Africa. Vol. 1. London: I. R. H. Porter.

Sibley, C. G. (1954). Subspecies and clines: the contribution of avian taxonomy. Systematic Zoology 3: 105--110.

Thomas, O., & SCHWANN, H. (1904). On a collection of mammals from British Namaqualand, presented to the National Museum by Mr C. D. Rudd. Proceedings of the Zoological Society, London, 1: 171--183.

Thorpe, R. S. (1976). Biometric analysis of geographic variation and racial affinities. Biological Review 51: 407--452.

Thorpe, R. S. (1984b). Coding morphometric characters for constructing distance Wagner networks. Evolution 38: 244--255.

White, M. J. D. (1978). Modes of Speciation. San Francisco: Freeman.

Wilson, E. O. & Brown, W. L. (1953). The subspecies concept and its taxonomic application. Systematic Zoology 2:

97--111.

Wright, S. (1965). The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution 19: 395--420.

CHAPTER 2

REVIEW OF BIOLOGY[1]

TAXONOMIC SYNONYMY

Cynictis penicillata Cuvier, 1829

Yellow mongoose

Herpestes penicillata G. Cuvier, 1829:158. Type locality "Cape" (designated as Uitenhage, eastern Cape Province by Roberts, 1951:151).

Mangusta Le Vaillantii A. Smith, 1829:437. Type locality South Africa.

Cynictis steedmanni Ogilbyi, 1833:49. Type locality Uitenhage, eastern Cape Province.

Cynictis typicus A. Smith, 1834:116. Renaming of *Le Vaillantii*.

Cynictis ogilbyii A. Smith, 1834:117. Type locality Bushman Flat and northern parts of Graaf-Reneit district.

Cynictis lepturus A. Smith, 1839: Plate 17 and text. Type locality "arid plains towards the Tropic of Capricorn" (=Marico district *fide* Roberts, 1951:154).

---

1. This chapter is essentially the text of a paper by P. J. Taylor and J. Meester, entitled '*Cynictis penicillata*', that is to be submitted to the journal, *Mammalian Species*.

Cynictis penicillata pallidior Thomas and Schwann, 1904:5 (vol. 2), 175 (vol. 1). Type locality Klipfontein, north of Steinkopf, Little Namaqualand, northwestern Cape Province.

Cynictis penicillata intensa Schwann, 1906:104. Type locality Deelfontein, north of Richmond, Cape Province.

Cynictis penicillata brachyura Roberts, 1924:68. Type locality Boschkop, near Johannesburg, Transvaal.

Cynictis penicillata bradfieldi Roberts 1924:69. Type locality Quickborn, 96km north of Okahandja, Damaraland, Namibia.

Cynictis bradfieldi cinderella Thomas, 1927:375. Type locality Ondongwa, central Ovamboland, northern Namibia (1074m).

Cynictis penicillata coombsii Roberts 1929:90. Type locality Swarthaak Farm, north of Soutpansberg Mountains, northern Transvaal (originally, and until recently, taken incorrectly to be "Swarthoek", a farm located south of the Soutpansberg Mountains, some 60km from Swarthaak: Taylor and Meester, 1989).

Cynictis penicillata kalaharica Roberts, 1932:4. Type locality Kaotwe Pan, central Kalahari, Botswana.

Cynictis penicillata bechuanae Roberts, 1932:4. Type locality Gaberones, southeastern Botswana.

Cynictis penicillata karasensis Roberts, 1938:235. Type locality Kochena, Great Karas Mountains, Great Namaqualand, Namibia.

CONTEXT AND CONTENT.

Order Carnivora, Family Herpestidae, Subfamily Mungotinae (After Gregory and Hellman, 1939; Wurster and Benirschke, 1968; Honacki et al., 1982; Corbet and Hill, 1986, Wozencraft, 1989a). This classification disagrees with the conventional one which regards the mongooses as a subfamily of Viverridae (Simpson, 1945, Rosevear, 1974; Stains, 1984; Meester et al., 1986). However, Wozencraft (1989b) has demonstrated, from a survey of a large number of characters, that there are no synapomorphies uniting the Viverridae (civets and genets) and Herpestidae (mongooses), and that combining these two families would result in a paraphyletic group. The genus Cynictis is monotypic, as is the species C. penicillata. As many as 12 subspecies of yellow mongooses have been recognised in the past (Allen, 1939; Ellerman et al., 1953; Roberts, 1951; Shortridge, 1934). On the basis of apparent clines in size and colour, Lundholm (1955) considered the species to be monotypic, a view that has gained general acceptance (Coetzee, 1977; Meester et al. 1986).

DIAGNOSIS.

Five toes on fore feet, four on hind feet; skull relatively high, greatest height, measured at external auditory meatus,

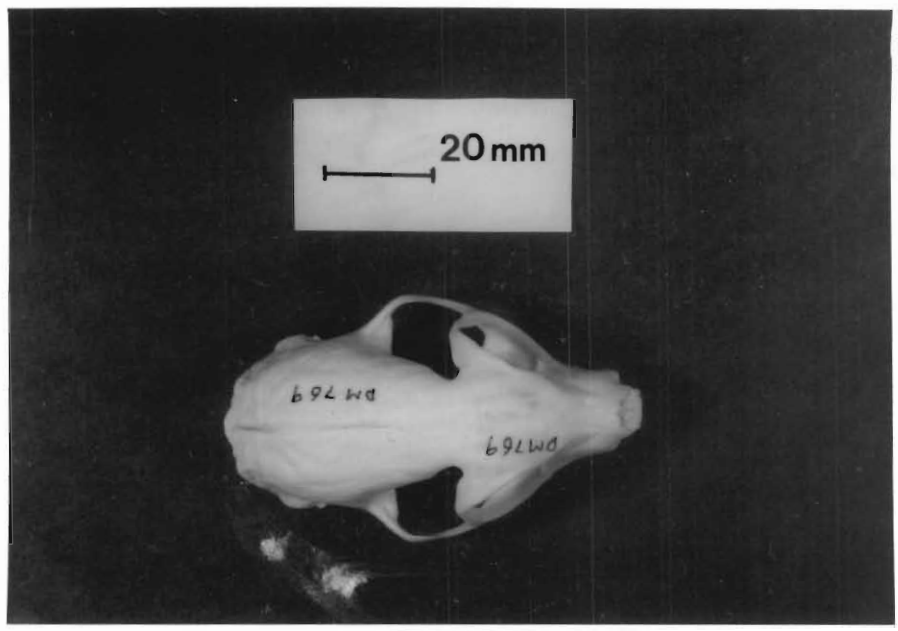
and including anterior part of bulla, just less than half of condylobasal length; orbit completely surrounded by bony ring; anterior part of bulla much enlarged, posterior portion only partly inflated; six cheekteeth; ears relatively large and, unlike other mongooses, projecting above the line of the head, seldom less than 9% of head and body length (Figs 2.1; 2.2).

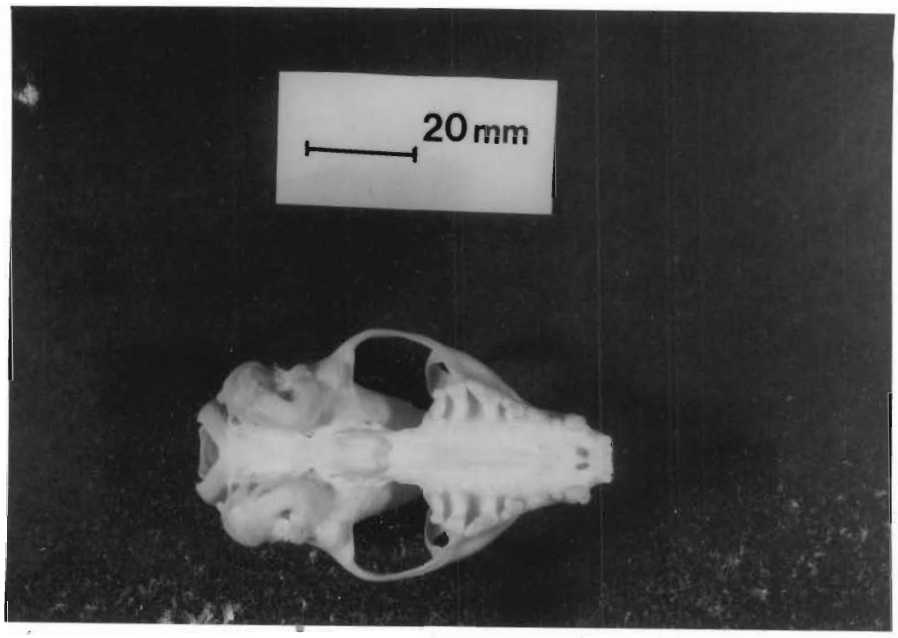
The only other diurnal mongoose species within its range with which the yellow mongoose may be confused is the slender mongoose Galerella sanguinea. The presence of a black tail tip in the latter, as opposed to a white tail tip in the yellow mongoose, is sufficient to distinguish these two species. The yellowish-grey coloration of C. penicillata also tends to distinguish it from the reddish, dark brown or grizzled appearance of G. sanguinea (Smithers, 1983). While C. penicillata bears a superficial resemblance, in general coloration and presence of a white tail tip, to Selous' mongoose Paracynictis selousi, the latter is nocturnal and somewhat larger in size (up to 75 cm in total length compared to usually less than 60 cm in C. penicillata: Smithers, 1983).

GENERAL CHARACTERS.

Pelage colour varies geographically from tawny-yellow in the south (South Africa, Namibia) to greyish-yellow and grizzled

Fig. 2.1. Dorsal, ventral and lateral views of cranium, and lateral view of mandible of Cynictis penicillata, female, from Victoria West, Cape Province, South Africa.


20 mm


20 mm

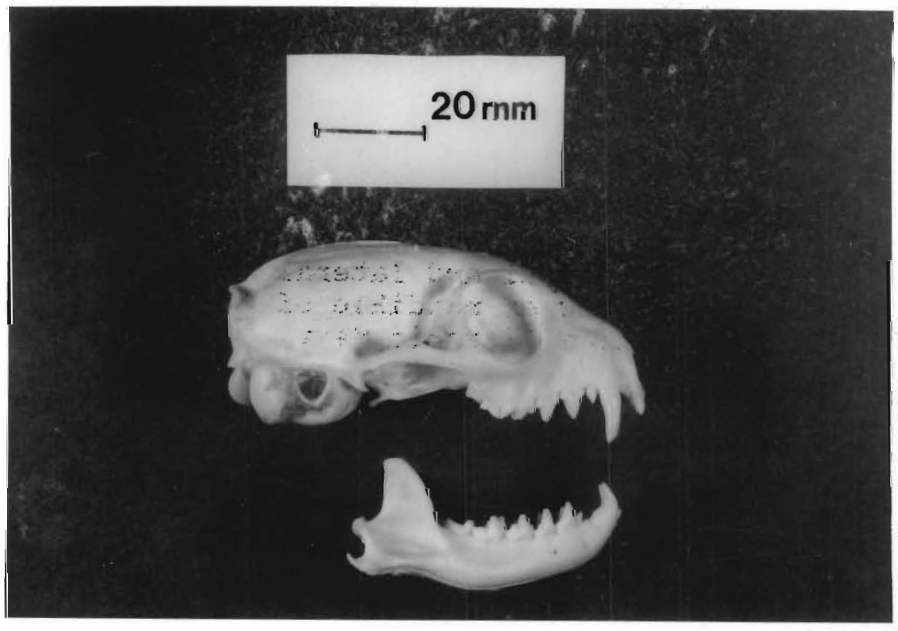

20 mm

Fig. 2.2. Yellow mongoose, Cynictis penicillata (photograph obtained from C. Baker).

in the north (Botswana; Smithers, 1983). The grizzled appearance of northern individuals results from contrasting, alternating black (eumelanin) and pale yellow (phaeomelanin) bands in individual guard hairs. Phaeomelanin bands are a richer orange colour, and eumelanin bands are reduced, in southern specimens (Lundholm 1955). A white tail tip is present in southern (Fig. 2.2), but not northern, specimens. Hair length is generally longer in southern specimens than in northern specimens, although it is always longest on the tail, giving the tail a bushy appearance (Fig. 2.2). Seasonal variation in pelage colour in southern specimens results in summer specimens having shorter hairs and a redder, brighter coat than winter specimens. The transitional coat, which appears in November and December, is pale yellow in colour, and patchy in appearance owing to the presence of old, moulting, black-tipped guard hairs over the newer summer coat. Seasonal changes are not conspicuous in the greyer-coloured northern specimens (Smithers, 1983).

Because of its relatively large, rounded ears, and bushy tail, the yellow mongoose has a somewhat fox-like, rather than typical mongoose-like, appearance (Shortridge, 1934; Fig. 2.2). A strip of naked skin is present on the mid line of the upper lip, although this does not completely divide the upper lip as it does in most mongoose genera (Pocock, 1916). Five digits are present in the fore foot and four on the hind foot. The first digit in the fore foot is raised

above the rest, and does not make an impression in the spoor. The hind foot sole is somewhat hairy, the fore foot palm being more extensively naked, almost to the wrist (Roberts, 1951). The claws are longer on the front than on the hind feet (Smithers, 1983).

The yellow mongoose is relatively small, compared to other mongooses. Lynch (1980) found no significant differences in size between males and females. Body size varies geographically, with northern specimens being distinctly smaller than southern specimens. Means, ranges (in parentheses), and sample sizes for body measurements (in mm) and body mass (in grams) of male, northern specimens from Botswana are as follows (Smithers, 1971): total length 496 (412 to 582), n = 36; tail length 210 (181 to 250), n = 36; hind foot length (cu) 67 (61 to 78), n = 38; ear length 30 (24 to 36), n = 33; mass 589 (478 to 797), n = 20. Corresponding measurements of southern specimens of both sexes from Orange Free State, South Africa, are as follows (Lynch, 1980): total length 580 (526 to 615), n = 20; tail length 240 (218 to 266), n = 20; hind foot length (su: + 8 mm to adjust su to cu) 71 (66 to 76), n = 20; ear length 35 (32 to 39), n = 20; mass 830 (715 to 900), n = 20.

Means, ranges (in parentheses) and sample sizes of selected body and skull measurements (in mm) of C. penicillata are as follows (based on measurements by PJT of specimens from

several Southern African museums and the British Museum (Natural History)): head and body length 333 (265 to 460), n = 235; tail length 228 (150 to 292), n = 234; condylobasal skull length 65.4 (56.2 to 73.7), n = 283; brain case width 28.1 (24.8 to 30.9), n = 284; mandibular ramus height 17.8 (15.2 to 20.8), n = 287; interorbital width 15.1 (12.6 to 18.2), n = 284; zygomatic width 39.1 (33.2 to 44.2), n = 278; bulla length 17.1 (15.0 to 18.8), n = 285; length of fourth upper premolar 6.03 (4.75 to 7.30).

DISTRIBUTION.

The yellow mongoose is endemic to and widely distributed throughout Southern Africa, being found in the Cape (except for mountainous and forested regions in the south and east), the Orange Free State, western and central Natal, Transvaal (except in the east and parts of the northwest), Botswana (except for the Okavango swamps and the extreme northeastern and eastern parts), extreme western Zimbabwe, Namibia (except for the Namib Desert,the Caprivi strip and the extreme north; Fig. 2.3; Lynch, 1983; 1989; Pringle, 1977; Rautenbach, 1982; Shortridge, 1934; Smithers, 1983; Stuart, 1981). The species is associated with drier, open habitats within the South West Arid Biome (Davis, 1962). A single Angolan record exists from Mupanda, near the southern border of Angola, between the Cunene and Okavango rivers (Monard, 1935, in Smithers, 1983).

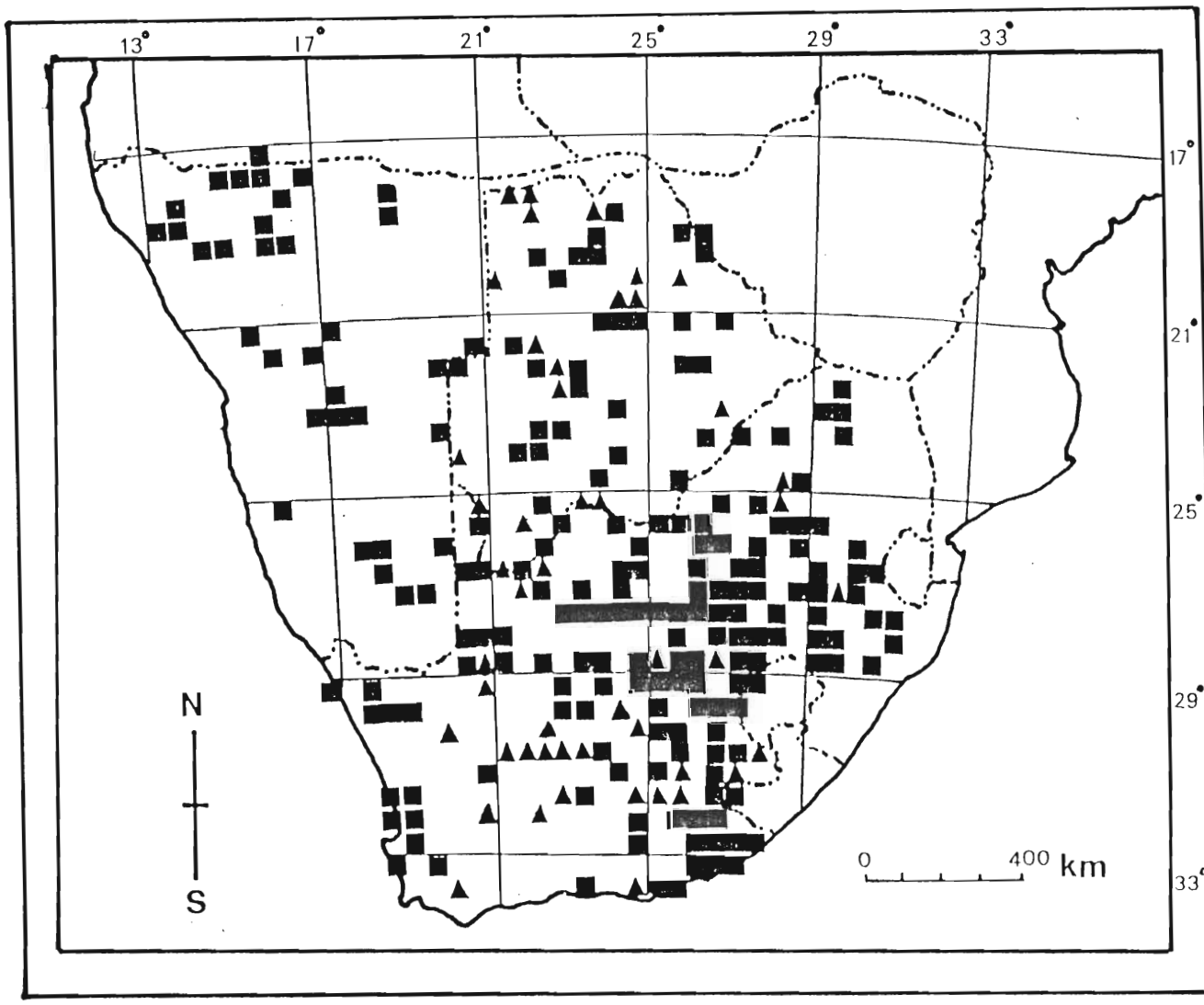


Fig. 2.3. Geographical distribution of Cynictis penicillata, plotted on half degree squares. Squares represent material records and triangles represent sight records.

The yellow mongoose has recently expanded its range into the wheatlands of the southwest Cape (Stuart, 1981). According to Snyman (1940) the species is particularly common in the western Orange Free State and western Transvaal, where population densities are very high. On the other hand, islands occur within the species' distribution, such as the Gaap Plateau in the northern Cape, where yellow mongooses are very scarce or absent (Snyman, 1940). Snyman lists four factors which determine the occurrence of C. penicillata in an area: (1) food supply (particularly their principal food source of termites Hodotermes and Trinervitermes); (2) occurrence of the ground squirrel Geosciurus capensis (which is usually responsible for digging the burrows that yellow mongooses cohabit); (3) soft or sandy soils for digging; (4) open country devoid of dense bush.

FOSSIL RECORD.

In Southern Africa, Hendey (1974) records the earliest presence of C. penicillata and ancestral forms in late Cenozoic deposits during the Makapanian mammal age (3 million BP to 700 000 BP), at the fossil sites of Makapansgat and Swartkrans. The species is also recorded from Southern African sites spanning the Cornelian (700 000 BP to 125 000 BP) and Florisian (125 000 BP to 12 000 BP) mammal ages (Hendey, 1974). Savage (1978) recorded Cynictis (an unidentified species which may have represented

Paracynictis selousi, since Savage incorrectly included selousi in Cynictis) from the early Pleistocene, East African site of Olduvai I.

FORM AND FUNCTION.

Like all other viverrids, the yellow mongoose possesses a glandular anal sac (Pocock, 1916), consisting of a depressed, glandular area surrounding the anus. According to Pocock (1916), a pair of gland orifices opens at a point somewhat higher up in the anal sac than the anus (unlike the situation in most viverrids in which these apertures are level with the anus). Contrary to Pocock's assertion, examination of a frozen, male yellow mongoose (skin and skull deposited in the Transvaal Museum, TM39223) by PJT showed the gland orifices to open close to and on either side of the anus. Two caudally-located, glandular depressions, not noted by Pocock (1916), were also noted. Apps et al. (1989) examined the anal sacs of a male and a female yellow mongoose, and found the peri-anal area of both sexes to be thinly covered by a dark brown, waxy material with an odour closely resembling that of dried beef. The anal sacs contained a milky fluid with a sour, cheesy smell, which was analysed by gas-liquid chromatography and mass spectrophotometry, and found to consist of 22 volatile compounds, including short-chain fatty acids, esters, alcohols, aldehydes, organic sulphurous compounds, and the

aromatic nitrogenous compound, indole (Apps et al. 1989). The odour volatiles of the yellow mongoose are considerably more diverse, and the intersexual differences more complex, than those of Herpestes auropunctatus and H. ichneumon (Apps et al., 1989). The anal glands function in scent marking of home ranges, and in allomarking between colony members (Earle, 1981).

Females have three pairs of abdominal mammae. Skull is of average build. Braincase is pear-shaped, narrowing to the postorbital constriction. Postorbital bars are closed in adults, and angled sharply backwards at the postorbital constriction. Rostrum is short and broad, the distance from the front of the eye socket to the incisors being about 30% of the total length of the skull. Zygomatic arch is weak. Supraoccipital crest is low, poorly developed. Sagittal crest is absent or weak. Undeveloped zygomatic arch and sagittal crest suggests relatively weak masseter and temporalis muscles adapted to a diet of soft food. Compared with other mongooses, the anterior bullae are well developed, about the same size as the posterior bullae (Fig. 2.1; Smithers, 1983).

The dental formula is i 3/3, c 1/1, p 4/4, m 2/2, total 40. Upper canines are long and sharp, and slightly flattened on the inside, while lower canines are strongly recurved. First upper and lower premolars are small and peg-like, and are

sometimes absent, particularly in the lower jaw. The carnassial teeth (upper fourth premolar and lower first molar) have retained some slicing ability. The lower first molar has three high, anterior cusps, and the hind portion is flattened. The second lower molar is adapted for crushing of insect and other soft food, having three cusps in front, a flat central section, and a low cusp at the back. The two upper molars are elongated labio-lingually, and lie at right angles to the tooth row (Fig. 2.1; Smithers, 1983).

External neuroanatomy of a number of viverrids was surveyed by Radinsky (1975). The mongooses could be characterised by the possession of a well-developed cruciate sulcus and little to no development of the presylvian sulcus. The yellow mongoose was reported to possess (in common with Bdeogale, Ichneumia, and Paracynictis) a short presylvian sulcus that delimits a small orbital gyrus, and (in common with Helogale, Mungos and Suricata) an undeveloped coronal sulcus (Radinsky, 1975).

Pocock (1916) has pointed out that the ear of C. penicillata differs from all other mongoose species, not only on the basis of its larger size, but also in the existence of a small shallow pocket behind the antitragus, which may be an homologue of a similar depression, the marginal bursa, found in the ear of hyaenas.

ONTOGENY AND REPRODUCTION.

In the northwestern Cape and Western Transvaal, mating, love-play, inhibited biting and mock-fighting was observed during August and September (Zumpt, 1969; 1976). In the southern Transvaal, Earle (1981) observed matings to commence in the first week of July. In a sample of 90 female C. penicillata, eight were pseudopregnant (Lynch, 1980), indicating the possibility of induced ovulation in the species. From observations on captive animals, Zumpt (1976) found the gestation period to be approximately 42 days. Ewer (1973; citing Zumpt and Jacobsen, personal communication) states that the gestation period is about 55 days, with estimates varying from 45 to 57 days. Of 12 pregnant female reproductive tracts analysed microscopically, Lynch (1980) estimated (based on the numbers of corpera lutea, embryos and placental capsules present) that only two females had suffered prenatal (preimplantation or postimplantation) losses.

Lynch (1980; citing Brand, 1963; Earle, 1977; and data from the South African Museum and the Johannesburg City Zoological Gardens) notes the existence of yellow mongoose birth records for the months of August to November. Ewer (1973; citing Zumpt and Jacobsen, personal communication) considers the birth season to be from October to January. The discovery of lactating females during January, February

and March indicates that the birth season probably extends at least until January (Rautenbach, 1982; Smithers, 1971; Stuart, 1981). Young are born in chambers in the burrows which are devoid of nest material (Smithers, 1983).

In Botswana, Smithers (1971) found that the average number of foetuses in pregnant females varied from 2 to 5, with a mean of 3.2 ($\underline{n}$ = 6). In the Transvaal, two pregnant females had 2 and 5 foetuses (Rautenbach, 1982). In Natal three pregnant females had a mean of 2.3 foetuses per animal (Rowe-Rowe, 1978). Lynch (1980) reported a mean of 2.3 foetuses per pregnant female in the Orange Free State. The above data suggest that litter size may be somewhat higher in the northern parts of the species' range.

Lynch (1980) recorded a mean of 1.8 young per litter. Based on his estimate of a mean of 2.3 foetuses per pregnant female, and based on his estimate of prenatal losses in 2 out of 12 females analysed, Lynch (1980) estimated that the total loss from ovulation until after parturition, is 0.8 ovum, embryo, foetus or young per female. Zumpt (1976) reported that, in a study of 41 litters, each was composed of one sex only. At birth, the male: female sex ratio was found to be 1.6:1, whereas in adults this changed to 1.2:1 (Zumpt, 1976).

From an examination of 676 yellow mongooses collected from

the western Transvaal, pregnant females were found from mid-July to the end of December, with a peak in October (Zumpt, 1969). In the Orange Free State, Lynch (1980) recorded pregnant females between August and November. In Botswana, Smithers (1971) found pregnant females in February, March, July, October and November. This indicates that the reproductive season may be more prolonged in yellow mongooses from the northern regions. The presence of two specimens in the Transvaal Museum, collected in a pregnant state from Windhoek, Namibia, during February, substantiates this view. Lynch (1980) reports an increase in adult male reproductive activity (involving several variables including testes, epididymes, accessory gland and endocrine organ masses and spermatazoa numbers) from about March / April, to a maximum during September / October, followed by a decrease to a low (a period of relative quiescence) in January / February. However, male Cynictis do not exhibit pronounced seasonal reproductive periodicity, and their reproductive cycle seems to be regulated by the cycle of the female.

Although Snyman (1940) indicated that C. penicillata may have more than one litter per season, this has not been substantiated by any later publications (Lynch, 1980; Zumpt, 1969; 1976). However, Lynch (1980) did find postpartum and pseudopregnant females in which a second, seasonal ovarian cycle had occurred, and he suggested that this provided a second opportunity for breeding in cases of failed mating or

loss of young. Two females from Windhoek, Namibia, stored in the Transvaal Museum (TM39947, TM39949), were collected in a pregnant, lactating condition, suggesting that, at least in northern specimens, some females have two litters per season.

Weaning of the young takes place at about 10 weeks of age (Zumpt, 1976). Lynch (1980) has described 5 morphometric groups (relative age classes) of Cynictis, and has also provided a classification of reproductive groups of male and female individuals (for example, prepubertal, pubertal, pregnant). Zumpt (1969) has investigated age determination in Cynictis, using known-age animals, and has described five age classes having absolute age limits. By comparing zygomatic width means of Zumpt's age classes, and Lynch's size classes, Lynch's size groups could be approximately calibrated: Lynch's group A matched Zumpt's group I (3 to 9 months); groups B and C matched group II (9 to 12 months), group D matched groups III and IV (over one year), and group E matched group V (unknown age). According to Lynch (1980), 75% of prepubertal females (those having no Graafian follicles in the ovaries) belonged to group A (3 to 9 months) and 25% belonged to group B and C (9 to 12 months). Twelve percent of pubertal females were under 9 months of age. Estrus females were all of group D (older than one year). Among males, prepubertal individuals could be subdivided into those in which the spermagenic cycle was

incomplete and the seminiferous tubules very small in diameter, and those in which epididymal spermatazoa were present. Individuals of the former group belonged to groups A, B and C (less than one year old), while those of the latter group, which were probably fertile, belonged to groups C and D (9 to 12 months and older). While it thus appears that males may be physiologically mature at about 9 months of age, they may not be behaviorally capable of reproducing (Lynch, 1980). Species such as Herpestes auropunctatus and Mungos mungo have been shown to have sperm in the testis at about four months of age. In Ichneumia albicauda, incomplete sexual behavior was noted at 15 months, but only at 2 years of age were both sexes sexually mature (Hinton and Dunn, 1967).

ECOLOGY.

The yellow mongoose is associated with semi-arid, open habitats within the South West Arid Zone, as typified by Karroo scrub in the Cape Province, grassland associations in the Orange Free State, semi-desert scrub in Botswana and the gravel plains and pro-Namib of Namibia. Where the species occurs in woodland associations, such as Combretum / Terminalia scrub of the Kalahari, it is usually associated with open areas such as vleis and grasslands surrounding waterholes (Smithers, 1983). The range of the species extends narrowly into savanna habitats in the northern

Transvaal and northwestern Natal, but Rautenbach (1982) found yellow mongooses to be less abundant in savanna than in pure grassland habitats. Stuart (1981) recorded Cynictis occurring in stands of Phragmites reeds along the Keisers and Koning Rivers, and from fairly dense Fish River valley bushveld, in the Cape Province. The species is entirely absent from desert, forest and montane habitats.

The yellow mongoose is a predominantly diurnal, colonial species, occupying permament burrows which it often cohabits with ground squirrels Xerus inaurus and suricates Suricata suricatta (Lynch, 1980; Roberts, 1951; Sclater, 1900; Shortridge, 1934; Smithers, 1983; Snyman, 1940). Xerus and Suricata have longer claws, and are better adapted to digging, than Cynictis, and the latter often occupies burrows initially excavated by the other two species. However, the yellow mongoose is capable of excavating its own burrows, and Earle (1981) described a complex burrow excavated by Cynictis which consisted of 66 entrance holes. Snyman (1940) and Lynch (1980) have described in detail the structure of the burrow system. Burrows vary in structure from simple systems with one or two holes to complex, extensive systems having forty or more holes. Tunnels are interconnected underground, and occur on two or three levels to a depth of about 1.5 m. Enlarged nest chambers are excavated at intervals aong the tunnels. Burrow-dwelling confers a significant thermoregulatory advantage, in that

the microenvironment is buffered against extremes in ambient temperature. In the Orange Free State in the hottest summer months, where an average, mean maximum ground temperature of 39°C was found, the corresponding soil temperature was 14°C cooler. In the coldest winter months, when a minimum mean of -3.6°C was recorded, soil temperature was 14°C warmer (Lynch, 1980).

Estimates of colony size vary. Mean colony sizes of 3.9 (n = 362 colonies; Zumpt, 1976), 4.1 (n = 8; Lynch, 1980) and 8 (n = 5; Earle, 1981) have been recorded in the southern and western Transvaal and the Orange Free State. In Botswana, colonies of up to 8 individuals occur, but the majority consist of 1 or 2 individuals (Smithers, 1971). A record of a colony of 50 animals in the Addo area of the Cape (FitzSimons, 1919) probably resulted from the author confusing Suricata with Cynictis (Smithers, 1983).

A male:female ratio of 1:1.2 was found by Lynch (1980) and Zumpt (1976), while Earle (1981) recorded a surplus of males (male:female = 1.2:1). Based on observations of five colonies, Earle (1981) found that the colony was centred around a family group, consisting of a male and female, their youngest offspring, and two other individuals, usually subadults or very old individuals. The remaining three or four individuals of a group had only a loose association with the group. While excavating entire burrows, Lynch

(1980) found that Cynictis were usually present singly or in pairs. Larger groups consisted of a family group of an adult pair, 2 or 3 juveniles, and possibly two subadults from the previous parturition season.

Stuart (1981) found that tagged animals were observed feeding up to 1.3 km from their burrows. According to Zumpt (1976), home ranges of yellow mongooses varied from 600 to 3000 metres in radius from a colony. Earle (1981) estimated that territories occupied an area of 5-6 hectares. Recent evidence has shown that yellow mongooses may have 3 to 5 burrows systems, each of which may be occupied for 6 to 8 weeks, and that actual territory size could cover an area of 3 km^2 or more (A. Rasa, personal communication).

Lynch (1980) investigated the possibility of interspecific competition between the yellow mongoose and the suricate. Both species are diurnal, insectivorous and share the same burrows. However, Suricata is highly social and forages cooperatively while Cynictis is more solitary and forages individually; Suricata is strictly diurnal while Cynictis is diurnal and crepuscular, becoming marginally nocturnal in summer; Suricata is strictly insectivorous (preferring Lepidoptera and Coleoptera) while Cynictis is insectivorous (preferring Isoptera) and carnivorous; Suricata is confined to open habitat, while Cynictis also occurs in wooded vegetation; Suricata excavates its own burrows while

Cynictis often uses those of Suricata and Xerus. These factors minimise competition and allow coexistence between the two species.

The association between Cynictis, Suricata and Xerus may be regarded as symbiotic, as each species benefits from the presence of the others. Cynictis benefits from the group vigilance of the social species. Being more aggressive than the social species, Cynictis may play a role in defending the burrow from terrestrial predators such as large snakes or water monitor lizards. Suricata and Xerus may alternately use the same burrows, with a consequent saving of time and energy.

Lynch (1980) lists 34 species of parasites from the yellow mongoose: 6 species of fleas (including the plague vector, Xenopsylla pirei), 10 species of ticks (including the economically important species, Rhipicephalus appendiculatus), 7 species of mites, 2 species of lice and 9 species of helminthes. Hinton and Dunn (1967) recorded the presence of a nematode parasite, Tenuostrongylus cynictis, in the yellow mongoose.

The yellow mongoose has few terrestrial predators. Large snakes and water monitor lizards may provide a threat to young or immature yellow mongooses. Large raptors are the most important natural predators (Hinton and Dunn, 1967).

Man is the most important predator, as the yellow mongoose has, in the past, been indiscriminantly shot by farmers who (probably mistakenly) consider that yellow mongooses are responsible for killing newborn lambs.

The yellow mongoose is an opportunistic feeder, feeding predominantly on insects but also on larger vertebrate prey (Smithers, 1981). Stuart (1981) examined the stomachs of 20 yellow mongooses in the Cape Province, and found Coleoptera (beetle) larvae and adults and Orthoptera (locusts) to have the highest occurrence. Other food items included termites, caterpillars, ants, mice, birds, reptiles, grass and seeds. From faecal samples of the species from Mountain Zebra National Park, Du Toit (1980) found the diet to consist predominantly of insects, in particular beetles, grasshoppers and termites. Other food items were fruit from Diospyros lycioides, and the occasional mice or bird. Zumpt (1968) found mice to have the highest occurrence in 95 stomachs collected from the Orange Free State, western Transvaal and northern Cape. Locusts occurred almost as frequently as mice, and termites and beetles were also recorded. The remains of ground squirrels, yellow mongooses and meat from unidentified larger carcasses were also recorded in several stomachs, indicating that the species feeds on carrion. Snyman (1940) reports on a yellow mongoose observed gnawing on the lips and muzzle of a dead ox. In captivity, Zumpt (1968) observed mothers devouring their

young on two occasions, although there was sufficient food in the cages. Food items taken in captivity are, in order of preference: termites, locusts, lean meat, eggs, lizards, boiled meat, beetles, mice and birds. In the field yellow mongooses have been observed to hunt birds such as the Blacksmith Plover, Mountain Chat and Ant-eating Chat. They have also been observed to eat the aloe-type plant Chortolirium angolense, though this may be for the water content.

In the Transvaal, invertebrates occurred more frequently (87%) than vertebrates (62%) in 76 yellow mongoose stomachs analysed by Herzig-Straschil (1977). Invertebrates included termites, locusts and a mixture of other invertebrates. Vertebrates included mammals, birds and amphibians. The most important invertebrate species was the harvester termite (Hodotermes sp.). This corresponds with a Botswana sample of 54 stomachs, in which Hodotermes mossambicus was the most important invertebrate food item (Smithers, 1971). The distribution of H. mossambicus corresponds very closely with that of the yellow mongoose (Smithers, 1983). Smithers (1971; 1983) found insects to have by far the highest percentage occurrence (91%), followed by murids (15%), scorpions (13%), reptiles (11%) and, at lesser percentages, centipedes, birds, frogs, hunting spiders and true spiders. Among the insects, termites occurred most frequently (occurring in 37% of stomachs), followed by dung beetles

(33%), crickets and grasshoppers (32%), beetle larvae (28%), and, at much lower percentages, ants and cockroaches.

A predominance of termites (in this case Trinervitermes trinervoides) in the diet of the yellow mongoose was reflected by their occurrence in 74% of 156 stomachs and / or colons from the Orange Free State (Lynch, 1980). Other important food items were, in order of importance, Orthoptera, Coleoptera and Lepidoptera. Also present, at lower percentage occurrences, were birds, spiders, amphibians, mammals (including remains of mice, springhares, shrews and hares), Hymenopterans, reptiles, Dermaperans, Dipterans, Dictyopterans (including cockroaches), Diplopodans and Chilopodans. Lynch (1980) found no seasonal differences in the proportion of the four most important food items in the diet of the yellow mongoose. In an analysis of yellow mongoose faecal samples from the Vaaldam in the Transvaal, Earle (1981) found that, during winter when insects were less abundant, fruit from Diospiros lycioides and Opuntia sp. were an important food source and could make up as much as 16% of the total food taken.

Yellow mongooses can become problem animals as they are known to prey on hens eggs and free-ranging chickens (Roberts, 1951). There is no real evidence for Fitzsimon's (1919) contention that they will kill and eat young lambs (Smithers, 1983).

The yellow mongoose is considered to be the main carrier of rabies in South Africa, and the geographical incidence of this disease in South Africa corresponds closely with the distribution of the species (Snyman, 1940; Zumpt, 1967; 1976). Snyman (1940) showed that, by 1940, Cynictis had been responsible for the recorded death of some 21 human beings and five head of cattle, besides causing some 80 known outbreaks of rabies. A large proportion of human deaths result from curious children approaching infected animals that lose their fear of humans and wander onto farms (Snyman, 1940).

The prevalence of the disease in the species is attributed, not to a greater susceptibility to the virus, but rather to their abundance in certain areas, and their burrow-dwelling habit which brings individuals into close proximity, thereby increasing the chances of transmitting the virus (Snyman, 1940). Zumpt (1969) found a close correlation between the seasonal incidence of rabies and the breeding cycle of the yellow mongoose. Annual peaks in rabies incidence and the pregnancy rate of female yellow mongooses both occurred in October. As subadults are forced to leave the colony before the birth of the current year's litter in October, young animals must compete for the establishment of territories at a time (winter) when food supplies are limited. These and other stresses may trigger off clinical rabies in the

mongoose population (Zumpt, 1976). However, the hypothesis that subadults are forced to leave the colony before the end of their first year has been challenged by recent evidence which shows that young may remain in their natal colony for several years as "helpers" (Rasa, personal communication).

Snyman (1940) found that rabies outbreaks occurred in restricted foci, and that the disease could flair up in the same area or farm after intervals of several years. He investigated the possibility of controlling rabies through the systematic extermination of yellow mongooses, suricates and ground squirrels on infected farms. The most effective method of extermination involved sealing and gassing burrows with cyanide gas, followed by setting traps for the survivors who managed to dig out of the burrows. On two infected, adjacent farms in the Bloemfontein district, 1591 colonies were gassed, and 1017 surviving "meerkats" (including 384 yellow mongooses) were trapped, over a period of three months. Since many animals must have died in the burrows, the populations must have been considerably greater than the numbers trapped. Zumpt and de Bruyn (1967) found that fumigating burrows with phosphine ("Phostoxin") was very effective in exterminating yellow mongooses, but also very cruel, resulting in a slow and painful death. Gases such as CO and CO_2 were found to be as effective, but cheaper and less dangerous to use than cyanide gas and phosphine. However, the effectiveness of eradication methods

in controlling rabies has been questioned, as it leads to a temporary reduction in a localised population followed by immediate recolonisation and exponential population growth (Zumpt, 1976).

Lynch (1980) investigated several methods of trapping yellow mongooses, including live-traps, flooding burrows with water, fumigating burrows with sulphur dust or phosphine, excavating burrows and shooting. Only the latter two techniques were found to be consistently successful.

The yellow mongoose has been known to live for up to 15 years in captivity (Nowak and Paradiso, 1983).

BEHAVIOR.

Based on observations of 5 colonies of yellow mongooses on Big Island in the Vaaldam in the Transvaal, over a seven month period from March to September, Earle (1981) reported on aspects of the social and feeding behavior of the species.

Yellow mongooses are primarily diurnal but are often active on warm, summer nights. Individuals emerge from their burrows before sunrise, sometimes as early as 06 h 00. After moving to middens to defaecate, they return to their burrows for 30 mins before reappearing to sunbathe. Whilst

sunbathing, individuals face north-south to gain maximum benefit from the sun. Several sunbathing postures, including standing and sitting positions, are adopted, usually exposing as much of the skin on the stomach and neck as possible. As much as 90 mins a day is spent sunbathing. After sunbathing, individuals commence foraging. Individuals forage independently although occasionally pairs may be seen together. Foraging involves digging and scratching in the ground and in dung heaps for insect larvae and termites, as well as pursuing and hunting vertebrates such as mice, lizards and game birds. On very hot days, yellow mongooses rest in their burrows from 11 h 00 to 14 h 30, followed by a further foraging period before they retire to their holes between 17 h 30 and 18 h 30.

Yellow mongoose territories correspond closely with their foraging ranges. The dominant male of a colony patrols a territorial demarcation route each day before foraging. Demarcation of yellow mongoose territories occurs primarily by means of anal and cheek glands, and secondarily by means of faeces and urine concentrated in middens which are often positioned along territorial borders. Back-rubbing is also employed as a visual and olfactory method of marking objects within the territory. Facial glands are used in the vicinity of burrow holes, and are thought to be aimed at intra-colony communication. Anal glands are used most often for marking, and secretions are deposited, with the individual in a squat

position, throughout the territory. On his territory demarcation trip, the dominant male deposits secretions every 5-10 m. Marking occurs more frequently where a territorial border is under greater pressure from adjacent colonies. Only the dominant pair makes any contribution to territory demarcation. The dominant female marks less frequently than the male, but actively assists in defending the territory.

Fights between dominant males of adjacent colonies occur frequently, and last about 3-4 s, after which each runs back to his own territory. Wounds are inflicted often, as dominant males often have scars on their faces. Within a colony, the dominance hierarchy consists of, in order of decreasing dominance, the dominant male, the dominant female, the youngest offspring, other adults, young adults and very old animals. Subordinate individuals exhibit submissive behavior towards dominant individuals while the latter exhibit dominance in the absence of submissive behavior from subordinates. To assess their mutual status two individuals approach each other and sniff the facial glands. The most dominant rises higher on its legs while licking or biting the other's neck. The subordinate lies on its side and sometimes emits a high-pitched scream. This behavior only occurs at inter-colonial level. At intra-colonial level, a dominant individual marks a submissive one by jumping over it and landing, using the anal glands in a

standing position. Each dominant male marks the individuals of his colony daily.

Matings commence in the month of July. Copulation lasts for about 30 s to 60 s, during which the male makes a soft purring sound while the female bites or licks the male's ears and neck continuously. Dominant females probably only mate with dominant males, while young females mate with dominant and young males.

The yellow mongoose is a rather quiet animal, with only five vocalisations being recorded by Earle (1981). A high pitched scream is emitted during fighting. A low warning growl warns off other animals, and a very low growl is emitted when an animal is threatened. A short barking sound is emitted in dangerous situations, causing all other animals in hearing range to disappear into their holes. A soft purring sound is emitted during copulation.

The white tail tip of the yellow mongoose is an effective visual signal. The relative bushiness of the tail may also be used in communication. The tail is normally held lower than the back, and this position also conveys neutrality. Danger is signalled by the tail in a S-position, and the tail is very bushy when fleeing danger. When a dominant animal successfully chases an intruder from its territory, or exerts its dominance over a subordinate, the tail is held

in a "satisfied" position, with the tail tip held higher than the back and therefore very conspicuous. When an animal is uncertain of itself, for example on entering a new territory, the tail is raised above the back, but with the tip pointing downwards.

A detailed behavioral study of C. penicillata is currently in progress (A. Rasa, personal communication).

GENETICS.

The karyotype of the yellow mongoose is characterised by a diploid number (2N) of 36, including 17 biarmed autosomes, a very small metacentric Y and a medium-sized, metacentric X (Fredga, 1972). The yellow mongoose karyotype can be distinguished from other mongooses by the large number of metacentric chromosomes, and the small size of the Y chromosome. The karyotype is invariant geographically, although a single, supernumery microchromosome is occasionally detected (Taylor and Meester, submitted, a).

Twenty eight allelic systems have been analysed by starch gel electrophoresis in eight yellow mongoose populations (Taylor et al., in press). Thirteen loci, representing 10 proteins and enzymes, were polymorphic (alcohol dehydrogenase, catalase, esterase, glucose dehydrogenase, glutamate-oxaloacetate transaminase, glycerol-3-phosphate

dehydrogenase, unidentified general protein, phosphogluconate dehydrogenase, phosphoglucomutase, transferrin). Mean heterozygosity was 3.4%. Different populations were very closely related genetically. However, most polymorphic alleles were detected only in single populations, resulting in a high value (0.585) for Wright's F_{ST} statistic. It was estimated that fewer than one individual per generation was exchanged between local populations, suggesting that gene drift, and not gene flow, is the major factor determining the population genetic structure of yellow mongoose populations.

Several yellow mongoose skulls, stored in various Southern African museums, show cranial and dental abnormalities which may be genetic in origin. These include one specimen (TM 25645; Transvaal Museum, Pretoria) with the infraorbital canal divided by a bony ridge; one specimen (TM 7885) with a modified cusp pattern on the lower second molar; one specimen (KM 14042; Kaffrarian Museum, King William's Town) with curiously shaped nasals, the right being indented and the left having a protruding bony deposition; one specimen (KM 14061) with elongate infraorbital canals; one specimen (KM 19724) with a supernumerary, right lower second premolar; and one specimen (SM 3547; State Museum, Windhoek) with an additional "foramen" on the right maxilla, giving a distorted shape to the interorbital constriction.

REMARKS.

A recent, craniometric study of the yellow mongoose (Taylor and Meester, submitted, b) resulted in the proposal of four subspecies of yellow mongooses: C. p. penicillata from South Africa, C. p. bradfieldi from Namibia, C. p coombsii from Botswana and northern Transvaal, and C. p. natalensis from Natal.

The financial assistance of the Foundation for Research and Development (FRD) to JM is gratefully acknowledged.

LITERATURE CITED.

ALLEN, G. M. 1939. A checklist of African mammals. Bulletin of the Museum of Comparitive Zoology at Harvard College, 83:1-763.

APPS, P. J., H. W. VILJOEN, AND P. TAYLOR. 1989. Volatile components from the anal glands of the yellow mongoose Cynictis penicillata. South African Journal of Zoology, 24:361-362

COETZEE, C. G. 1977. Order Carnivora. Pp. 1-42, in The mammals of Africa: an identification guide (J. MEESTER AND H. W. SETZER, eds.). Smithsonian Press, Washington D. C.

CORBET, G. B., AND J. E. HILL. 1986. A world list of mammalian species. British Museum (Natural

History), London. 254 pp.

CUVIER, G. 1829. Le regne animal. Second ed.

DAVIS, D. H. S. 1962. Distribution patterns of Southern African Muridae, with notes on some of their fossil antecedents. Annals of the Cape Provincial Museums, 2:56-76.

DU TOIT, C. F. 1980. The yellow mongoose Cynictis penicillata and other small carnivores in the Mountain Zebra National Park. Koedoe, 23:179-184.

EARLE, R. A. 1981. Aspects of the social and feeding behavior of the yellow mongoose Cynictis penicillata (G. Cuvier). Mammalia, 45:143-152.

ELLERMAN, J. R., T. C. S. MORRISON-SCOTT, AND R. W. HAYMAN. 1953. Southern African Mammals, 1758-1951: a reclassification. British Museum (Natural History), London. 363 pp.

EWER, R. F. 1973. The carnivores. Weidenfield and Nicolson, London. 494 pp.

FITZSIMONS, F. W. 1919. The natural history of South Africa. Longmans, London.

FREDGA, K. (1972). Comparitive chromosome studies in mongooses (Carnivora, Viverridae). I. Idiograms of 12 species and karyotypic evolution in Herpestinae. Hereditas, 71:1-74.

GREGORY, W. K. AND M. HELLMAN. 1939. On the evolution and major classification of the civets (Viverridae) and allied fossil and recent Carnivora: a

phylogenetic study of the skull and dentition. Proceedings of the American Philosophical Society, 81:309-392.

HENDEY, Q. B. 1974. Faunal dating of the late Cenozoic of Southern Africa, with special reference to the Carnivora. Quaternary Research, 4:149-161.

HERZIG-STRASCHIL, B. 1977. Notes on the feeding habits of the yellow mongoose Cynictis penicillata. Zoologica africana, 12:225-229.

HINTON, H. E. AND A. M. S. DUNN. 1967. Mongooses. Their natural history and behavior. Oliver and Boyd, Edinburgh and London. 144 pp.

HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPPL. 1982. Mammal species of the world. Allen Press and Association of Systematics Collections, Lawrence, Kansas, 694 pp.

LUNDHOLM, B. G. 1955. A taxonomic study of Cynictis penicillata (G. Cuvier). Annals of the Transvaal Museum, 22:305-319.

LYNCH, C. D. 1980. Ecology of the suricate, Suricata suricatta and yellow mongoose, Cynictis penicillata with special reference to their reproduction. Memoirs van die Nasionale Museum Bloemfontein, 14:1-145.

LYNCH, C. D. 1983. The mammals of the Orange Free State. Memoirs van die Nasionale Museum Bloemfontein, 18:1-218.

LYNCH, C. D. 1989. The mammals of the north-eastern Cape Province. Memoirs van die Nasionale Museum Bloemfontein, 25:1-116.

MEESTER, J. A. J., I. L. RAUTENBACH, N. J. DIPPENAAR, AND C. M. BAKER. 1986. Classification of Southern African mammals. Transvaal Museum Monograph, 5:1-359.

NOVAK, R. M. AND J. L. PARADISO. 1983. Walker's mammals of the world. Fourth ed. The Johns Hopkins University Press, Baltimore, Maryland, 2:569-1362.

OGILBY, W. 1833. Proceedings of the Zoological Society, London: 49.

POCOCK, R. I. 1916. On the external characters of the mongooses (Mungotidae). Proceedings of the Zoological Society, London, 1:349-374.

PRINGLE, J. A. 1977. The distribution of mammals in Natal. Part 2. Carnivora. Annals of the Natal Museum, 23:93-115.

RADINSKY, L. 1975. Viverrid neuroanatomy: phylogenetic and behavioral implications. Journal of Mammalogy, 56:130-150.

PROFESSOR O. ANNE E RASA, Department of Zoology, University of Pretora, Pretoria, 0002.

RAUTENBACH, I. L. 1982. Mammals of Transvaal. Ecoplan Monograph No. 1, Ecoplan, Pretoria. 211 pp.

ROBERTS, A. 1924. Some additions to the list of South African mammals. Annals of the Transvaal Museum, 10:59-76.

ROBERTS, A. 1929. New forms of African mammals. Annals of the Transvaal Museum, 13:82-121.

ROBERTS, A. 1932. Preliminary description of fifty-seven new forms of South African mammals (Mainly 38 from Vernay-Lang Kalahari expedition, 1930). Annals of the Transvaal Museum, 15:1-19.

ROBERTS, A. 1938. Descriptions of new forms of mammals. Annals of the Transvaal Museum, 19:231-245.

ROBERTS, A. 1951. The mammals of South Africa. "The mammals of South Africa" Book Fund, Johannesburg, 700 pp.

ROSEVEAR, D. R. 1974. The carnivores of West Africa. British Museum (Natural History), London. 548 pp.

ROWE-ROWE, D. T. 1978. The small carnivores of Natal. Lammergeyer, 25:1-48.

SAVAGE, R. J. G. 1978. Carnivora. Pp. 249-267, in Evolution of African mammals (V. J. MAGLIO AND H. B. S.. COOKE, eds.). Harvard University Press, Cambridge and London, 641 pp.

SCHWANN, H. 1906. A list of the mammals obtained by Messr. R. B. Woosnam and R. E. Dent in Bechuanaland. Proceedings of the Zoological Society, London, 1:101-111.

SCLATER, W. L. 1900. The mammals of South Africa. I. R. H. Porter, London, 1:1-324.

SHORTRIDGE, G. C. 1934. The mammals of South West Africa. William Heinemann, London, 1:1-437.

SIMPSON, G. G. 1945. The principles of classification and a

classification of mammals. Bulletin of the American Museum of Natural History, 85:1-350.

SMITH, A. 1829. Dr A. Smith's contributions to the natural history of South Africa. Zoological Journal, London, 4:437.

SMITH, A. 1834. African zoology. Mammalia. South African Quarterly Journal, 2:116, 117.

SMITH, A. 1839. Illustrations of the zoology of South Africa. Mammalia. Smith, Elder and Co., London, 1 (un-numbered).

SMITHERS, R. H. N. 1971. The mammals of Botswana. Museum Memoir No. 4. The Trustees of the National Museums of Rhodesia, Salisbury. 340 pp.

SMITHERS, R. H. N. 1983. The mammals of the Southern African subregion. University of Pretoria, Pretoria. 736 pp.

SNYMAN, P. S. 1940. The study and control of the vectors of rabies in South Africa. Onderstepoort Journal of Veterinary Science and Animal Industry, 15:9-140.

STAINS, H. J. 1984. Carnivores. Pp. 491-521, in Orders and families of Recent mammals of the world (S. ANDERSON AND JONES, J. KNOX JR., eds.). John Wiley and Sons, New York. 686 pp.

STUART, C. T. 1981. Notes on the mammalian carnivores of the Cape Province, South Africa. Bontebok, 1:1-58.

TAYLOR, P. J., AND J. A. J. MEESTER. 1989. The type locality of Cynictis penicillata coombsii Roberts, 1929 and

Gerbillus paeba coombsii Roberts, 1929. Zeitscrift für Säugetierkunde, 54:329-330.

TAYLOR, P. J., AND J. MEESTER. Submitted, a. Karyotypic analysis of the yellow mongoose Cynictis penicillata. Zeitschrift fur Saugetierkunde.

TAYLOR, P. J., AND J. MEESTER. Submitted, b. Morphometric variation in the yellow mongoose Cynictis penicillata Cuvier, 1829, in Southern Africa. Annals of the Transvaal Museum.

TAYLOR, P. J., G. K. CAMPBELL, D. VAN DYK, J. P. WATSON, J. PALLET, AND H. ERASMUS. In press. Genic variation in the yellow mongoose (Cynictis penicillata) in Southern Africa. South African Journal of Science.

THOMAS, O., AND H. SCHWANN. 1904. On a collection of mammals from British Namaqualand, presented to the National Museum by Mr C. D. Rudd. Proceedings of the Zoological Society, London, 1:171-183.

THOMAS, O., AND H. SCHWANN. 1904. Abstracts, Proceedings of the Zoological Society, London, 2:5.

WOZENCRAFT, W. C. 1989a. Classification of the recent Carnivora. Pp. 569-593, in Carnivore Behavior, Ecology and Evolution (J. L. GITTLEMAN, ed.). Chapman and Hall, London.

WOZENCRAFT, W. C. 1989b. The phylogeny of the recent Carnivora. Pp. 495-535, in Carnivore Behavior, Ecology and Evolution (J. L. GITTLEMAN, ed.). Chapman and Hall, London.

WURSTER, D. H. AND K. BENIRSCHKE. 1968. Comparitive cytogenetic studies in the order Carnivora. Chromosoma, 24:336-382.

ZUMPT, I.F. 1968. The feeding habits of the yellow mongoose, Cynictis penicillata, the suricate, Suricata suricatta and the Cape ground squirrel, Xerus inauris. Journal of the South African Veterinary and Medical Association, 39:89-91.

ZUMPT, I. F. 1969. Factors influencing rabies outbreaks: the age and breeding cycle of the yellow mongoose, Cynictis penicillata (G. Cuvier). Journal of the South African Veterinary and Medical Association, 40:319-322.

ZUMPT, I. F. 1976. The yellow mongoose (Cynictis penicillata) as a latent focus of rabies in South Africa. Journal of the South African Veterinary Association, 47:211-213.

ZUMPT, I. F. AND H. W. DE BRUYN. 1967. The merits of "phostoxin" in the eradication of small Viverridae. Journal of the South African Veterinary and Medical Association, 38:456-457.

CHAPTER 3

COLOUR VARIATION[1]

INTRODUCTION

Two general approaches to colour analysis in mammals, qualitative and quantitative, can be identified. In most cases colour variation is analysed by means of general qualitative descriptions based on comparisons of museum study skins. Colour terminology often conforms to a recognized nomenclatural system such as Ridgeway's (1912) 'Colour Standards and Nomenclature' (see for example Roberts, 1951), or Munsell's (1905) 'A Colour Notation' (see for example Hall, 1981). Unlike Ridgeway's charts, Munsell's charts can be used for a quantitative as well as a qualitative approach to determining colour (Miller, 1958; Oyama, Takehara and Ooi 1967; Smithe, 1974).

---

1. This chapter, together with abstract, is essentially the text of a paper, by P. J. Taylor, J. Meester and I. L. Rautenbach, that is in press in Annals of the Transvaal Museum under the full title 'A quantitative analysis of geographic colour variation in the yellow mongoose Cynictis penicillata (Cuvier, 1829) in Southern Africa'.

Quantitative methods of colour determination, such as Munsell charts (Bowers, 1956), disc colorimeters (Nickerson, 1946; Bowers, 1956) and spectrophotometric devices (Sumner, 1927; 1930; Bowers, 1956; Genoways 1973; Demeter and Lazar, 1984), have not been widely adopted by mammalogists. It is often assumed that colour is too variable a character, and the mammalian pelage too heterogeneous, to allow accurate and meaningful measurements of colour. The primary aim of this paper was to critically test the validity of such an assumption by using two different measuring devices (Munsell charts and a tristimulus colorimeter), to analyse seasonal and geographic colour variation in the yellow mongoose, a diurnal, burrow-dwelling carnivore endemic to and widely distributed throughout Southern Africa. The results of the two methods were compared with each other and with qualitative findings based on comparisons of large numbers of specimens.

Marked geographic changes in coat colour occur in C. penicillata, which have proved to be difficult to resolve by means of conventional qualitative methods (a cursory reading of colour descriptions for the species in Roberts, 1951; Lundholm, 1955 and Smithers, 1983 will quickly prove this). Partly as a result of the subjectivity involved in colour determination, the taxonomy of the species is confused and in need of revision. Up to 12 subspecies were previously recognised, differing only slightly in size and colour

(Roberts, 1951; Ellerman, Morrison-Scott and Hayman, 1953). On the basis of apparently smooth clines in colour and size, Lundholm (1955) regarded the species as being monotypic, a view that is currently held (Smithers, 1983; Meester, Rautenbach, Dippenaar and Baker, 1986). In attempting to develop a quantitative and objective approach to colour determination, a further aim of this study was therefore to obtain an accurate description of the pattern, rate and nature (continuous or discontinuous) of geographic colour variation in the yellow mongoose, from which meaningful taxonomic conclusions could be drawn.

A third aim of this study was to investigate the environmental correlates of colour, by comparing maps of environmental variables and trend surface maps of colour variables, and by using statistical techniques (multiple linear regression analysis) to obtain measures of association between climatic and colour variables.

MATERIALS AND METHODS

Colour measurement

Sixty four yellow mongoose study skins were selected (by P.J.T.) from a much larger collection of specimens housed in the Transvaal Museum, Pretoria, so as to reflect the range of observable local and regional differences in colour,

while covering the geographic range of the species as evenly as possible (an important requirement for trend surface analysis: see below). The selection process can be assumed to approximate random sampling since it was dictated largely by the availability of specimens at any one locality (most localities were represented by one or a few specimens only).

Individual colour measurements were taken on the dorsal surface of the rump, using 'Standard Revised Munsell Soil Colour Charts' (Oyama et. al., 1967) and a Hunterlab D25-2, I.C.I. (International Committee on Illumination) tristimulus colorimeter, belonging to the South African Bureau of Standards in Pretoria. Both methods relate directly to the internationally recognized Munsell Colour System (Munsell, 1954), which defines colour in terms of a three-dimensional 'colour solid', having orthogonal axes corresponding to three different physical properties of colour. These are generally termed hue (position on the visible spectrum, e.g., red or blue), value (tone, e.g., dark or light) and chroma (colour saturation, e.g., rich or faded). In this study the three properties of colour were measured independently using Munsell charts and a tristimulus colorimeter as follows.

The dorsal rump colour of study skins was matched with Munsell colour charts under standard conditions (a north-facing window). As standard Munsell colours are arranged in

equal steps of increasing hue, value and chroma, and each standard Munsell colour possesses unique numerical coordinates of hue, value and chroma, individual measurements of the three variables could be obtained for each skin in the sample.

Tristimulus colorimeter measurements were taken by placing each study skin under the instrument so that the mid-dorsal region of the rump fitted tightly against a standard aperture of approximately 5 cm diameter. The standard area was illuminated by a standard achromatic light source called illuminant C 45/0 (incident light 45°, reflected 0°). Tristimulus readings were obtained directly from the instrument, representing the reflectance of light from the measured surface in each of the primary colours, red (X), green (Y) and blue (Z). By convention Y is also taken to represent overall reflectance from the sample, or 'brightness' (equivalent to Munsell value).

Tristimulus readings were converted to trichromatic coefficients as follows: $x = X/(X + Y + Z)$; $y = Y/(X + Y + Z)$; $z = Z/(X + Y + Z)$. For each sample x and y were plotted on a standard chromaticity chart (Fig. 3.1) in order to obtain measurements of 'dominant wavelength' (equivalent to Munsell hue) and 'excitatory purity' (equivalent to Munsell chroma). In the chromaticity chart shown in Fig. 3.1, dominant wavelength is determined as the point at which the

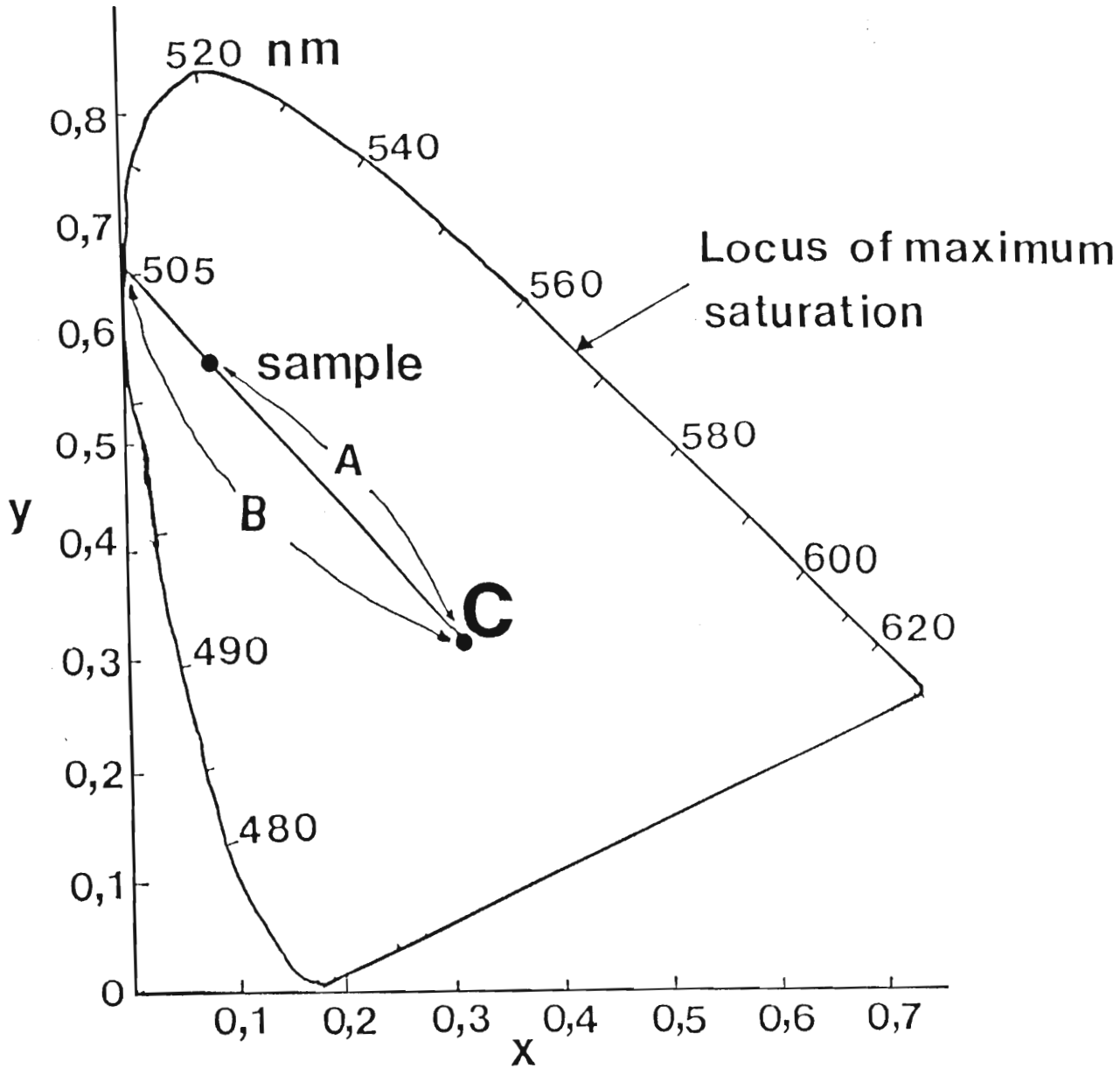


Fig. 3.1. Standard I.C.I. (International Committe on Illumination) chromaticity chart showing method of determination of dominant wavelength (DOM) and excitatory purity (PUR). Modified from Hardy, 1936. See text for explanation.

locus of maximum saturation is intersected by a line drawn from C (achromatic point for standard illuminant C) through the point represented by the sample (i.e., 505 nanometers in the example in Fig. 3.1). Conceptually, dominant wavelength can be understood as the amount of 'mixture' that occurs between the different primary colours (reflected in the position of x, y on the chromaticity chart). Excitatory purity is measured as the percentage of the distance from C to the sample point, of the total distance from C to the locus of maximum saturation along the line connecting the two points (i.e., %(A/B) in Fig. 3.1). The closer the x, y point is to C the more faded it is, while as the point approaches the locus, the colour of the sample approaches saturation at a particular wavelength. The close correspondence between Munsell chart and I.C.I. colorimeter variables is explained by the fact that the standard Munsell colours were originally defined in terms of their positions on standard I.C.I. chromaticity charts (Newhall, Nickerson and Judd, 1943). Further explanation of standard colorimetric procedures can be found in Hardy (1936); Nickerson (1946); and Smithe (1974).

To avoid confusion the properties of colour will hereafter be referred to as hue, value and chroma (i.e., in lower case letters), while references to specific variables will be in upper case letters. Colorimeter-based variables will hereafter be abbreviated to DOM (dominant wavelength), BRT

(brightness) and PUR (excitatory purity). Thus the chart-based variables HUE, VALUE and CHROMA measure the same properties as DOM, BRT and PUR respectively.

Analysis of colour variables

Analysis of colour variables was performed in three stages: 1) analysis of statistical properties of variables; 2) analysis of seasonal and geographic variation; 3) analysis of environmental correlates of colour.

Statistical properties of variables

The usefulness of continuous variables in describing biological processes depends on statistical properties such as resolution, precision, accuracy and conformity to a normal distribution in a homogeneous sample. As the colour variables used in this study have not been routinely used in biological applications, simple quantitative measures of their statistical properties were obtained in order to assess their reliability, before conducting further statistical analyses.

Statistical properties of variables, used in this study, are defined as follows. Resolving ability $(\underline{R})^2$ was taken to be

---

2. The term 'resolving ability' was coined here as the term

the number of class intervals (ie. scale divisions) included in the sample range:

$$\underline{R} = \frac{(\underline{X}_{max} - \underline{X}_{min})}{\underline{d}}$$

where $\underline{X}_{max}$ and $\underline{X}_{min}$ represent the largest and smallest values of $\underline{X}$ respectively, and $\underline{d}$ represents the smallest possible unit measurement (i.e., resolution in the conventional sense). $\underline{R}$ is therefore inversely proportional to resolution in its conventional sense.

Thus, for a sample of skulls in which greatest length is to be measured, and the range is 50 mm, a tenfold increase in resolving ability ($\underline{R}$) is possible using vernier callipers which measure to the nearest 0,1 mm ($\underline{R}$ = 50/0,1 = 500) than would be possible using a metre rule which measures to the

---

'resolution' usually refers to the smallest possible unit measurement, e.g., 1/10 sec, 1 mm. Because of the diversity of units of colour variables in this study the term resolution would be meaningless. One nanometer (DOM) cannot be compared with one arbitrary unit (HUE, VALUE and CHROMA) or 1/10 of a percent (BRT, PUR). Resolving ability, as defined here, conveys the same general meaning as resolution but is independent of scale.

nearest 1 mm (R = 50/1 = 50).

Accuracy and precision are defined sensu De Blase and Martin (1981: 13, 276). Accuracy is defined as the amount of correspondence between replicate pairs of measurements taken independently by two or more persons (i.e., a measure of approximation of the true value), while precision is defined as the amount of correspondence between replicate pairs of measurements taken by the same person. In this context precision is the exact converse of measurement error.

A measure of accuracy of chart-based variables was obtained by asking three independent observers to score the same sample of 25 C. penicillata study skins. Pairs of replicate scores for HUE, VALUE and CHROMA were compared by means of the percentages of matches and Pearson's product-moment correlation coefficients. For practical reasons it was not possible to obtain an equivalent measure of accuracy for colorimeter-derived variables.

An index of measurement error (ME: the converse of precision) was obtained for all six variables, as the mean absolute deviation calculated between two replicate sets of measurements taken by the same person (P.J.T.), expressed as a percentage of the range:

$$\underline{ME} = \frac{\Sigma \left| \underline{X}_{i,1} - \underline{X}_{i,2} \right|}{\underline{n}} \times \frac{100}{\underline{X}_{max} -- \underline{X}_{min}}$$

where $\underline{n}$ is the number of replicate pairs of measurements, $\underline{X}_{max} -- \underline{X}_{min}$ is the range and $\underline{X}_{i,1}$ and $\underline{X}_{i,2}$ are measurements of the same specimen taken by the same person at times t=1 and t=2 (one year apart for chart variables and a few days for colorimeter variables. A longer time was necessary for chart variables, to eliminate the bias due to the possibility of remembering which scores had previously been assigned to certain specimens). Given two sets of 10 skull length measurements (in mm) measured on the same sample of 10 skulls by the same person, ME is calculated as follows:

Specimen	Set 1	Set2
1	15,9	15,7
2	13,5	13,8
3	13,9	13,8
4	15,4	15,4
5	15,3	15,6
6	14,7	14,5
7	14,5	14,4
8	12,4	12,3
9	15,1	14,7
10	14,5	14,3

$\underline{n} = 10;$

$(\underline{X}_{max} -- \underline{X}_{min}) = (15,9 - 12,3) = 3,6$; and

$$\underline{ME} = \frac{\sum |\underline{X}_{i,1} - \underline{X}_{i,2}|}{\underline{n}} \times \frac{100}{\underline{X}_{max} -- \underline{X}_{min}} ;$$

$$= \frac{|15,9 - 15,7| + \ldots + |14,5 - 14,3|}{10} \times \frac{100;}{3,6}$$

$$= 0,19 \times 27,78;$$

$$= 5,3\%$$

In the above example measurement error accounts for 5,3% of the range of variability in skull length. The above formula was designed to be comparable between variables, and therefore independent of the unit of measurement (since different colour variables used different units of measurement), and to be meaningful. When ME accounts for a high proportion of the range, say 15% or greater, then the ability of the variable to measure biological trends in the data becomes increasingly reduced.

To test the normality of the variable sample distributions, frequency distribution histograms were plotted and $\underline{g}_1$ (skewness), $\underline{g}_2$ (kurtosis) and Kolmogorov-Smirnov ($\underline{D}$) statistics were computed for each of the six colour variables. These tests were performed using the program STATS of the statistical software package BIOΣTAT I

(Pimentel and Smith, 1986a). Using the statistical software package NTSYS-PC (Rohlf, 1986), Pearson product-moment correlation coefficients were calculated for all pairs of variables, and these were summarized by means of a correlation phenogram conforming to the unweighted pair group method with averages (UPGMA: Sneath and Sokal, 1973). Both BIOΣTAT and NTSYS-PC were run on an Olivetti M24 PC.

Seasonal and geographic variation

Means for all six variables were calculated for a summer (collected in January; $n = 6$) and a winter (collected in June; $n = 12$) sample of study skins from a locality, Wesselsbron, in the Orange Free State, and t-tests of colorimeter variables were used to analyse the significance of seasonal differences. Analysis of variance (ANOVA) was used to test for equality of variances of colorimeter variables between seasonal samples.

Thorpe (1976) pointed out that two categories of techniques exist for analysing geographic variation, those that depend on spatial distribution of localities (e.g., contouring techniques) and those that do not (e.g., clustering and ordination techniques). Both approaches were used in this study. Trend surface analysis of colorimeter variables was used to map the directionality and rate of change of colour variation across the species range. On the other hand, using

both Munsell chart and colorimeter-derived variables, bivariate plots of OTU (see Fig. 3.4 for geographic extent of OTUs) means, and univariate Dice-grams for each OTU, were used to detect possible taxonomic groupings among OTUs.

Trend surface analysis of DOM, BRT and PUR was performed using the program PTSA from the statistical software package BIOΣTAT II (Pimentel and Smith 1986b). In trend surface analysis (a special case of multiple regression) the measured quantity is predicted as a function of latitude and longitude, and plotted as smoothed geographic surfaces of increasing complexity (linear, quadratic, cubic and higher). Residuals (deviations of actual from predicted values) may also be calculated and plotted. Ideally, regional trends are represented by trend surfaces and local effects by way of plots of residuals. Further discussions and applications of this technique can be found in Marcus and Vandemeer (1966), Sneath and Sokal (1973) Thorpe (1976), Johnson (1978), Sokal and Rohlf (1981), and Pimentel and Smith (1986b) .

The technique of trend surface analysis, although often superior as a means of representing continuous data, is most applicable to studies for which data on a regular grid are available (e.g., geological data), a near impossibility for biological data. Blackith and Reyment (1971) point out that 'at the purely statistical level trend-surface analysis seems almost indefensible: there is, therefore a special

responsibility on the user'. In view of this, the assumptions of the technique are discussed briefly below in relation to the colorimetric data used in this study:

1) Independent X variables (latitude and longitude) are measured without error. This is obviously true for geographical coordinates of fixed localities;

2) The regression function follows the appropriate linear or curvilinear model. Regression statistics were used to evaluate the fit of each polynomial, hence its map, to the present data.

3) Measurements of Y (dependent variable) at each locality follow a normal distribution. In this study most localities were represented by only a single specimen so that this assumption could not be critically tested. Nevertheless tests of normality were presented for the entire sample, and these results can be cautiously applied to the level of single localities.

4) Measurements of Y from each locality come from populations having the same variance. The same argument as above applies. Measures of sample variance are not available for each locality.

5) X variables (latitude and longitude) are independent. Colinearity, or correlation, between latitude and longitude results from non-regular distribution of data points, an almost universal problem with biological data sets. In selecting localities for this study an attempt was made to cover the range as regularly as possible, in order to

minimize the effects of colinearity. Moreover, latitude and longitude of localities sampled in this study were not significantly correlated (n = 53; r = 0,32; P > 0,05). Nevertheless, statistics obtained from trend surface analysis were treated with caution, and the overall aim, in using this approach, was simply to visualize broad geographic trends in DOM, BRT and PUR. The biological reality of geographic colour trends was verified from *a posteriori* visual comparisons of study skins.

In order to eliminate the effect of seasonal bias in the data the complete sample was subdivided into a winter sample (skins collected from May to October) and a summer sample (January to April). Skins collected in November and December tended to have a transitional coat and were excluded from the sample. Analyses were performed separately on winter skins and summer skins as well as on the combined sample.

Environmental correlates of colour

For the purpose of obtaining climatic variables for multiple regression analysis, climatic data for actual annual rainfall (mm), mean annual temperature (°C) and mean daily relative humidity taken at 08h00 hours (%), were obtained from three sources: South African Weather Bureau publications WB35 (1972) and WB40 (1986) and the Botswana Government publication (1984), 'Climatological Summaries for

Botswana'. For each locality represented in the sample, climate data were obtained from the nearest climate station for which appropriate data were available, with the exception of rainfall data for South African localities, for which mean values were obtained for rainfall districts (WB35) in which individual localities were situated. In most cases climatic data were available from climate stations in the same or adjacent sections (quarter degree grid squares). Where climate stations were not situated in the immediate vicinity of localities, particular attention was paid to climate maps, and altitude of climate stations, to ensure that the climate was similar to the locality for which the data were required.

Multiple linear regression analysis (using the program MCREG from BIOΣTAT I) was used to analyse the relationship between colorimeter variables, DOM, BRT and PUR (dependent variables), and the three climatic variables (independent variables). The relative importance of the three climatic variables, in determining patterns of colour variation, was determined using $\underline{t}$-tests to assess the significance of partial regression coefficients. Maps of actual annual rainfall (mm), total daily radiation ($cal.^{-3}\ day^{-1}$), mean annual temperature (°C) and vegetation types were presented for visual comparison with trend surface maps of colorimeter-derived variables.

RESULTS AND DISCUSSION

Statistical properties of variables

Accuracy of chart variables (HUE, VALUE, CHROMA) was determined by the degree of similarity between pairs of replicate measurements taken by three different people (Table 3.1). Although the percentage of matches was fairly low (12--48%), statistically significant correlations were obtained ($\underline{r}$ = 0,45--0,88; $\underline{P}$ < 0,05) between replicate sets of measurements. The low percentages of matches between replicate sets of scores indicates a low probability of two people matching a particular skin to the same standard Munsell colours. This is to be expected due to individual differences in colour perception and differences in the nature of the light illuminating the surface to be measured.However, the statistical significance of correlations between replicate sets of scores indicates that different people will tend to recognize the same <u>relative</u> trends in HUE, VALUE and CHROMA. The method is therefore inaccurate in an <u>absolute</u> sense (approximating the true value), but surprisingly accurate in a <u>relative</u> sense (approximating a real trend in the data).

Resolving ability of colorimeter variables (DOM, BRT, PUR)

Table 3.1

Percentages of matches (%M) and correlation coefficients (r) between replicate pairs of Munsell chart scores, taken by three individuals, of overall and underfur dorsal surfaces of C. penicillata study skins.

	Overall (n = 25)		Underfur (n = 18)	
	%M	r	%M	r
Individual 1 versus individual 2				
HUE	44	0,88	36	0,45
VALUE	48	0,85	56	0,60
CHROMA	48	0,68	48	0,70
Individual 1 versus individual 3				
HUE	44	0,77	40	0,79
VALUE	28	0,80	44	0,58
CHROMA	44	0,61	40	0,76
Individual 2 versus individual 3				
HUE	12	0,79	44	0,46
VALUE	44	0,70	48	0,44
CHROMA	28	0,45	40	0,76

Table 3.2

Measurement error (ME; %) in six quantitative variables used to analyse colour variation in the yellow mongoose Cynictis penicillata. Method of calculation of ME given in text. n represents the number of replicate pairs of measurements.

Variable (abbreviation)	Unit of measurement	n	ME(%)
Hue (HUE)	Munsell units	25	6,7
Value (VALUE)	Munsell units	25	15,0
Chroma (CHROMA)	Munsell units	25	13,1
Dominant wavelength (DOM)	Nanometers	17	12,7
Brightness (BRT)	% Reflectance	17	3,3
Excitatory purity (PUR)	% Saturation	17	3,9

is generally much higher ($\underline{R}$ = 10, 189 and 425 respectively) than for chart variables (4, 5, 6 for HUE, VALUE and CHROMA respectively). This results from the greater resolving ability of a photometric device compared with the human eye.

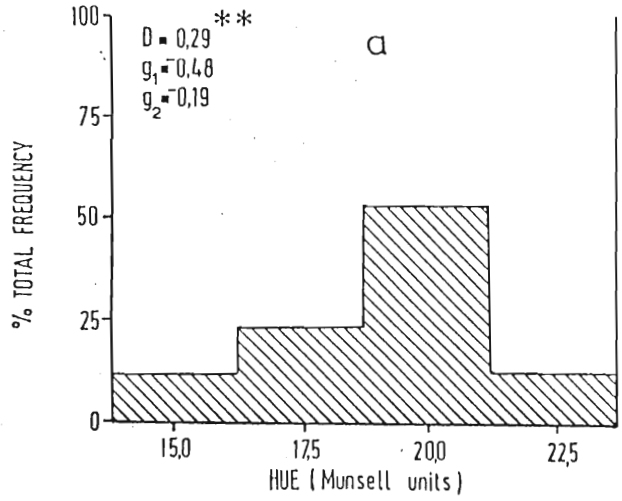
Measurement error (the converse of precision) varied from 6,7% to 15% for chart-based variables, and from 3,3% to 12,7% for colorimeter-based variables (Table 3.2). Comparable estimates of measurement error of craniometric variables in C. penicillata varied from 0,28% to 2,45% (Taylor and Meester, unpublished data). Colour variables tend to be less precise than craniometric variables, although measurement error never exceeded 15% of the sample range, and was usually less than 10% (Table 3.2). Measurement errors of this magnitude should not obscure major trends in colour variation. Errors in taking tristimulus colorimeter measurements resulted from differences in the way that skins were mounted in the instrument. Depending on how hard the skins were pressed against the measuring aperture, different tristimulus readings of the same skin could be obtained because of slight differences in the orientation of individual hairs. The extent of this source of variation in the present case was negigible in comparison to the range of colour variation in the sample, and it was further reduced by standardising the amount of pressure used to press skins against the aperture of the colorimeter. However, where the range of

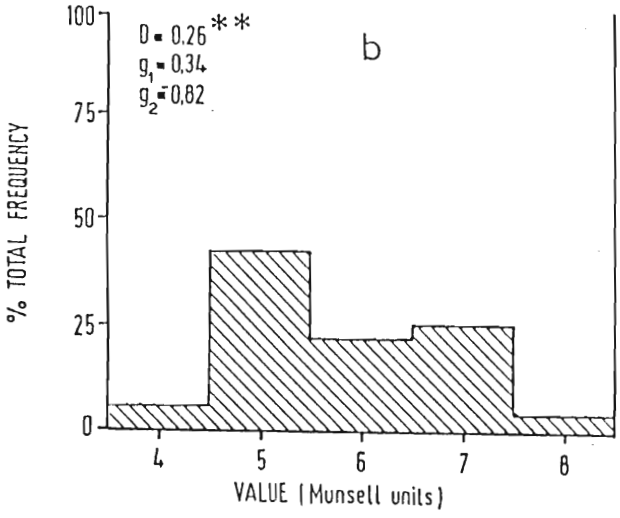
colour variation is small, skins are very dark in colour, or where the area of the measured surface of a study skin does not completely seal the aperture, measurement error may become a crucial factor, prohibiting the effective use of this method (Dippenaar, personal communication). However, a simple test of measurement error would validate or prohibit the use of a tristimulus colorimeter in a particular instance.

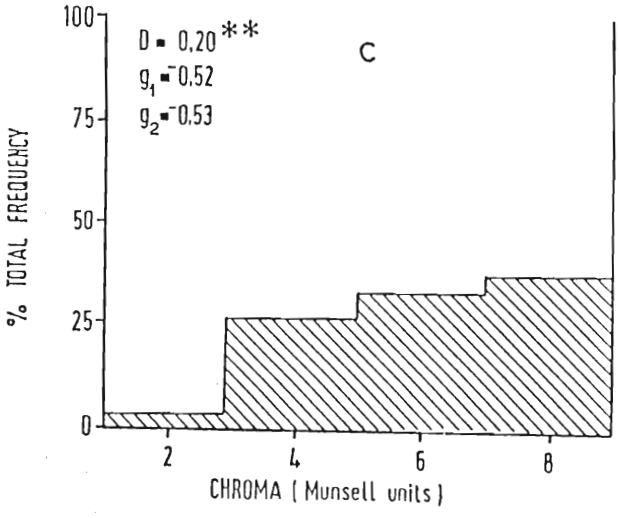
Figure 3.2 shows the distribution of all six colour variables in the entire sample (n = 64). Frequency histograms based on the entire sample are useful for detecting obvious sampling biases in individual variables, although departures from normality may also result from a non-homogeneous sample, rather than inherent limitations of variables. Tests of normality need not therefore be applicable at the level of single localities, but obvious departures from normality not attributable to sampling protocol will probably apply both at species and population level.

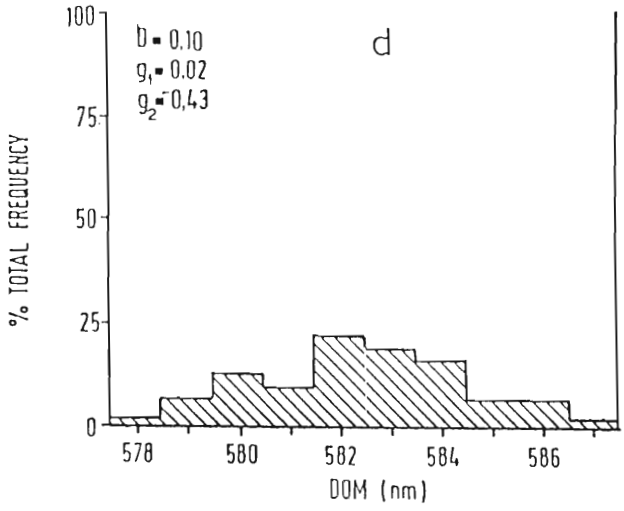
While chart-derived variable distributions departed significantly ($P < 0,01$) from normality, as determined by the Kolmogorov-Smirnov (D) test, they did not appear to show significant levels of skewness or kurtosis (Fig. 3.2). Significant D values were probably related to the small number of frequency classes in these variables. In the case

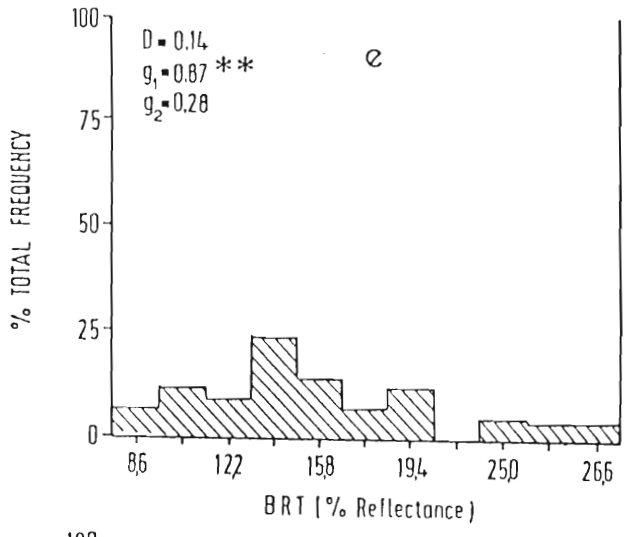
Fig. 3.2. Frequency distribution histograms, *t*-tests of skewness (g_1) and kurtosis (g_2), and Kolmorov-Smirnov tests of normality (D), for six quantitative variables used to measure colour in a sample of study skins of 64 adult *C. penicillata* (* indicates significance at the 5% level, ** at the 1% level). Abbreviations of variables explained in text.

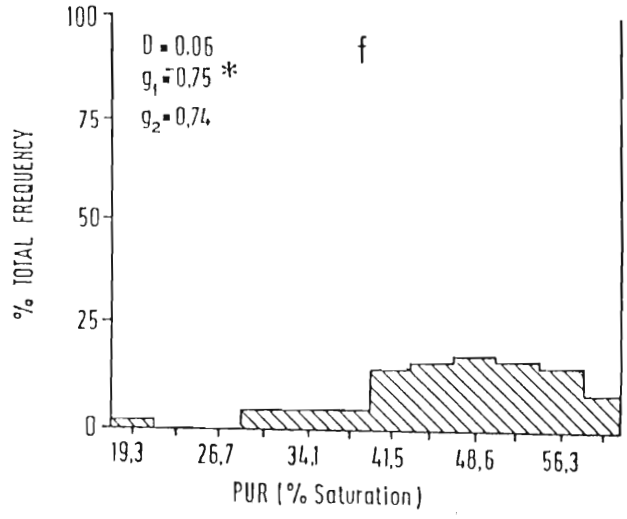

D = 0,29 **
g1 = 0,48
g2 = 0,19
a
% TOTAL FREQUENCY
100
75
50
25
0
15,0
17,5
20,0
22,5
HUE (Munsell units)


D = 0.26 **
g1 = 0,34
g2 = 0,82
b
% TOTAL FREQUENCY
100
75
50
25
0
4
5
6
7
8
VALUE (Munsell units)


D = 0,20 **
g1 = 0,52
g2 = 0,53
c
% TOTAL FREQUENCY
100
75
50
25
0
2
4
6
8
CHROMA (Munsell units)


D = 0.10
g1 = 0.02
g2 = 0,43
d
% TOTAL FREQUENCY
100
75
50
25
0
578
580
582
584
586
DOM (nm)


D = 0.14
g1 = 0.87 **
g2 = 0.28
e
% TOTAL FREQUENCY
100
75
50
25
0
8,6
12,2
15,8
19,4
25,0
26,6
BRT (% Reflectance)


D = 0.06
g1 = 0,75 *
g2 = 0,74
f
% TOTAL FREQUENCY
100
75
50
25
0
19,3
26,7
34,1
41,5
48,6
56,3
PUR (% Saturation)

of CHROMA it is clear from the asymmetrical nature of the frequency distribution histogram that the highest score (8) represented in the Munsell charts was lower than the highest actual intensity of coloration in the sample of study skins. Colorimeter-derived variables followed normal distributions (non-significant D values) although BRT and PUR had skewed distributions (Fig. 3.2: g_1 = 0,87 and -0,75; P = 0,01 and 0,05 respectively). From the appearance of the frequency distribution histograms for BRT and PUR there is a suggestion of bimodality associated with high measurements of BRT and low measurements of PUR. This result indicates the possibility of there being two populations in the sample, and appears to be due to the non-homogeneity of the sample rather than to inherent limitations in the variables BRT and PUR. As the Kolmogorov-Smirnov test is a more sensitive indicator of normality than the skewness or kurtosis statistics (Pimentel and Smith, 1986a), the above results suggest that parametric statistical techniques can be applied to colorimeter-derived but not to chart-derived variables. In subsequent analyses, therefore, the use of parametric techiques was restricted to colorimeter variables, and non-statistical methods were used to analyse chart variables.

While a high degree of integration existed generally between all pairs of colour variables, variables relating to hue and chroma properties of colour were particularly highly

correlated and variables relating to colour value were relatively weakly, negatively correlated with the other variables (Fig. 3.3). This suggests that there are two dimensions of colour variation in the yellow mongoose. The high degree of correlation between equivalent pairs of chart-derived and colorimeter-derived variables is an empirical demonstration of the direct relationship that exists between the two techniques, as described earlier.

Seasonal variation

Means for all six colour variables for winter ($\underline{n}$ = 18) and summer ($\underline{n}$ = 6) samples from a single locality are shown in Table 3.3. According to both methods of analysis (Munsell charts and tristimulus colorimeter), summer skins are redder (lower HUE, higher DOM), darker (lower VALUE, BRT) and richer (higher CHROMA, PUR) than winter skins (Table 3.3). Yellow mongooses moult once a year in November and December and new summer hairs appear in January and February. Progressive growth and eumelanization (increase in black pigments) of individual summer hairs, and the bleaching effect of sunlight, combine to produce the winter coat after about April or May. In addition to the seasonal colour changes mentioned above (which can easily be verified from inspection of skins), winter coats have longer guard hairs and are more grizzled in coloration than summer coats (due to alternating pale yellow and black annulations of

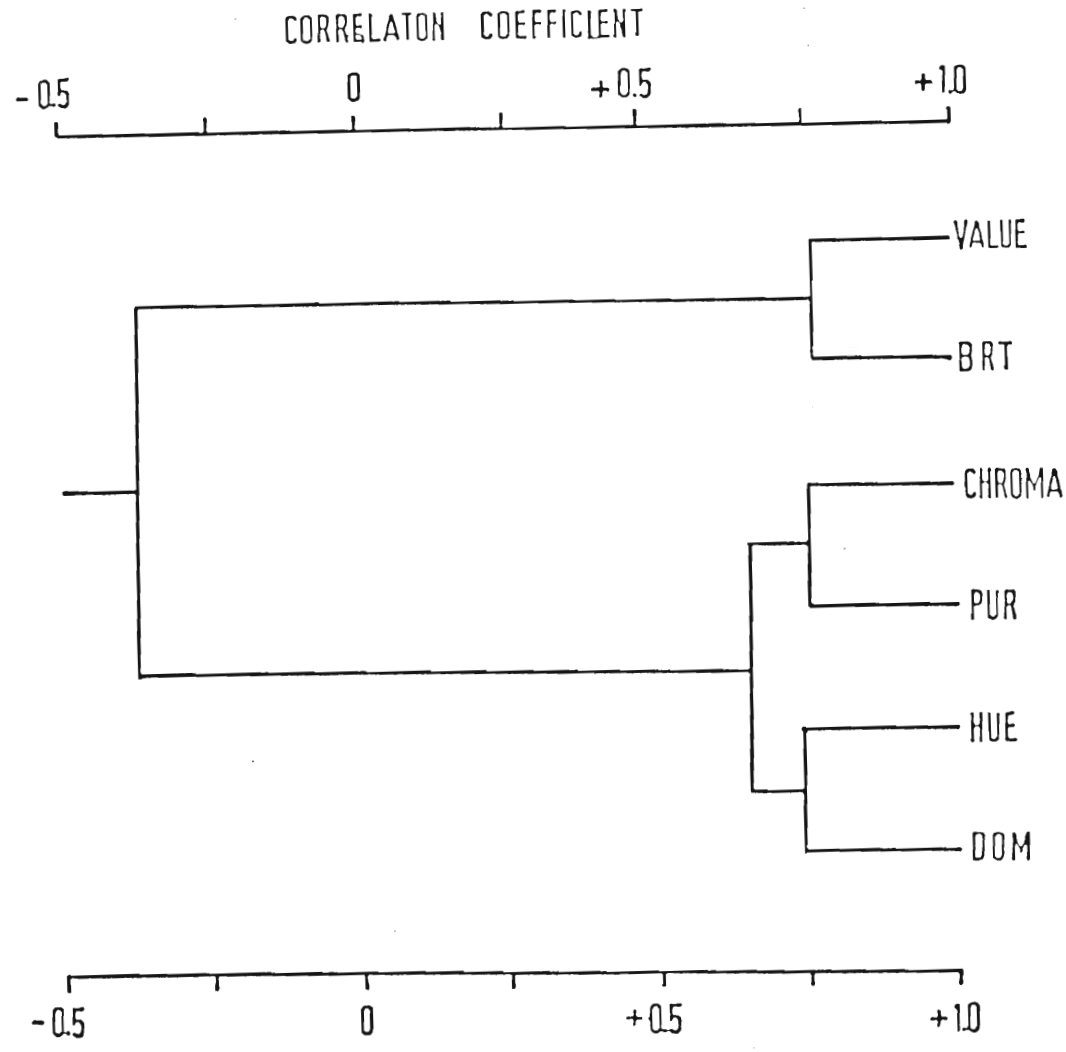


Fig. 3.3. Phenogram summarising patterns of correlation among six variables used to measure colour in a sample of adult C. penicillata study skins. Abbreviations of variables explained in text.

Table 3.3

Means ($\underline{X}$), standard deviations ($\underline{sd}$) and ranges ($\underline{X}_{min}$ - $\underline{X}_{max}$) of six colour variables in summer (collected in February: n = 6) and winter (collected in July: n = 12) samples of *C. penicillata* study skins from Wesselsbron in the Orange Free state. Abbreviations of variables explained in Table 3.2.

VARIABLE	SUMMER			WINTER		
	$\underline{X}$	$\underline{sd}$	$\underline{X}_{min}$ - $\underline{X}_{max}$	$\underline{X}$	$\underline{sd}$	$\underline{X}_{min}$ - $\underline{X}_{max}$
HUE	18,8	1,37	17,5 - 20,0	19,4	1,13	17,5 - 20,0
VALUE	6,0	0	All 6	6,2	0,57	5 - 7
CHROMA	8,0	0	All 8	6,5	1,24	4 - 8
DOM	583,5	1,38	582 - 585	582,7	0,98	581 - 584
BRT	14,93	0,99	13,8 - 16,1	15,77	2,87	12,1 - 20,2
PUR	54,47	2,22	50,8 - 56,7	51,00	4,27	43,9 - 55,9

individual guard hairs).

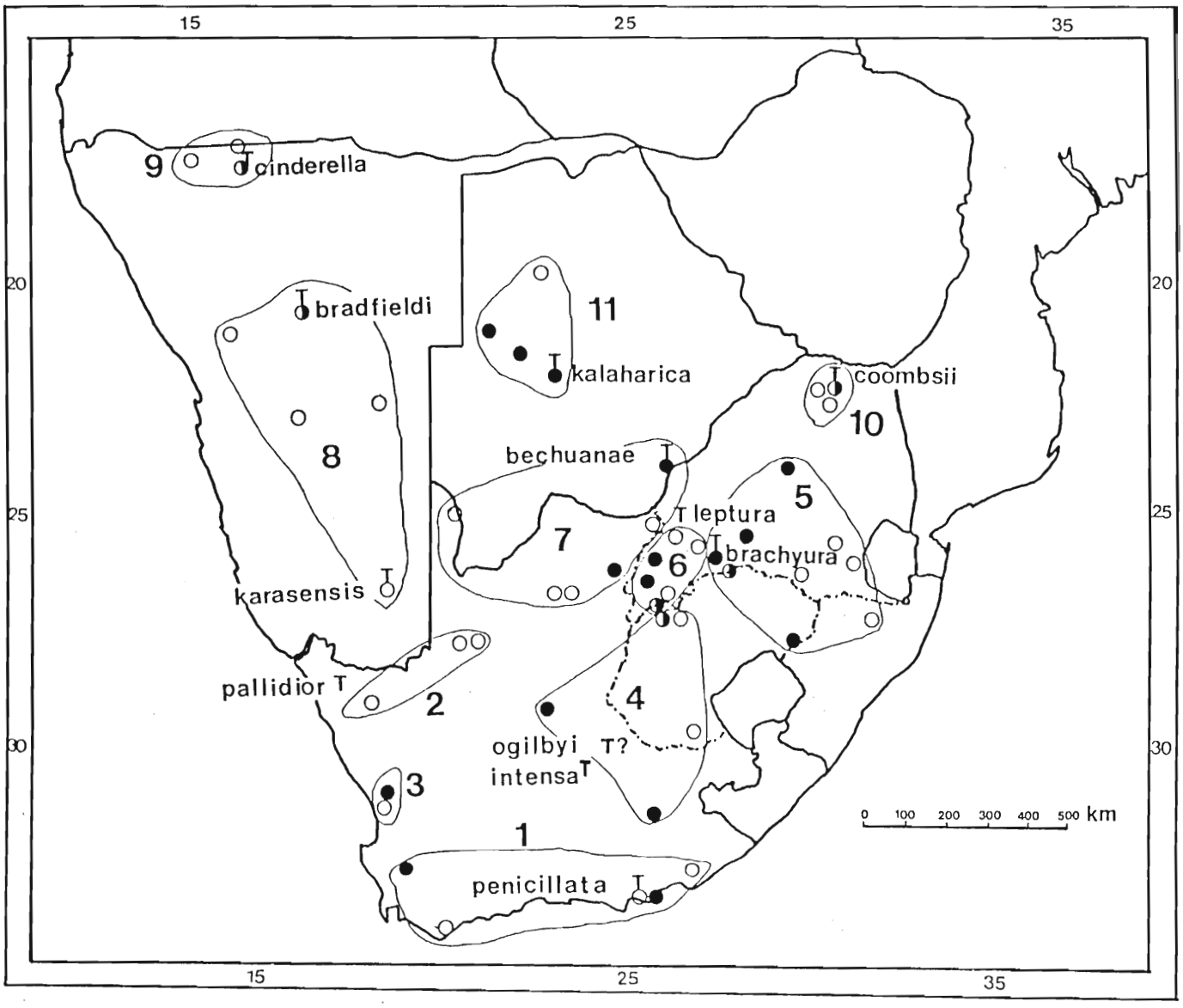
Seasonal means of colorimeter variables did not differ significantly (t = 1,48, 0,90, and 1,86 for DOM, BRT and CHR respectively; P > 0,05). Comparison of sample variances revealed significant differences in BRT (F = 8,40, P < 0,05), but not in DOM or PUR (F = 1,96 and 3,69 respectively; P > 0,05).While there are therefore consistent seasonal differences in colour in C. penicillata from a single locality, the non-significance of these differences justifies the pooling of skins collected in different seasons, for the purposes of subsequent analyses of geographic variation. Nevertheless, trend surface analyses were performed on both single-season and combined-seasons samples in this study, to compare the patterns of variation and statistical reliability of geographic trends produced by the two different samples. Concordance in geographic trends between these two sets of results provides a rough index of the robustness of the technique of trend surface analysis in describing actual geographic patterns of colour variation in C. penicillata. Ideally, analyses should be performed on single-season samples, but in the present study seasonal biases in the available study skin collection led to small sample sizes and uneven geographical coverage when single-season samples were considered.

Geographic variation

Trend surface analysis

Trend surface maps of DOM, PUR and BRT are shown in Figures 3.5--3.7 (combined-seasons sample) and Figures 3.8--3.10 (single-season sample). Variation in DOM and PUR does not follow a smooth cline as cubic (third degree) rather than linear (first degree) models provide the best fit to the data (Table 3.4: in analyses of the summer sample third degree polynomials accounted for a significant proportion of added explained variability (i.e., SS) in DOM and PUR and therefore represent the best fit to the data). Cubic trend surface maps of DOM and PUR (Figs 3.5, 3.6, 3.8, 3.9) show a predominantly north-south geographic trend with a richer, redder coloration in the south becoming faded and yellow towards the north. There is a zone of rapid geographic change, reflected by closely-spaced contours on trend surface maps, in DOM and PUR (more pronounced in the summer sample: Figs 3.8, 3.9) which separates specimens from northern Namibia, Botswana and northern Transvaal from specimens occurring to the south. This is correlated with the observation that specimens from the northern regions indicated are noticeably different in colour from southern specimens. Northern specimens have a dull, grizzled - greyish colour compared with a richer, redder coat colour in southern specimens.

Fig. 3.4. Map showing localities from which study skins of 64 C. penicillata were selected (from a larger sample of museum specimens) for colour measurement. Closed circles indicate localities from which summer skins were obtained; open circles indicate localities from which winter skins were obtained; half - closed circles indicate localities from which both summer and winter skins were obtained. Numbered groups of localities represent OTUs. T indicates positions of type localities of subspecies recognised by Roberts (1951); when combined with locality symbols, T indicates the inclusion of type specimens in the sample (except in the case of penicillata). OTUs correspond with ranges of previously recognised subspecies as follows: 1 = penicillata + intensa; 2 = pallidior (in part); 3 = pallidior (in part); 4 = ogilbyi; 5 = brachyura; 6 = leptura; 7 = bechuanae; 8 = karasensis + bradfieldi; 9 = cinderella; 10 = coombsii; 11 = kalaharica.


15
25
35
20
25
30
9
cinderella
bradfieldi
8
11
kalaharica
coombsii
10
bechuanae
5
leptura
7
6
brachyura
karasensis
pallidior
2
4
ogilbyi T?
intensa
3
1
penicillata
0 100 200 300 400 500 km

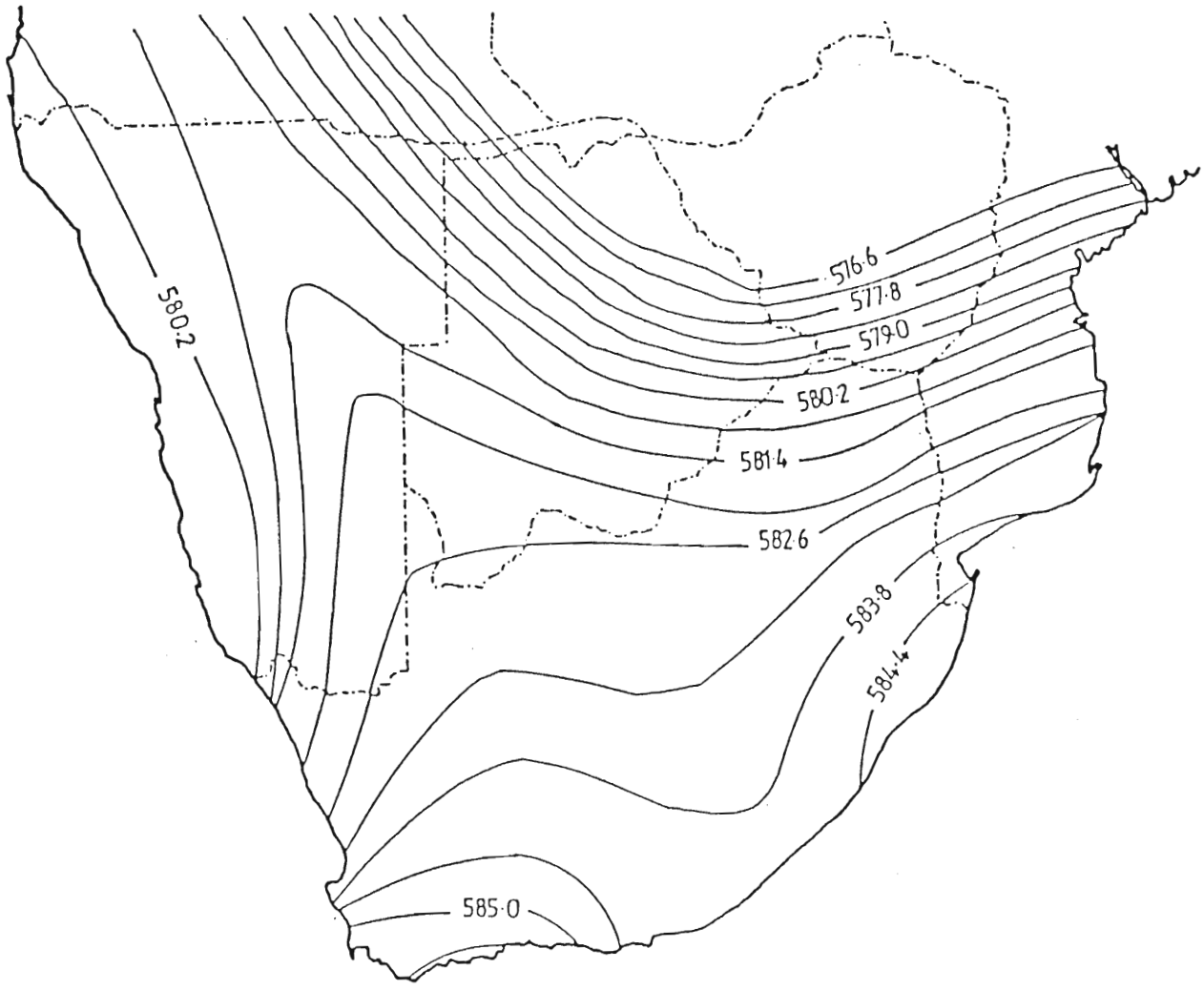


Fig. 3.5. Third degree (cubic) trend surface map of DOM in 64 C. penicillata (summer and winter skins combined). Contour values represent wavelengths in nanometers: increasing values indicate a shift from a yellower to a redder coloration.

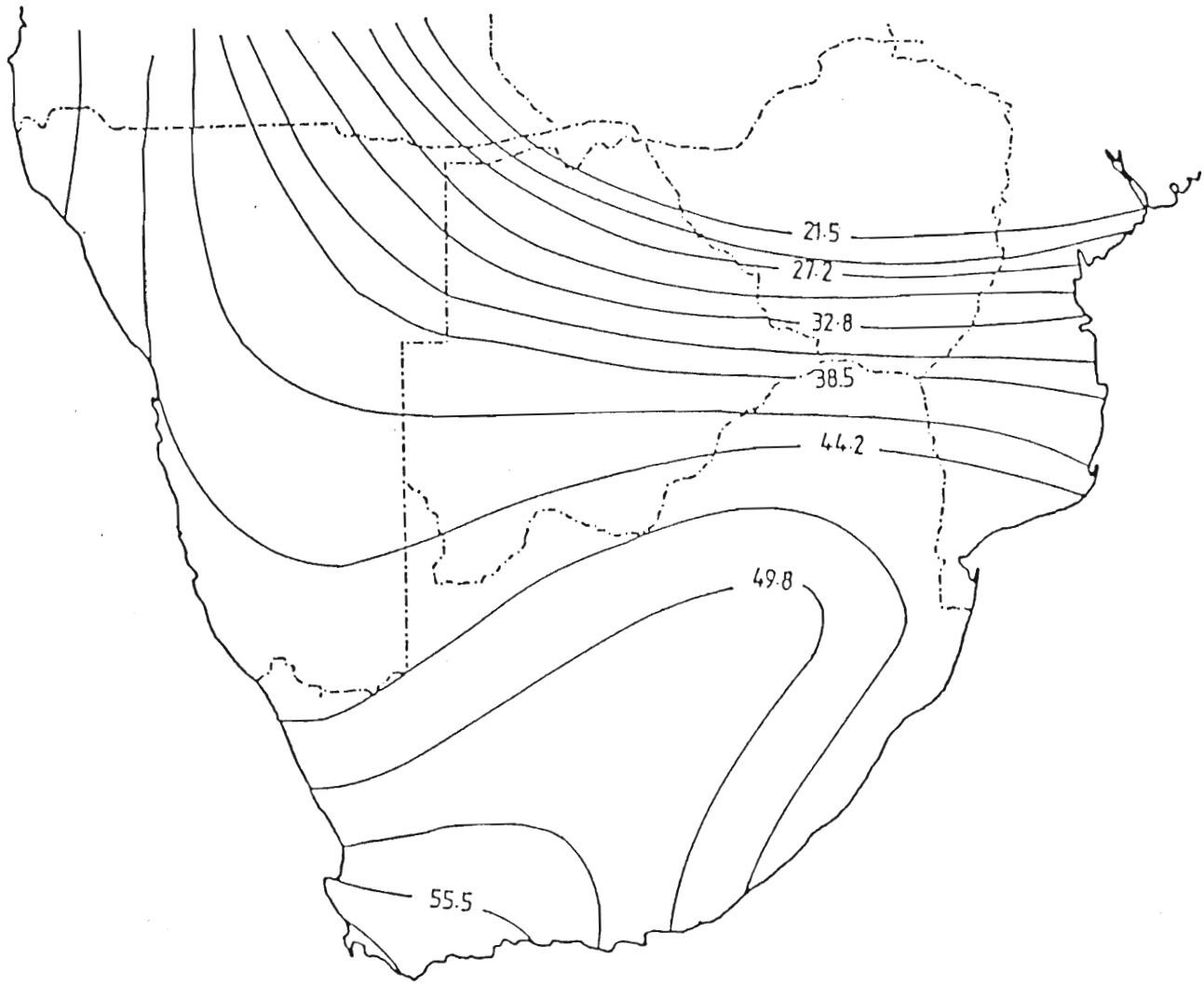


Fig. 3.6. Third degree (cubic) trend surface map of PUR in 64 C. penicillata (summer and winter skins combined). Contour values represent colour saturation: increasing values represent increasing colour saturation.

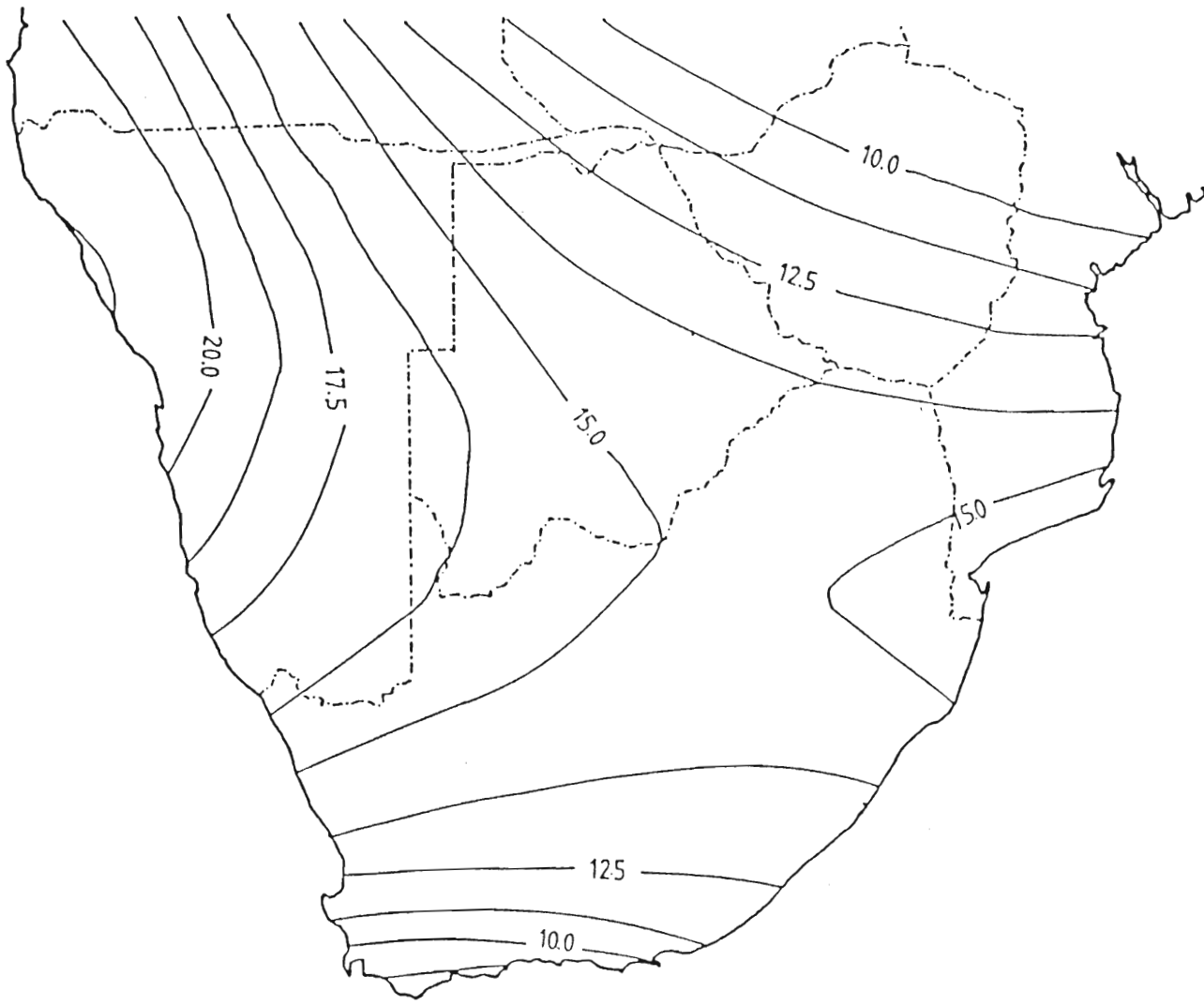


Fig. 3.7. Second degree (quadratic) trend surface map of BRT in 64 C. penicillata (summer and winter skins combined). Contour values represent reflectance of light from a sample relative to a pure white standard (i.e., paleness): increasing values represent increasing paleness.

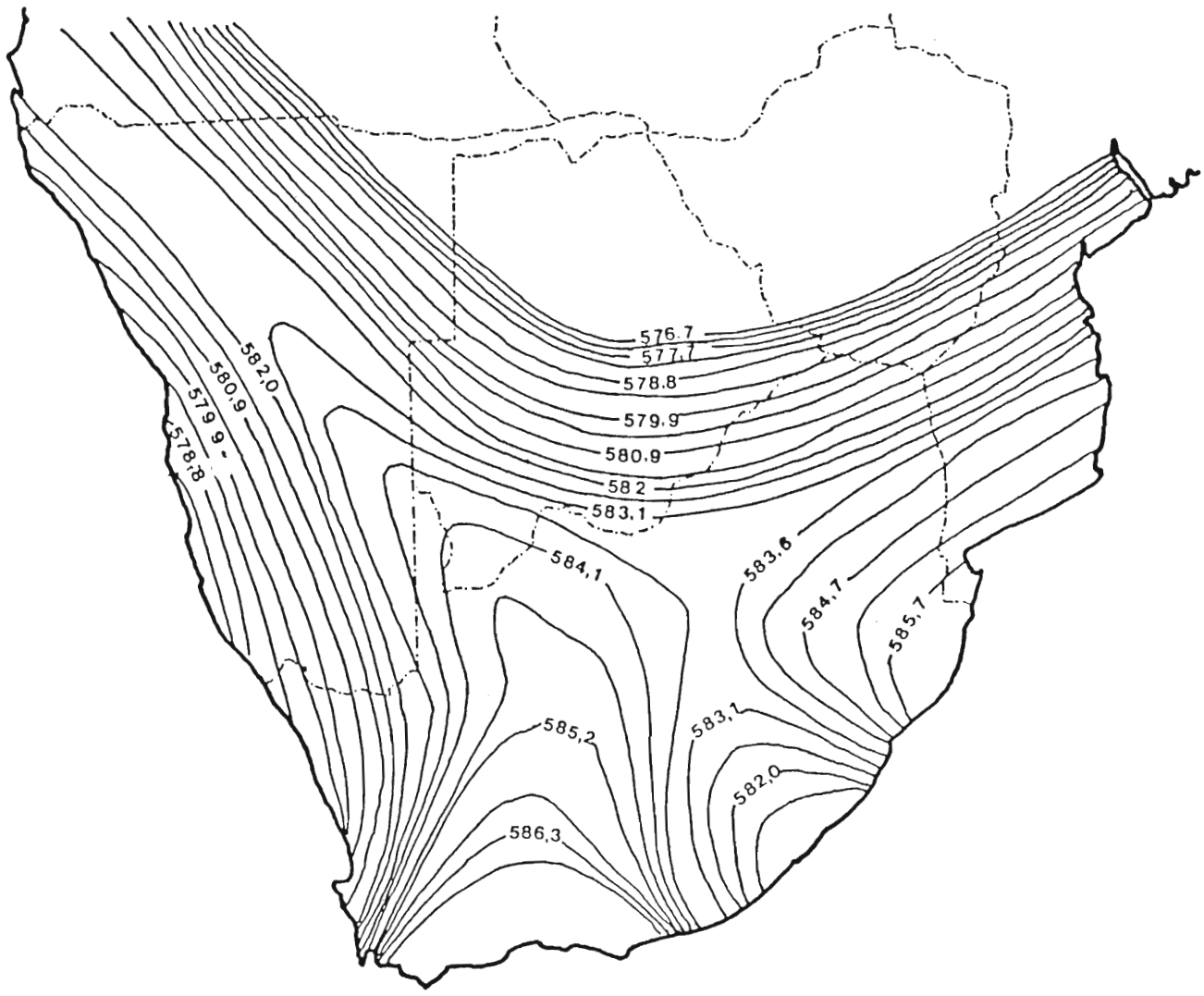


Fig. 3.8. Third degree (cubic) trend surface map of DOM in 24 C. penicillata (summer skins). Contour values represent wavelengths in nanometers: increasing values indicate a shift from a yellower to a redder coloration.

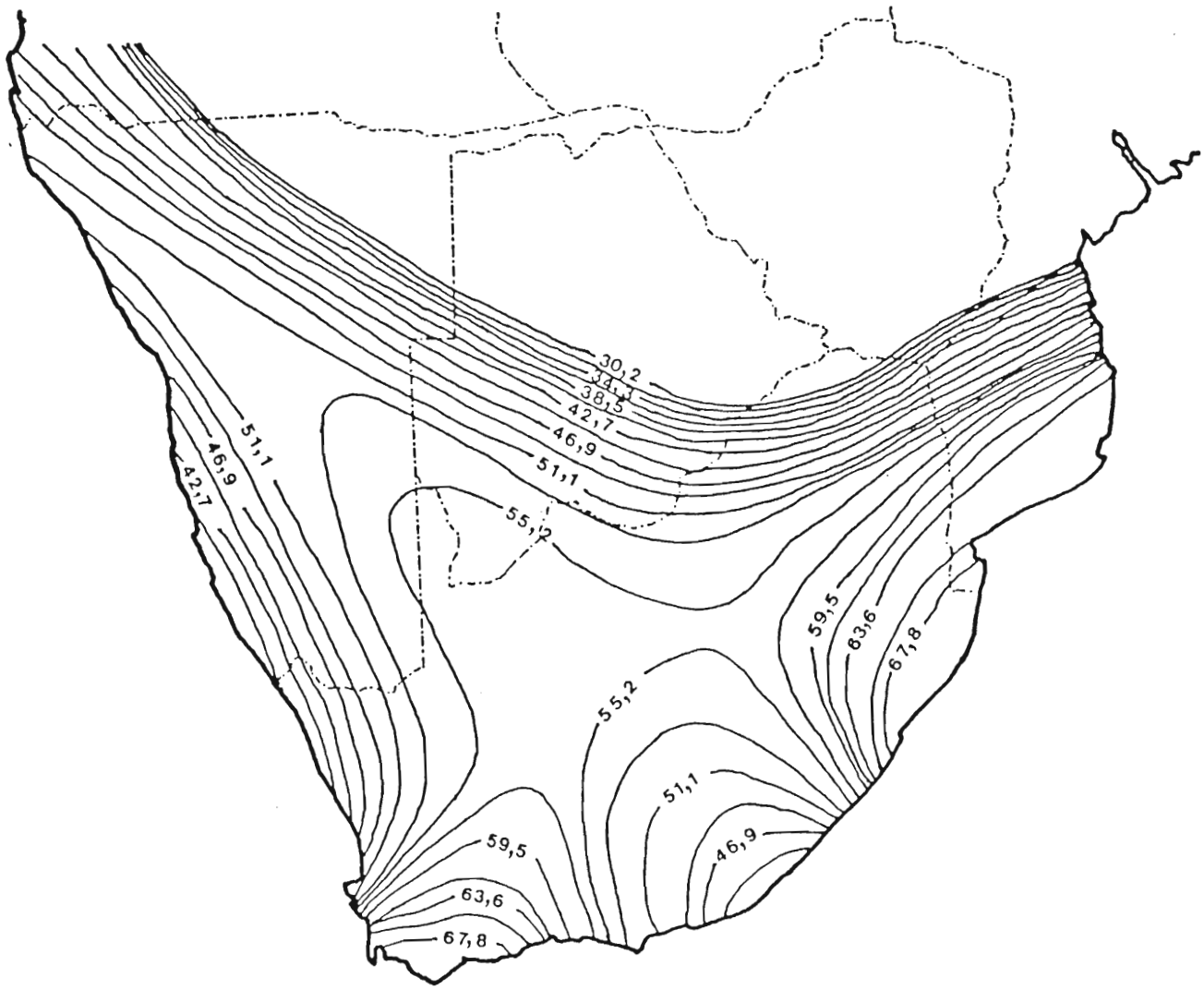


Fig. 3.9. Third degree (cubic) trend surface map of PUR in 24 C. penicillata (summer skins). Contour values represent colour saturation: increasing values represent increasing colour saturation.

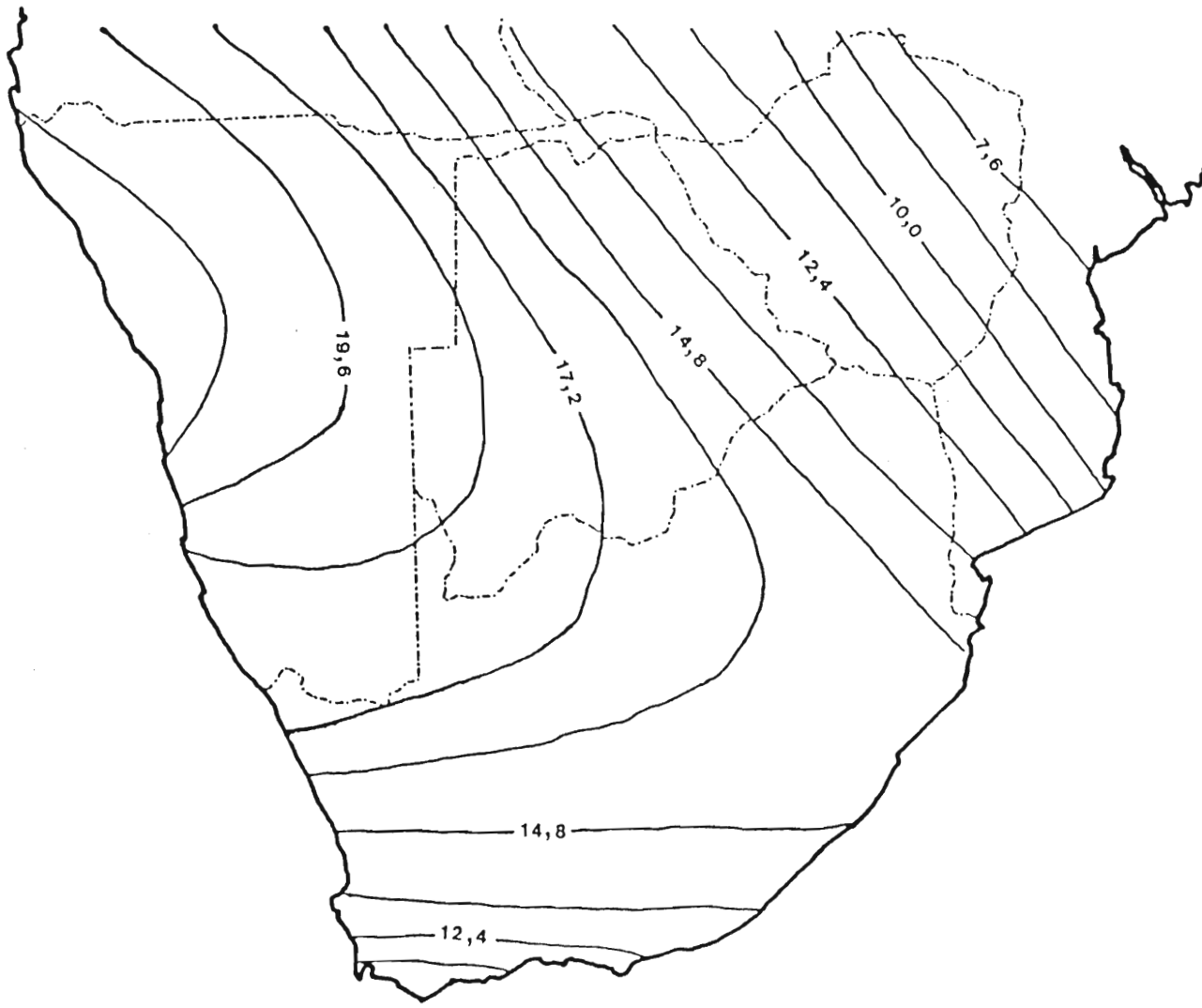


Fig. 3.10. Second degree (quadratic) trend surface map of BRT in 35 C. penicillata (winter skins). Contour values represent reflectance of light from a sample relative to a pure white standard (i.e., paleness): increasing values represent increasing paleness.

There is also a westerly component to the geographic pattern in DOM, with skins from the northwestern Cape and western Namibia tending to be yellower than more easterly localities; this is much more marked in the summer sample (Fig. 3.8). A similar westerly decrease in PUR is evident in the summer sample (Fig. 3.9) but not in the combined sample (Fig. 3.6). Also more evident in the summer samples is a tendency towards a redder (higher DOM) and richer (higher PUR) coloration in the eastern Transvaal and Natal. In addition there is a southeasterly decrease in DOM and PUR which probably results from the influence of a particular, semi-albinotic specimen from Carolina in the southeastern Transvaal. Patterns in DOM and PUR are therefore similar for the combined and the summer samples, although trends tend to be more pronounced in the summer sample.

A quadratic model explained a substantially greater proportion of total SS in BRT than did a linear model (26,6% rather than 18,2% in the winter sample; Table 3.4) although this could not be supported statistically ($F = 1,1$; $P > 0,05$). A cubic model only accounted for an additional 1,7% of explained SS, compared with the quadratic model, and can therefore be ignored as a suitable model for explaining trends in BRT. Although analyses of the summer sample explained higher proportions of the total variability in BRT than did the winter sample analyses, the absence of (observably paler) summer specimens from the arid western

Table 3.4

Regression statistics (explained sum of squares, as a percentage of the total (expl. % SS), F tests of this, first and second degrees of freedom (df1 and df2), and significance probability (P) of first to fourth degree polynomials describing geographical trend surfaces of DOM, BRT, and PUR in samples of C. penicillata study skins (* indicates significance at the 5% level, and ** at the 1% level; NS indicates statistical non-significance). Abbreviations of variables explained in Table 3.2.

			1ST DEGREE (Testing total expl. % SS)				2ND DEGREE (Testing added expl. % SS)				3RD DEGREE (Testing added expl. % SS)				4TH DEGREE (Testing added expl. % SS)			
Var.	Nature of sample	n	Expl. % SS	F	df1:df2	P	Expl. % SS	F	df1:df2	P	Expl. % SS	F	df1:df2	P	Expl. % SS	F	df1:df2	P
DOM	Combined	64	28,4	12,1	2:61	**	31,3	0,8	3:58	NS	37,6	1,4	4:54	NS	44,4	1,2	5:49	NS
	Winter	35	25,4	5,5	2:32	**	26,0	0,1	3:29	NS	43,2	1,9	4:25	NS	52,4	0,8	5:20	NS
	Summer	24	40,9	7,3	2:21	**	57,2	4,8	3:18	NS	83,2	5,4	4:14	**	89,5	1,1	5: 9	NS
BRT	Combined	64	17,5	6,5	2:61	**	23,6	1,6	3:58	NS	27,8	0,8	4:54	NS	38,7	1,7	5:49	NS
	Winter	35	18,2	3,6	2:32	*	26,6	1,1	3:29	NS	28,3	0,1	4:25	NS	49,1	1,6	5:20	NS
	Summer	24	38,5	6,6	2:21	**	39,9	0,1	3:18	NS	61,0	1,9	4:14	NS	64,4	0,2	5: 9	NS
PUR	Combined	64	25,0	10,2	2:61	**	27,4	0,6	3:58	NS	38,8	2,5	4:54	*	47,9	1,7	5:49	NS
	Winter	35	18,2	3,6	2:32	*	19,3	0,1	3:29	NS	25,0	0,5	4:25	NS	34,7	0,6	5:20	NS
	Summer	24	40,0	7,0	2:21	**	76,5	9,3	3:18	**	90,2	4,9	4:14	**	92,7	0,6	5: 9	NS

Cape resulted in a purely north-south trend in the summer sample, for all polynomial models. A quadratic model (of the combined-season or the winter sample) accommodated both north-south and east-west trends in BRT. The east-west component (which could be easily verified by visual observation of study skins) was not accommodated by a linear model. Since the quadratic model was the most consistent with observations of study skins, quadratic trend surface maps were presented for BRT (Figs 3.7 & 3.10).

The westerly increase in BRT (Figs 3.7 & 3.10) indicates a change from a darker to a paler pelage coloration. There is also a tendency for coat colour to darken (decreasing BRT) northwards and southwards from the central portion of the species range. Maps from combined and winter samples are very similar although a more predominant west-east pattern is evident in the winter map (compare Fig. 3.10 with Fig. 3.7). The winter sample was used, rather than the summer sample, for analysing BRT, because of the seasonal bias in the sample whereby most of the paler specimens from the drier western regions were collected during winter. Geographic trends in BRT were smoother than in DOM and PUR.

Although broad patterns of variation in colour variables did not vary between trend surface maps from combined and single-season samples, trend surfaces from the summer sample accounted for markedly higher proportions of explained

variability (i.e., sums of squares, SS) in all three variables than did winter or combined samples (Table 3.4). This was due to the virtual removal of seasonal effects in the summer sample.

Bivariate plots of OTUs

Bivariate plots of OTU means of all six colour variables (see Fig. 3.4 for geographic extent of OTUs) are shown in Fig. 3.11. With three exceptions (see caption of Fig. 3.4), OTUs correspond with the ranges of 12 subspecies previously recognized by Roberts (1951). Similar trends were indicated in bivariate plots of chart-derived and colorimeter-derived variables. While the plot of HUE and CHROMA indicates a somewhat smooth northerly cline in colour the plot of DOM and PUR suggests a more discontinuous pattern with a northern (OTUs 2, 8, 9, 10, 11) and a southern (OTUs 1, 3, 4, 5) group present. Specimens from northern Cape, the southern border of Botswana and southwestern Transvaal (OTUs 6 & 7) are somewhat intermediate in colour and represent a possible zone of intergradation between northern and southern populations, although they fall closer to the northern group (Fig. 3.11).

Study skins of specimens from the northwestern Cape (OTU 2; i.e., pallidior, in part) are markedly paler than skins of C. penicillata found elsewhere, as evidenced by bivariate

plots involving means of VALUE (Fig. 3.11a, c) and BRT (Fig. 3.11d, f). Specimens from more southerly localities in the western Cape (OTU3), referred by Roberts (1951) to pallidior, are clearly darker in colour than typical pallidior (OTU 2) and closer in value (as well as in hue and chroma) to OTU 1 (intensa + penicillata). Plots involving BRT (but not VALUE) show specimens from OTU 9 (cinderella, northern Namibia) to be grouped close to OTU 2, and distinct from other OTUs (Fig. 3.11d, f).

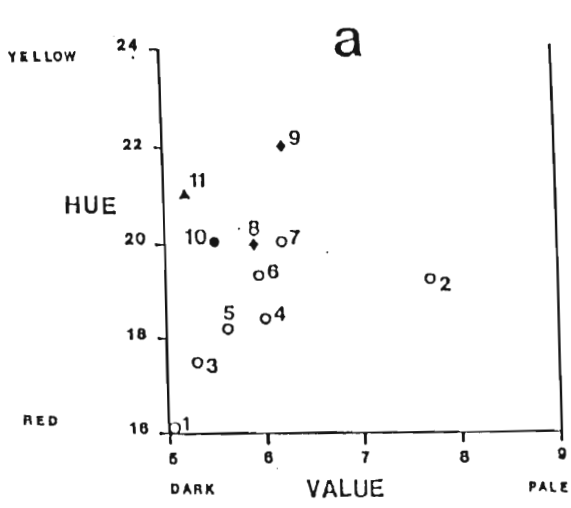
The modified Dice-Leraas grams in Fig. 3.12 illustrate means, ranges, two standard errors of the mean and one and a half standard deviations for each colour variable, for all 11 OTUs. The significance of mean OTU differences (as shown in bivariate plots) can only be established by taking into account intra-OTU variability in colour variables. In the case of OTUs having small samples sizes (OTUs 2, 3; $n = 3$), 95% confidence limits of the mean (i.e., two standard errors) exceeded the range in all variables (Fig. 3.12), making interpretation of these OTU means somewhat arbitrary. The extreme ranges in PUR (Fig. 3.12c) and CHROMA (Fig. 3.12f) in OTU5 resulted from a single partially albinotic individual from Carolina in the eastern Transvaal which had a very faded coat colour.

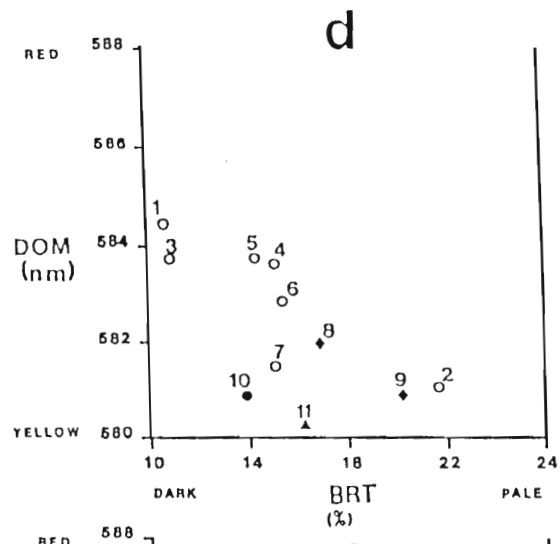
From analysis of variance (ANOVA) of OTU means in DOM, BRT and PUR, significant geographic variation was found in all

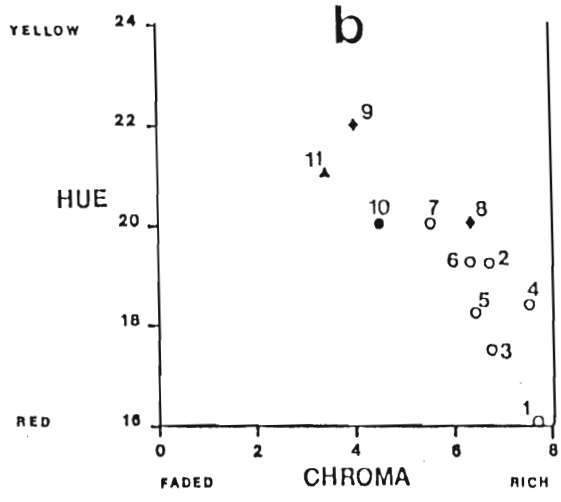
Fig. 3.11. Bivariate plots of OTU means for six colour variables in 64 C. penicillata. Numbers refer to OTUs in Fig. 3.4. Symbols refer to broad geographic regions: open circles - Cape Province, Orange Free State, southern Transvaal, Natal; closed circles - northern Transvaal; closed diamond - Namibia; closed triangle - Botswana. Abbreviations of variables explained in text.

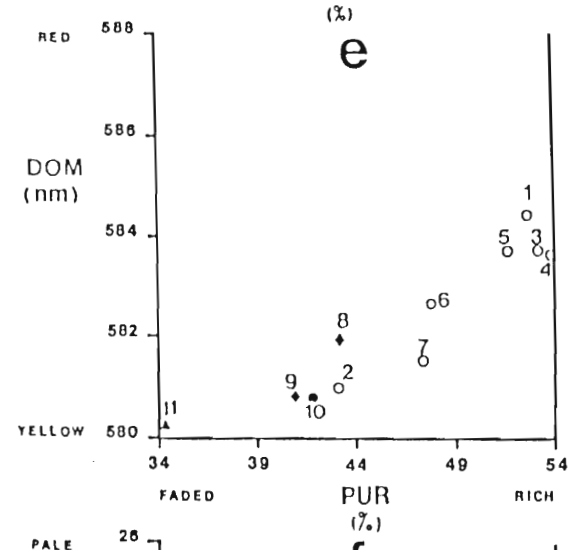
MUNSELL CHARTS

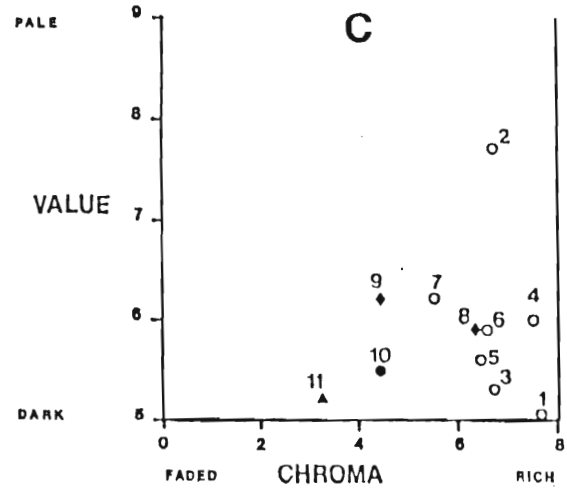
COLORIMETER











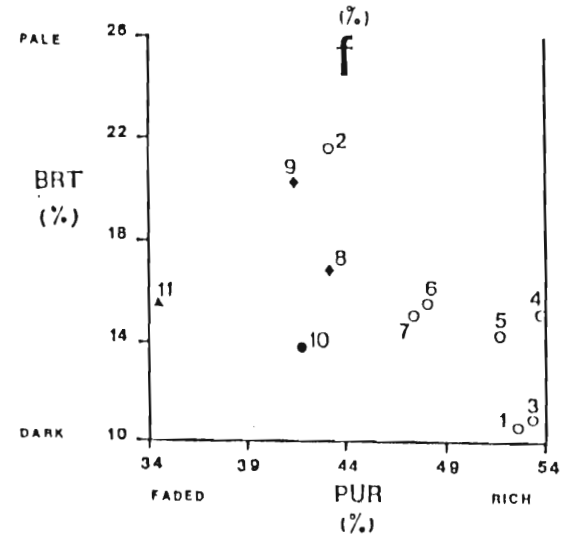
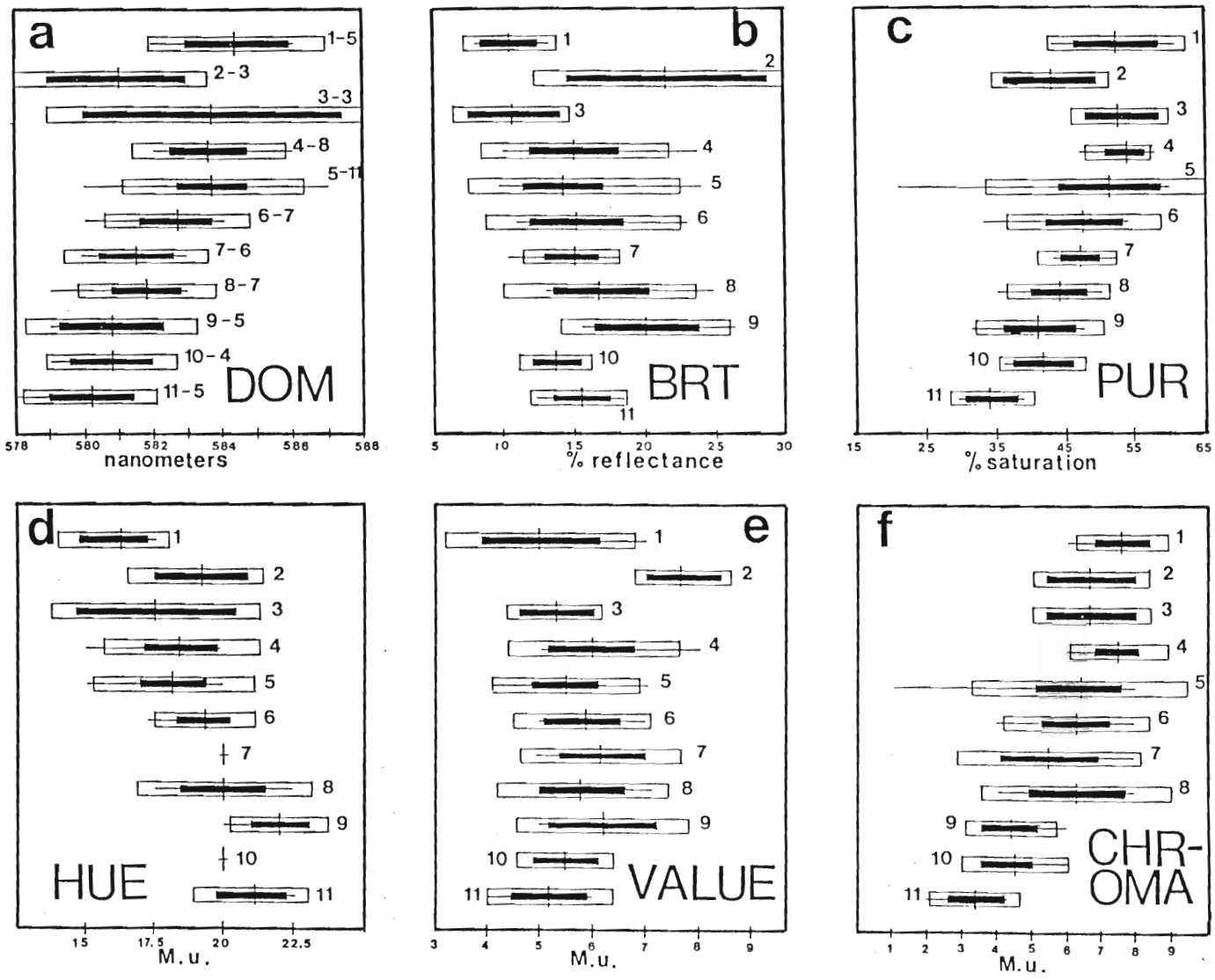


Fig. 3.12. Modified Dice-Leraas diagrams for six colour variables in 11 OTUs in a sample of 64 C. penicillata. The first number to the right of the gram is the OTU number (see Fig. 3.4), the second (in the top left box only) is the sample size. The horizontal line represents the range, vertical line the mean, open rectangle one and a half standard deviations, and closed rectangle two standard errors of the mean.


a
1-5
2-3
3-3
4-8
5-11
6-7
7-6
8-7
9-5
10-4
11-5
DOM
578 580 582 584 586 588
nanometers
b
1
2
3
4
5
6
7
8
9
10
11
BRT
5 10 15 20 25 30
% reflectance
c
1
2
3
4
5
6
7
8
9
10
11
PUR
15 25 35 45 55 65
% saturation
d
1
2
3
4
5
6
7
8
9
10
11
HUE
15 17.5 20 22.5
M.u.
e
1
2
3
4
5
6
7
8
9
10
11
VALUE
3 4 5 6 7 8 9
M.u.
f
1
2
3
4
5
6
7
8
9
10
11
CHR-
OMA
1 2 3 4 5 6 7 8 9
M.u.

three variables (F = 4,53, 2,96 and 4,17; P < 0,01; < 0,05 and < 0,01 respectively). Means that differ by their combined one and a half standard deviation limits approximate the 90% joint non-overlap rule (Mayr, Linsley, and Usinger, 1953: 148) which serves as an (albeit rather arbitrary) indication of subspecific differences. Figure 3.12 shows that, apart from OTUs 7 and 11 which differ in PUR at the 90% joint non-overlap level, means of adjacent OTUs generally overlap their combined one and a half standard deviation limits. These results indicate that the amount of intra-OTU variation precludes the confident delimitation of subspecies, based only on colorimetric data.

Metachromism

Geographical colour variation in *C. penicillata* can be interpreted in terms of the principle of metachromism or evolutionary change in mammalian tegumentary colours (Hershkovitz, 1968). Mammalian coat colours are derived from the distribution of two basic pigment types, orange phaeomelanins and black eumelanins, in individual hairs. Based on his study of South American marmosets and tamarins, Hershovitz proposed that the initial stages of metachromic evolution involved the modification of a primitive 'agouti' state (comprising alternating phaeomelanin and eumelanin zones in individual hairs) in two directions: complete saturation by either phaeomelanin or eumelanin pigments.

Further metachromic processes involved the progressive bleaching of these saturated pigments: phaeomelanins from rich reds through oranges and yellows to cream, and eumelanins from black through greys to white. This chromatic succession could be geographic or phylogenetic, and, in the case of marmosets, was genetically controlled and often non-adaptive.

In the yellow mongoose the coloration throughout is essentially an agouti one, since alternating phaeomelanin (orange) and eumelanin (black) zones are almost always present in individual guard hairs. Nevertheless, as indicated by the north-south pattern of variation in hue and chroma (see above discussion) phaeomelanins have undergone a metachromic, bleaching progression from a saturated orange-red coloration in the south to a bleached, yellow coloration in the north. Concordant with this difference is a tendency towards saturation by phaeomelanin pigments in southern specimens (fewer, narrower black bands in guard hairs) and towards saturation by eumelanin pigments in northern specimens (wider black bands). These differences give rise to the more grizzled appearance of northern specimens, particularly evident in Botswana specimens.

To a large extent variation in value in the yellow mongoose tends to reflect the amount of eumelanin in the pelage: in pale specimens having the highest colour value, eumelanin

zones in individual guard hairs are greatly restricted and in some animals may even be entirely absent (giving rise to a completely yellow coloration). While the northerly decrease in BRT (i.e., darker coloration) recorded in Figs 3.7 and 3.10 clearly reflects an increase in eumelanins associated with a more grizzled appearance, the southerly decrease is a result, not of increased eumelaninization, but rather of the presence of darker orange phaeomelanins.

Considerable evidence exists which suggests that metachromic processes are genetically controlled. Hershkovitz (1968) showed that hybrids of closely related species of marmosets have a coloration that is intermediate between the parental colorations. Changes identical to those involved in metachromic processes can be produced experimentally by different alleles at certain gene loci known to be involved in coat colour inheritance in mammals. Thus different alleles at the 'agouti' (or A) locus produce modifications of the basic agouti coloration resulting in progessive saturation by either phaeomelanins or eumelanins (Searle, 1968: 69), while alleles at the 'dilute' (or D) locus cause progessive desaturation or bleaching of pigments (Searle, 1968: 71). Sumner (1931) found that individuals of three subspecies of Peromyscus, which differed markedly in degree of paleness of the pelage (i.e., value), retained their typical coloration when bred for many generations in a constant environment. Crossbreeding experiments demonstrated

segregation of colour characters, and the probable existence of multiple genetic factors controlling coat colour.

It is of significance that the quantitative colour variables used in this study appear to directly measure metachromic parameters such as the relative amounts of eumelanin and phaeomelanin in the pelage and the degree of bleaching of phaeomelanins. Analysis of these variables can therefore reveal the course of metachromic evolution in a particular taxon, as has been attempted in the present study. It is suggested that combining the precise methodological framework of the Munsell Colour System (including I.C.I. tristimulus colorimetry) with the theoretical framework embodied in the concept of metachromism provides an objective and operational foundation for future studies involving coat colour variation in mammals.

Ecological correlates of colour

Results

From multiple linear regression analysis (Table 3.5), the combined influence of the three climatic parameters explained significant percentages of total variability in DOM (23%; $\underline{F} = 6,0$; $\underline{P} < 0,01$), BRT (15%; $\underline{F} = 3,5$; $\underline{P} < 0,05$) and PUR (20%; $\underline{F} = 5,0$; $\underline{P} < 0,01$). From $\underline{t}$-tests of partial regression coefficients, mean annual temperature (MAT) was

significantly associated with DOM and PUR (Table 5: $\underline{r}_p$ = -0,4 and -1,7; $\underline{t}$ = 2,9 and 3,0 respectively; $\underline{P} < 0,01$), while BRT was not significantly associated with any of the climatic variables (Table 5: $\underline{P}$ always > 0,05).

From comparison of trend surface maps (Figs 3.5--3.10) and maps of environmental variables (Figs 3.13 & 3.14), total daily radiation (TDR) and mean annual temperature (MAT; Fig. 3.14) both exhibit a north-south pattern of variability over Southern Africa, and may partly explain the predominantly latitudinal pattern of variation in DOM (Figs 3.5 & 3.8) and PUR (Figs 3.6 and 3.9). This relationship is confirmed statistically in the case of temperature, as noted above (data on TDR were not available from many climate stations in Southern Africa so that this variable was not included in multiple regression analysis).

The trend surface maps for BRT (Figs 3.7 & 3.10), bear some resemblance to the pattern of variation in actual annual rainfall (AAR) over Southern Africa (Fig. 3.14) and follow the pattern predicted by Gloger's rule (Kuhnelt, 1965), in that paler colours are associated with the drier western regions of the subcontinent (Namaqualand and the pro-Namib), and darker colours with the more humid, higher rainfall eastern parts. The 100 mm isohyet is particularly important in influencing BRT. This is most clearly evidenced in the strikingly pale-coloured specimens from the lower Orange

Table 3.5

Results of multiple linear regression analysis of DOM, BRT and PUR (dependent variables) on three climatic variables (independent variables), actual annual rainfall (mm; AAR), mean annual temperature (°C; MAT) and relative humidity at 08h00 (%; RH) in 64 *C. penicillata* study skins from 53 localities in Southern Africa. R^2 = coefficient of determination; F values refer to ANOVA tests of significance of explained variability; r_p = partial regression coefficient; t refers to t-tests of significance of r_p; P = significance probability (NS: non - significant; *: significant at the 5% level; **: significant at the 1% level).

				CLIMATE VARIABLES								
COLOUR VARIABLE	R^2	F	P	AAR (mm)			MAT (°C)			RH (%)		
				r_p	t	P	r_p	t	P	r_p	t	P
DOM	0,23	19,6	**	0,001	0,5	NS	-0,4	2,9	**	0,002	0,1	NS
BRT	0,15	3,5	*	-0,002	0,6	NS	0,2	0,8	NS	-0,1	1,7	NS
PUR	0,20	5,0	**	-0,002	0,3	NS	-1,7	3,0	**	0,02	0,2	NS

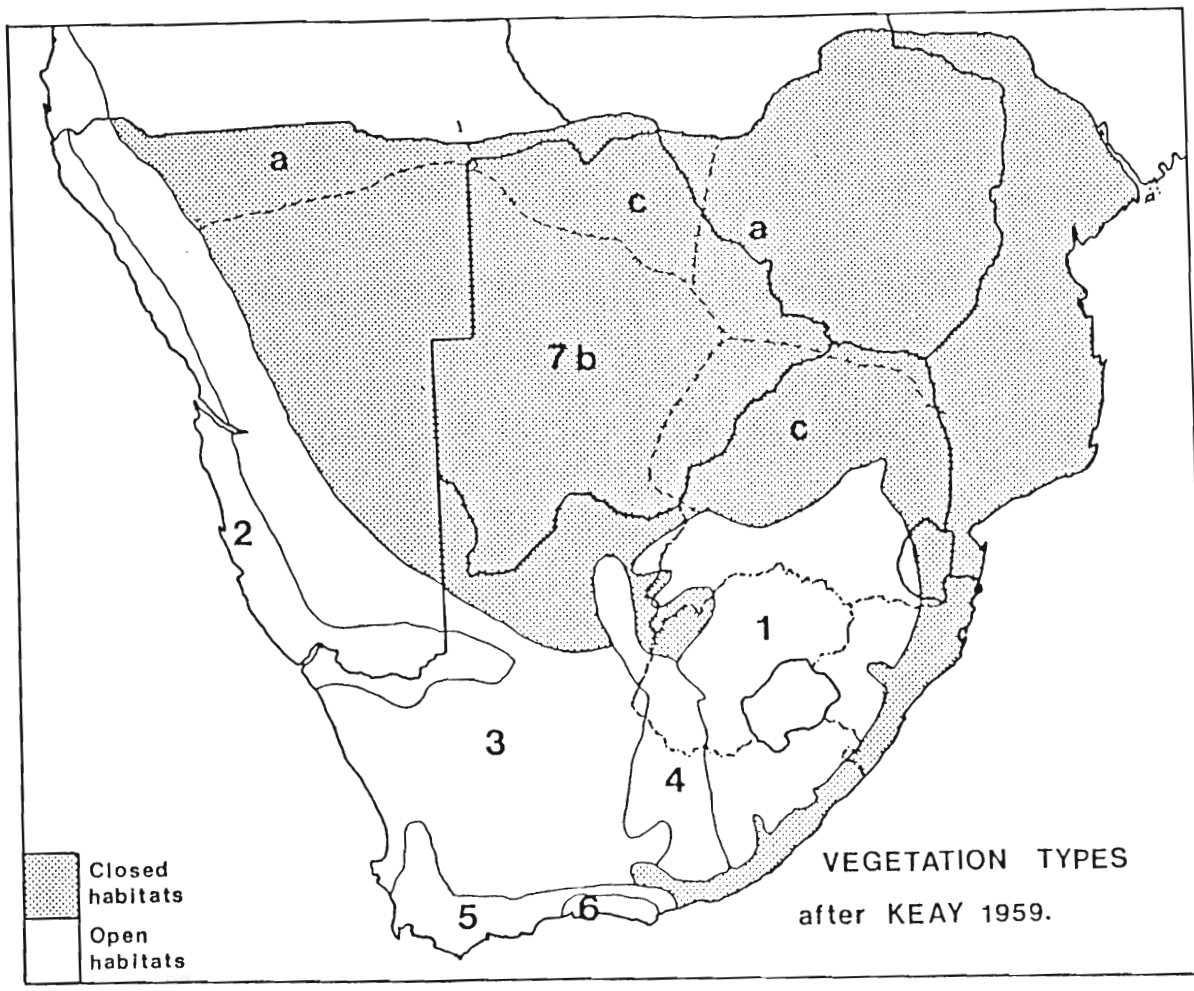
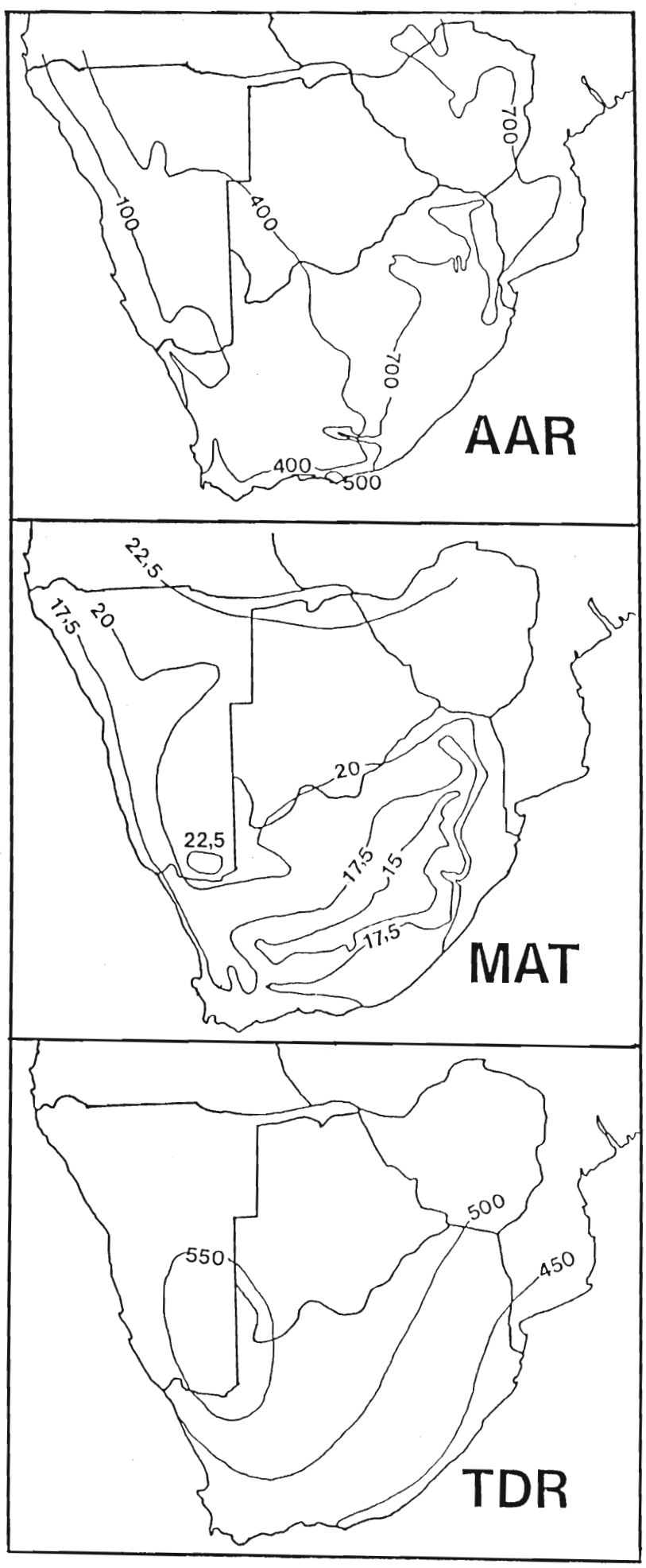


Fig. 3.13. Map showing distribution of major vegetation types in Southern Africa (after Keay, 1959). 1 - grassland; 2 - Namib Desert; 3 - semidesert steppe (mainly Karroo shrubs); 4 - transitional Karroo; 5 - Cape maccia; 6 - evergreen forest; 7 - woodland: a - mopane; b - Acacia; c - undifferentiated.

Fig. 3.14. Climatic maps showing variation over Southern Africa in actual annual rainfall (mm; AAR), mean annual temperature (°C; MAT) and total daily radiation (cal. cm^{-3} day^{-1}).


100
400
700
700
400
500
AAR
22,5
20
17,5
20
22,5
17,5
15
17,5
MAT
500
550
450
TDR

River valley, much of which receives less than 100 mm rainfall (OTU2; see Figs 3.11 & 3.12). Meester (1963) found that 20 or 24 inch isohyets corresponded with subspecies boundaries separating arid-adapted western and moisture-adapted eastern subspecies in three species of shrews of the genus Crocidura. A pale Namib subspecies of suricate, Suricata suricatta marjoriae, is currently recognised (Meester et. al., 1986). As the Namib Desert corresponds with the region receiving less than 100 mm in Namibia, the 100 mm isohyet corresponds with the subspecies limits of S. s. marjoriae. Since the distribution of C. penicillata does not penetrate the Namib desert, and the species occurs in regions receiving less than 100 mm only in the lower Orange River valley, pallidior (OTU2; Fig. 3.4) may in fact merit subspecific recognition, with the 100 mm isohyet serving as a subspecies boundary.

This apparent relationship between BRT and AAT is not borne out statistically by multiple linear regression, as partial regression coefficients for both relative humidity (RH) and actual annual rainfall (AAR) are not statistically different from zero (Table 3.5, and above). Non-significance probably arises from the north-south component of variation in BRT (Figs 3.7 & 3.10), which is uncorrelated with the pattern of variation in AAT over Southern Africa. It may be that a combination of climatic factors determines variation in value (i.e., paleness) in C. penicillata, although rainfall

(and humidity) probably plays a dominant role.

Adaptive function of coat colour

It is difficult to establish whether the correlations discussed above have any causal significance, and if so, whether they have a genetic (adaptive or non-adaptive) or non-genetic basis. It is a well-established fact that light (in particular ultraviolet light) causes fading of colours in unprotected displays of natural history specimens, and as yellow mongooses are diurnal, regional differences in intensity of direct solar radiation (i.e., TDR) may play an important part in explaining colour variation in the species. However, as new summer hairs (which have had little exposure to sunlight) show marked differences geographically, and as there is not a direct relationship between any of the trend surface maps (Figs 3.5--3.10) and the map for TDR (Fig. 3.14: the zone of maximum TDR in southern Namibia does not correspond with extreme values in DOM, PUR or BRT; furthermore the uneven rate of change of DOM and PUR is not reflected by parallel changes in TDR), factors over and above the direct influence of ultraviolet radiation are important in explaining geographic patterns of colour variation in the species.

Wemmer (in Lynch, 1981) comments that coat colour in mongooses is a character that is obviously responding to

selection. Two possible adaptive functions of coat colour in mammals are camouflage and thermoregulation. Examples of concealing coloration in mammals include the melanistic coloration of Galerella sanguinea nigrata inhabiting the black-coloured rocky terrain of northwestern Namibia (Lynch, 1981), melanistic races of five rodent species inhabiting the Malpais black lava bed in the Tularosa Basin of New Mexico (Hershkovitz, 1968) and the pale-coloured subspecies Peromyscus polionotus leucocephalus occupying the extremely white quartz sands of Santa Rosa island off north western Florida (Sumner, 1930).

Coat colour variation in C. penicillata does not show any obvious correlations with soil colour. The rich, reddish-coloured Kalahari sands of Botswana are associated with a faded, yellow pelage coloration, the opposite of what one would expect on the basis of soil colour. Lynch (1981) has suggested that the brighter coat colours found in Galerella sanguinea (compared to the grey coloration that predominates in Galerella pulverulenta), result from the fact that the latter relies more on vegetation cover for concealment. There is therefore greater selection for concealing colours, and hence a wider range of colour variation, in G. sanguinea occupying more exposed open habitats, than in G. pulverulenta occupying less exposed habitats. It is possible that the richer, tawny coloration of C. penicillata from more open (grassland, karroid and semi-desert) habitats has

a concealing function against the generally tawny-coloured soil and vegetation background, whereas C. penicillata from treed Kalahari sandveld habitats in Botswana (Fig. 3.13) are more reliant on tree cover for concealment from avian predators. The redder, richer coloration of C. penicillata from the southern Cape, compared to the Orange Free State and southern Transvaal (Figs 3.5, 3.6, 3.8, 3.9) could be explained by comparing the redder coloration of an exposed soil background in sparsely vegetated Karroo habitats to the yellower coloration of a grassy background in more densely vegetated grassland habitats. Very red specimens may be found in parts of southern Transvaal, but where these were encountered in the field in the Cullinan district they were found to occupy burrows on the edges of cultivated fields which remained fallow for part of the year. Coat colour bore a strong resemblance to the colour of the soil in the cultivated lands. Specimens collected in an undisturbed nature reserve in the nearby Onderstepoort district were found to have a yellower coloration. Thus it is possible that in exposed habitats, coat coloration may have an adaptive function in providing concealment for individuals. However, this remains to be established on the basis of detailed field studies.

Pelage coloration may play a part in thermoregulation in that heat load resulting from solar radiation in the visible spectrum may be reduced by having a highly reflective (i.e.,

white or pale) pelage. However, since most heating results from radiation in the infrared range, and all objects are black bodies in this respect, the significance of white colours in reducing heat load is questionable. If thermoregulation was an important factor in explaining coat colour variation in the yellow mongoose one would expect high BRT (which measures total reflectance from a sample relative to a pure white standard) to be associated with higher temperatures. As there is no correlation between trend surface maps of BRT (Figs 3.8 & 3.10) and the map for MAT (Fig. 3.14), thermoregulation does not appear to play a significant role in explaining colour variation in C. penicillata. This is to be expected as yellow mongooses are capable of escaping the danger of overheating by resting in cool burrows during the heat of the day. The significant association between MAT and both DOM and PUR (Table 5, and above) is difficult to explain in terms of thermoregulation and need not have any causal significance.

The close correlation between the 20 °C isotherm (Fig. 3.14) and the zone of rapid geographic change in trend surface maps of DOM and PUR (Figs 3.5, 3.6, 3.8, 3.9) may be an indirect effect of the relationship between temperature and other factors such as vegetation type. The western and southern limits of closed (treed) vegetation types (Fig. 3.13) in Southern Africa also corresponds with the zone of rapid geographic change of DOM and PUR. Populations of

mongooses occupying arid Acacia sandveld (usually on Kalahari sands) in northern Namibia, Botswana and northern Transvaal have a markedly duller, yellower, and somewhat more grizzled coat colour than more southerly populations, as described above. The population in northern Transvaal (OTU 10: coombsii of Roberts, 1951) forms a geographic isolate, occupying a remnant block of Kalahari sands just north of the Soutpansberg mountain range. As C. penicillata is ecologically restricted to the South West Arid biome (Davis, 1962), the typical mesic savanna of northern Transvaal and eastern Botswana forms an ecological barrier separating this population from those to the west and south. Specimens from the northern Transvaal (OTU 10) bear a much closer resemblance in colour (see Fig. 3.11e; and in size: Taylor and Meester, in preparation) to true Kalahari specimens (OTU 11) than to specimens from grassland habitats in southern and central Transvaal (OTU 5).

Based on the distribution of rupicolous lizards (Platysaurus spp. and Cordylus warreni subspp.), Broadley (1978) plotted an hypothetical maximum eastwards limit of aeolian sand during the Pliocene, which includes most of the Transvaal. According to Broadley, Kalahari sand movement, in producing geographical isolates in rocky outcrop refugia, was the principal factor promoting speciation in the genus Platysaurus. Eastwards movement of aeolian sands was also implicated in the distribution of subspecies of the legless

skink Typhlosaurus lineatus (Broadley, 1968; Jacobsen 1987). The nominate race occurs in the Kalahari proper, while three further subspecies occur in relict pockets of sand north of the Soutpansberg and in western Zambia (T. l. subtaeniatus is sympatric with C. penicillata). Broadley hypothesized that during an interpluvial period T. lineatus extended its range eastwards. During the subsequent pluvial the ranges shrank leaving isolated populations which have subsequently diverged morphologically.

It is likely that a similar sequence of historical events accounted for the observed patterns of colour variation (and size variation: Taylor and Meester in preparation) in C. penicillata. Certainly the isolated population occurring on a relict pocket of sand in the northern Transvaal must have arisen from a previous eastwards extension of the species' range associated with the postulated eastwards migration of Kalahari sands mentioned above. Cooke (1962) has proposed that marked vegetational changes occurred over Africa during pluvial and interpluvial periods of the Pleistocene. During pluvial periods the present area of Kalahari sandveld may have contracted somewhat, and this area may have been bordered on the west and east by mesic bushveld similar to that presently covering most of the northern Transvaal and eastern Botswana. These changes would have led to some degree of contraction and fragmentation of the previous range of C. penicillata, (since the species is generally

excluded from mesic bushveld habitats), and to a reduced area of contact between populations occurring on Kalahari sands and populations to the south inhabiting Karroo scrub and grassland habitats. Under these conditions of partial (or even complete) geographic isolation, it is possible that genetic divergence was accompanied by metachromic evolution (through dilution of phaeomelanin pigments, and an increase in eumelanins; see above discussion on metachromism). Colour changes may represent adaptations to different local environments, as discussed above, or they may simply have originated as pleiotrophic effects of unrelated genetic changes affecting morphology, behavior or physiology.

While such an hypothesis would help to account for the pattern of variation in trend surface maps of DOM and PUR (Figs 3.5, 3.6, 3.8, 3.9), it may be unrealistic to assume that vegetational changes during the Pleistocene were as profound as envisaged above, given the duration of Pleistocene pluvials and interpluvials (C. K. Brain, postscript to Cooke, 1962). An alternative hypothesis, which also assumes a genetic origin of colour differences, recognizes a parapatric rather than an allopatric origin of metachromic divergence. Given that the primary zone of differentiation in trend surface maps of DOM and PUR corresponds closely to the 20 °C isotherm, as well as to the westward and southward limits of Kalahari sands and related vegetational associations, steep genetic clines may have

arisen along selection gradients as predicted in certain population genetical computer models (Endler, 1977).

Neither of the above models appear to account for the longitudinal trends in DOM and PUR (most evident in summer sample trend surface maps; Figs 3.8 & 3.9), which are not correlated with a transition to Kalahari sands (as is the case for the primary latitudinal trend). The westward decrease in DOM and PUR appears to be associated with an increase in BRT (paler skins from the north-western Cape are also yellower and duller). This inverse relationship between BRT and DOM and PUR is also demonstrated in the easterly increase in DOM and PUR, with decreasing BRT (darker skins from the eastern Transvaal tend to be redder and richer. The additional trend, in summer trend surface maps, for DOM and PUR to decrease toward the south-east results from the effect of a single extreme individual, and can be ignored for the purpose of this discussion). On the other hand the northerly decrease in DOM and PUR is accompanied by a decrease in BRT (not an increase as is the case in the north-western Cape) associated with the grizzled appearance of specimens from Botswana, northern Transvaal, and northern Namibia. Thus populations occurring on Kalahari sands are distinguished (in having a darker, grizzled coloration) from pale-coloured populations from the north-western Cape having similar values for DOM and PUR. Considering all three variables, therefore, Kalahari populations are conspicuously

different from other populations, and the arguments above relating to the divergence of northern and southern populations, still apply.

ACKNOWLDEGEMENTS

Dr C. K. Brain, Director of the Transvaal Museum, is gratefully acknowledged for making available the facilities of the Transvaal Museum during the course of this study. We are also very grateful to Mr A. Timms of the Paints Division of the South African Bureau of Standards for allowing us to make use of their tristimulus colorimeter. The financial assistance of the Foundation for Research Development (F.R.D.) in making this project possible is gratefully acknowledged.

REFERENCES

BLACKITH, R. E. and REYMENT, R. A., 1971. Multivariate morphometrics. Academic Press, London and New York.

BOWERS, D. E., 1956. A study of methods of colour determination. Systematic Zoology **5**: 147--160, 182.

BROADLEY, D. G., 1968. A revision of the African genus Typhlosaurus Wiegmann (Sauria: Scincidae). Arnoldia

(Rhodesia) **3**: 1--20.

BROADLEY, D. G., 1978. A revision of the genus Platysaurus A. Smith (Sauria: Cordylidae). Occasional papers of the National Museums and Monuments of Rhodesia, Series B, **6**: 129--185.

COOKE, H. B. S., 1962. The Pleistocene environment in Southern Africa. Hypothetical vegetation in Southern Africa during the Pleistocene. Annals of the Cape Provincial Museums 2: 11--15.

DAVIS, D. H. S., 1962. Distribution patterns of Southern African Muridae, with notes on some of their fossil antecedents. Annals of the Cape Provincial Museums **2**: 56--76.

DEBLASE, A. F., and MARTIN, R. E., 1981. A manual of mammalogy, 2nd edn. Wm. C. Brown Company Publishers, Dubuque, Iowa.

DEMETER, A., and LAZAR, P., 1984. Morphometric analysis of field mice Apodemus: character selection for routine identification (Mammalia). Annales historico-naturales Musei nationalis hungarici **76**: 297--322.

DEPARTMENT OF METEOROLOGICAL SERVICES, 1984. Climatological summaries for Botswana. Department of Meteorological Services, Botswana Government.

DIPPENAAR, N. J. (Personal communication). Transvaal Museum, P. O. Box 413, Pretoria, 0001.

ENDLER, J. A., 1977. Geographic variation, speciation and

clines. Princeton University Press, Princeton, New Jersey.

GENOWAYS, H. H., 1973. Systematics and evolutionary relationships of spiny pocket mice, genus Liomys. Special Publications, Museum, Texas Tech University **5**: 1--368.

HALL, E. R., 1981. The mammals of North America, 2 vols, 2nd edn. John Wiley, New York.

HARDY, A. C., 1936. Handbook of colorimetry. The Technology Press, Massachusetts Institute of Technology, Cambridge, Massachusetts.

HERSHKOVITZ, P., 1968. Metachromism or the principle of evolutionary change in mammalian tegumentary colours. Evolution **22**: 556--575.

JACOBSEN, N. H. G., 1987. A new subspecies of Typhlosaurus lineatus Boulenger 1887 (Reptilia: Scincidae) from Venda, Southern Africa. South African Journal of Zoology **22**: 318--320.

JOHNSTON, R. L., 1978. Multivariate statistical analysis in geography. Longman, England.

KEAY, R., W. J., 1959. Vegetation map of Africa south of the Tropic of Cancer. Oxford University Press, London.

KÜHNELT, W., 1965. Gundriss der Ökologie. Veb Gustav Fischer Verlag, Jena.

LUNDHOLM, B. G., 1955. A taxonomic study of Cynictis penicillata (G. Cuvier). Annals of the Transvaal Museum **22**: 305--319.

LYNCH, C. D., 1981. The status of the Cape grey mongoose, Herpestes pulverulentus Wagner, 1839 (Mammalia: Viverridae). Navorsinge van die Nasionale Museum Bloemfontein 4: 121--168.

MARCUS, L. F. and VANDERMEER, J. H., 1966. Regional trends in geographic variation. Systematic Zoology **15**: 1--13.

MAYR, E., LINSLEY, E. G. and USINGER, R. L., 1953. Methods and principles of systematic zoology. McGraw-Hill, New York.

MEESTER, J., 1963. A systematic revision of the shrew genus Crocidura in Southern Africa. Transvaal Museum Memoir No. 13, Transvaal Museum, Pretoria.

MEESTER, J. A. J., RAUTENBACH, I. L., DIPPENAAR, N. J. and BAKER, C. M., 1986. Classification of Southern African mammals. Transvaal Museum Monograph No. 5. Transvaal Museum, Pretoria.

MILLER, R. S., 1958. The Munsell System of colour notation. Journal of mammalogy **39**: 278--286.

MUNSELL, A. H., 1954. A colour notation, 10th ed. Munsell Colour Co. Inc., Baltimore, Md.

NICKERSON, D., 1946. Colour measurement and its application to the grading of agricultural products. A handbook on the method of disc colorimetry. U. S. Department of Agriculture, Miscellaneous Publications **580**: 1--62.

OYAMA, M., TAKEHARA, H. and OOI, Y., 1967. Revised standard soil colour charts. Published in cooperation with the Japan Colour Research Institute.

PIMENTEL, R. A. and SMITH, J. D., 1986a. BioΣtat I. A tutorial manual. Sigma Soft, Placentia, CA.

PIMENTEL, R. A. and SMITH, J. D., 1986b. BioΣtat II. A tutorial manual, 2nd edn. Sigma Soft, Placentia, CA.

RIDGEWAY, R., 1912. Colour standards and colour nomenclature. Published by the author, Washington, D. C.

ROBERTS, A., 1951. The mammals of South Africa. Trustees of 'The Mammals of South Africa Book Fund', Johannesburg.

SEARLE, A. G., 1968. Comparitive genetics of coat colour in mammals. Logos/Academic, London/New York.

SMITHE, F. B., 1974. Naturalist's colour guide supplement. The American Museum of Natural History, New York.

SMITHERS, R. H. N., 1983. The mammals of the Southern African subregion. University of Pretoria, Pretoria.

SNEATH, P. H. A. and SOKAL, R. R., 1973. Numerical taxonomy. W. H. Freeman, San Francisco.

SOKAL, R. R. and ROHLF, F. J., 1981. Biometry, 2nd edn. W. H. Freeman and Company, San Francisco.

SUMNER, F. B., 1927. Linear and colorimetric measurements of small mammals. Journal of Mammalogy **8**: 177-206.

SUMNER, F. B., 1930. Genetic and distributional studies of three subspecies of Peromyscus. Journal of Genetics **23**: 275-376.

THORPE, R. S., 1976. Biometric analysis of geographic variation and racial affinities. Biological Reveiws **51**: 407-452.

WB35, 1972. District rainfall for South Africa and the annual march of rainfall over Southern Africa. Weather Bureau, Department of Transport.

WB40, 1986. Climate of South Africa: statistics up to 1984. Weather Bureau, Department of Environmental Affairs.

CHAPTER 4

MORPHOMETRIC VARIATION[1]

INTRODUCTION

The yellow mongoose Cynictis penicillata is a diurnal, burrow - dwelling carnivore endemic to, and widely distributed throughout, Southern Africa (Smithers, 1983). Owing to marked geographic differences in size and colour, as many as 12 different subspecies have been recognised in the past (Shortridge, 1934; Allen, 1939; Ellerman, Morrison - Scott and Hayman, 1953; Roberts, 1951). In a study of C. penicillata involving measurements of external, cranial, dental and pelage characters, Lundholm (1955) argued that variation in size and colour followed a smooth cline and that the species should therefore be considered as monotypic, a view that is currently held (Meester, Rautenbach, Dippenaar and Baker, 1986). A taxonomic revision of the species is necessary as: 1) Lundholm's (op. cit.) study was based on only a few specimens for most of the subspecies; 2) Statistical techniques were not employed; 3) Lundholm's graphs are open to interpretation: if subspecies are arranged from north to south (instead of west to east as in Lundholm's graphs) then two distinct groups of subspecies can be distinguished. In fact Lundholm mentions (1955: 318, 319) that 'It is possible that there is a rather sharp

1. This chapter, together with abstract, is essentially the paper by P. J. Taylor and J. Meester, that has been submitted to Annals of the Transvaal Museum under the full title 'Morphometric variation in the yellow mongoose Cynictis penicillata

change between forms adapted to the southern and the northern vegetation type, but more material will solve this problem'.

In species (or superspecies) having continuous distributions (as in Cynictis) the limits of subspecies (or parapatric species) would be expected to be represented by transition zones coinciding with partial or complete, present or past, geographical or ecological barriers (Lidicker, 1962; Endler, 1977; Moore, 1977). Thorpe (1984a) has pointed out that transition zones (stepped clines, hybrid zones, zones of intergradation) are the focus of attention in many evolutionary studies, particularly with respect to concepts of speciation (see Endler, 1977; Moore, 1977; Barton and Hewitt, 1985 for recent reveiws of clines and transition zones). Determining whether a transition zone is primary or secondary in nature may help to demonstrate whether speciation is parapatric (Ender, 1977; White, 1978) or allopatric (Mayr, 1963; 1982) in nature. However the origin of a transition zone (primary or secondary) cannot be deduced from its properties, such as gradient and width (Endler, 1977). Using phylogenetic analysis to reconstruct the historical pattern of range expansion in the grass snake (Natrix natrix), Thorpe (1984a) was able to distinguish between transition zones that were due to secondary contact of populations, and those that were not. This approach also allows one to distinguish between current ecological and

historical (phylogenetic) factors as the primary cause of observed patterns of geographic differentiation.

The aims of this study can be summarised as follows: 1) to examine the extent of individual, age and secondary sexual craniometric variation in a single population of C. penicillata; 2) to conduct a taxonomic revision of the species based on morphometric relationships of populations; 3) to determine the geographic extent of any discrete taxa (phena), and to demonstrate the existence of transition zones (subspecies or species boundaries) or possible zones of sympatry between them; 4) to attempt to reconstruct the historical pattern of range expansion in C. penicillata, using a cladistic approach (Thorpe, 1984a, b), and, from this, to attempt to explain the origin of transition zones and the pattern and mode of speciation in the species.

MATERIAL AND METHODS

Material

Skulls were obtained from the following institutions: Transvaal Museum, Pretoria (TM); National Museum, Bloemfontein (NM); State Museum, Windhoek (SM); Kaffrarian Museum, King William's Town (KM); Natal Museum, Pietermaritzburg (NAM); National Museum, Bulawayo (NMZ); British Museum of Natural History (BM); Durban Museum of

Natural History (DM); MacGregor Museum, Kimberley (MM). A total of 734 skulls from 272 localities was examined (sample sizes of each locality are listed in Taxonomy section, under subspecies accounts).

Fourteen cranial measurements were taken on each skull using digital callipers with a resolution of 0.01mm. All measurements were rounded off to three significant figures. The procedure used for selecting craniometric variables in this study, based on cluster analysis of inter - variable correlation coefficients from a larger initial sample of 48 variables, is described in detail in Appendix I. Full descriptions and illustrations of all measurements are given in Appendix I. The following 14 uncorrelated measurements are those selected for morphometric analysis (Numbers in brackets correspond with those given in Fig. 4.13 of Appendix I).

MTR (2) Mandibular tooth row, from anterior edge of P_2 alveolus to posterior edge of M_2 alveolus. **MRH (3)** Mandibular ramus height, from dorsal edge of coronoid process to ventral edge of angular process. **CBL (10)** Condylobasal length of skull. **ZYW (18)** Greatest zygomatic width, taken between outer margins of zygomatic arches perpendicular to skull axis. **BCW (19)** Brain case width, at dorsal root of squamosals. **ICD (20)** Inter - canine distance, taken on lingual surface of canine alveoli. **POC (22)**

Postorbital constriction. **WAB (23)** Width at bullae, taken on ear openings perpendicular to skull axis. **CNW (24)** Greatest width across occipital condyles, taken perpendicular to skull axis. **SOH (28)** Supraoccipital height, from junction of nuchal and sagittal crests to dorsal edge of foramen magnum. **BUL (31)** Greatest bulla length. **LP^4 (41)** Length of P^4 taken along cingulum. **WP^4 (44)** Greatest cross - sectional crown width of P^4. **IOW (46)** Least interorbital width.

Skulls were sorted into five relative age classes using criteria modified from Zumpt (1969) as follows (asterisk denotes criteria that were given priority in ageing a skull in which the different criteria conflicted): Class 1 (juveniles; < 9 months): temporary or erupting teeth; second molars unerupted*; orbit open (i.e. postorbital bar incomplete); sutures open; cranium rounded and smooth. Class 2 (subadults; 9--12 mths): permament teeth*, no wear; orbit nearly closed; sutures open; cranium oblong; sagittal crest undeveloped, nuchal mildly developed. Class 3 (adults; 1--2 yrs): mild wear on molars; orbit closed*; sutures faint, basisphenoid - basioccipital, fronto - parietal and squamo - parietal may be closed; saggital crest mildly developed, nuchal crest developed. Class 4: moderate, conspicuous wear on upper and lower premolars and molars*; sutures closed, though fronto - maxillary and naso - maxillary may be visible; crests well developed. Class 5: all teeth severely worn*; orbit and sutures closed; crests strongly developed.

Approximate absolute age - intervals for the first three relative age classes were obtained from the study of Zumpt (1969) which employed known - age specimens.

Non - geographic variation

One hundred and eighty - two skulls from Wesselsbron in the Orange Free State were sorted into sexes and relative age classes (1--5, as described above). Univariate and multivariate analyses were employed to analyse individual, age and secondary sexual variation in the Wesselsbron sample. Basic statistics (means, two standard errors of the mean and coefficients of variation) were obtained for each age / sex class, and tests of skewness and kurtosis were computed for the largest sample (males of age class 4). Two - way analysis of variance (ANOVA) was used to simultaneously assess the importance of sex and age variation in each of the 14 skull measurements. For those measurements in which there was no significant ($P < 0,01$) age - sex interaction, *a posteriori* multiple range tests (SNK: Student - Newman - Keuls; see Sokal and Rohlf, 1981: 261--262) were performed on the age class means in order to identify non - significant subsets.

A Model I two - way ANOVA design was employed, which correctly considers both sex and age to be fixed factors. The conventional application of two - way ANOVA to analyse

mean differences has been criticised, since the two factors are no longer independent when cell sizes are unequal (Straney, 1978; Leamy, 1983). An alternative approach to non - geographic analysis has been suggested which relies on the partitioning of variance components (sex, age, sex - age interaction and error), rather than mean differences. Since fixed factors cannot generate variances it is necessary to regard both factors (Model II design: Leamy, op. cit.) or just one factor (mixed design: Straney, op. cit.) as random. A similar approach, which avoids the problems of considering sex and age as random, and which produces very similar results to variance components partitioning (Leamy, op. cit.), is to calculate the percentage contribution of sum of squares (SS) of each source of variation to the total SS. The latter technique requires that the number of age classes is kept constant, a requirement which is adhered to in this study. For this reason and because of its greater computational ease (%SS can be calculated directly from a conventional two - way ANOVA table), this technique was used in the present study, so that the results could be compared with those from the conventional Model I two - way ANOVA.

Multivariate analysis of non - geographic variation in C. penicillata involved the use of multigroup principal components analysis (MPCA), multivariate analysis of variance (MANOVA) and discriminant functions analysis (DFA). Thorpe (1988) considers that, when a number of groups is to

be compared, a multigroup PCA (MPCA) is superior to a simple PCA because the within - group components (such as growth) and the between - group differentiation may perturb one another when samples are pooled irrespective of group. In a study of male feral minks, Wiig (1985) found that size accounted for 60% of within - group (geographic sample) variation but only half a percent of between - group variation. For this reason MPCA rather than a simple PCA was used to analyse non - geographic variation in C. penicillata. MANOVA and DFA were performed on component scores from separate MPCAs of males and females, rather than on the original data, as both approaches produce equivalent results (Thorpe, 1988). The advantage of using component scores rather than the original data is that size can be removed by discarding the first principal component, to test its effect on between - group discrimination.

A six step procedure was followed: 1) 14 - variable MPCAs of individuals of age classes 2--5 were performed on males and females separately; 2) the percentage of variation explained by successive principal components was determined for the male and female factor matrices from MPCAs in step 1 (within age - group variation); 3) one - way ANOVA was used to test for significant differences among age class means for each component from male and female MPCAs in step 1 (between age - group variation); 4) MANOVA was used to test for significant differences among age class mean centroids in

successive samples comprising age classes 2--5, 3--5, 2--4 and 4--5, in males and females separately; 5) MANOVA was used to test for secondary sexual dimorphism in age class 4 individuals; 6) using DFA, age classes of males and females were plotted in canonical space.

Geographic variation

The number of premolars in C. penicillata is variable (three or four, in the upper and lower jaws) due to the variable presence of the upper and lower first premolars (Smithers, 1983). The number of first premolars in the upper and lower jaws was recorded in all of the skulls for which cranial measurements were taken. First premolars were recorded as absent if there was no trace of an alveolus or tooth. Teeth in which an alveolus or part of the root of the tooth was present were recorded as broken, or accidentally lost. The frequencies of individuals having one or two missing premolars in the upper and lower jaws were calculated for each of the 39 geographic samples (OTUs) described below.

Morphometric analyses of geographic variation were performed on a sample of 287 skulls from 180 localities, representing the sample of 'adult' (age class 4--5 individuals: see RESULTS) males and females. Due to absence of secondary sexual dimorphism males and females could be combined (see RESULTS).

Since most of the localities sampled were represented by only one or two adult skulls, it was necessary to pool specimens from adjacent localities to obtain sample sizes of at least four adult skulls. In forming pooled localities (OTUs) care was taken not to cross any major geographical or vegetational boundaries. Pooling of localities was also based on geographical proximity of adjacent localities and similarity in overall skull size (condylobasal length of skull) between individuals from adjacent localities. The geographic extent of 39 OTUs is shown in Fig. 4.2. Localities represented only by 'non - adult' (age classes 2--3) skulls were included in Fig. 4.2 to give a more complete picture of the true geographic extent of OTUs (and of the species' distribution based on museum records). Localities represented only by non - adult skulls were added to OTUs according to their geographic proximity to adjacent localities and by comparing condylobasal length of individuals of the same age class between adjacent localities. However, only adult skulls from each OTU were subjected to morphometric analysis.

Standard statistics (means, standard deviations, coefficients of variation and ranges) of two external and 14 cranial measurements were calculated for each OTU, and analysis of variance (ANOVA) and sum of squares simultaneous

test procedures (SS-STP) were performed on each variable, using the program UNIVAR (FORTRAN program developed by Power, 1970 and recompiled in PC version by N. J. Dippenaar). SS-STP diagrams were presented for six selected cranial variables. Because of the small sample sizes of many OTUs, the significance probability level for ANOVA and SS-STP analyses was taken as 0,001.

Diffences among OTUs in multivariate space were analysed by principal components analysis (PCA) and cluster analysis (CA) of OTU means for all 14 craniometric variables. PCA was performed on both correlation and variance - covariance matrices. The latter analysis yielded more biologically meaningful results than the former (see RESULTS) and only the latter was presented in this study. Since standardisation of the raw data matrix results in the conversion of a covariance matrix into a correlation matrix (Pimental and Smith, 1986b), PCA was performed on unstandardised data. For the sake of consistency, and because analyses of unstandardised and standarised data produced almost identical results (due to the dominant influence of size: see RESULTS), all other multivariate analyses were performed on unstandardised data.

Phenograms were obtained from CA of both inter - OTU average taxonomic distance (ATD) and correlation coefficient matrices from the unstandardised data, using the unweighted

pair group method with averages (UPGMA: Sneath and Sokal, 1973). Distance phenograms tend to reveal overall size differences among OTUs while correlation phenograms tend to reflect shape differences (Sneath and Sokal, 1973). A minimum spanning tree, based on ATD, was superimposed on the PCA graph to detect inter - point distortions. The statistical validity of groups of OTUs distinguished from CA phenograms and PCA graphs was tested using discriminant functions analysis (DFA). Because of the dominant influence of skull size (the first principal component from PCA accounted for 93% of total variation) and the fact that only two principal components gave meaningful patterns of variability (see RESULTS), only three variables (having high loadings on the first two components: CBL, WAB and ZYW) were selected for DFA. Reducing the number of variables relative to the sample size of the smallest sample also increases the performance of DFA. Furthermore, because of the high degree of inter - locality correlation between variables (resulting from the common influence of size), including all 14 variables not only includes redundant information, but it may also lead to computational errors in discriminant analysis due to a near - zero determinant (a consequence of collinearity: see discussion in APPENDIX I).

In order to test for intergradation (hybridisation) between morphometric groups a further DFA (also based on three variables) was performed, on specimens rather than OTUs.

Following the approach used by Genoways and Coate (1972); Genoways (1973); and George, Choate and Genoways (1981), two reference samples were selected representing 'pure' samples of two distinct phena (see RESULTS), and these were subject to DFA. Using the discriminant model 'standard canonical analysis of discriminance for raw variables' (Pimental, 1979: 196), and based on grand centroids and canonical vectors of weights obtained from DFA of the reference samples, discriminant scores were calculated for specimens belonging to a test sample of individuals from OTUs intermediate in skull size and geographic position between the two reference samples (i.e. OTUs 12, 15, 17, 22--24, 26--29, 37--39: see Fig. 4.2).

For the purpose of cladistic analysis, the 39 OTUs in Fig. 4.2 were further pooled into 15 biogeographically and phenotypically homogeneous regions, allowing for biogeographical boundaries and based on proximity of OTUs on PCA graphs and CA phenograms (Figs. 4.3--4.5: see RESULTS), as follows: (1) NE Namibia = OTU 27; (2) NW Namibia = OTU 26; (3) Central Namibia = OTUs 28 & 29; (4) Southern Namibia (including southern Botswana and northwestern Cape) = OTUs 22, 23 & 37; (5) Central Botswana = OTUs 20 & 21; (6) North - central Cape = OTU 39; (7) NE Cape = OTUs 24 & 38; (8) Northern Botswana = OTUs 18 & 19; (9) Northern Transvaal = OTU 11; (10) Central Transvaal = OTUs 12 & 13; (11) Southern Transvaal = OTUs 14--17; (12) Orange Free State = OTUs 1--

10; (13) Natal = OTU 25; (14) Western Cape = OTUs 30--33; (15) Eastern Cape = OTUs 34--36.

Means and standard deviations of all 14 variables were obtained for each of the 15 regions, using UNIVAR. Variables were gap - coded (see Thorpe, 1986b) by arranging means for each variable in ascending order and searching for gaps of greater than one mean within - group standard deviation between adjacent means. Intervals between gaps were coded as 0, 1, 2 etc., starting from the highest values. Larger individuals were assumed to be 'primitive' (i.e. given a character state of zero) since decreasing size is associated with a transition from saturated, red coat colours to a more faded yellow coloration in Cynictis (Taylor, Meester and Rautenbach, in press). According to Hershkovitz' (1968) theory of metachromism, saturated, reddish colours precede faded, yellowish colours in the course of metachromic evolution. Five variables which showed no gaps of one standard deviation or greater (SOH, ICD, CNW, POC, LP^4) were excluded from the analysis leaving nine variables. Manhattan distances (Sneath and Sokal, 1973) were manually calculated for all pairs of variables, and distance Wagner trees and networks (Farris, 1970; Jensen, 1981) were constructed manually from the Manhattan distance matrix.

Two methods of tree formation were used: 1) construction of a Wagner tree, taking the southern - most region (E Cape) as

being ancestral (this population had a character state of zero for all characters); and 2) mid - point rooting of a Wagner network. The 'microphylogenetic' approach outlined above, for estimating hypothesised range expansion in a species, is described in more detail in Thorpe, 1986a, b.

Further explanation and discussion of the multivariate techniques referred to above may be found in Blackith and Reyment, 1971; Genoways, 1973; Thorpe, 1976; Pimentel, 1979; Neff and Marcus, 1980; and Pimentel and Smith, 1986b. All univariate analyses (except where UNIVAR was employed, as noted above) were conducted using the computer package BIOΣTAT I (Pimentel and Smith, 1986a). All multivariate analyses were conducted using programs from BIOΣTAT II (Pimentel and Smith, 1986b), with the exception of cluster analysis and the calculation of the minimum spanning tree, which were conducted using the computer package, NTSYS-PC (Rohlf, 1986).

DISCUSSION OF RESULTS

Non - geographic variation

COEFFICIENTS OF VARIATION (CV: Table 4.1). Characters having low intrapopulation CV's have greater systematic importance than those with high CV's since real differences between taxa will not be masked by intrapopulation

differences. However the CV is also affected by the accuracy and repeatability of a measurement, and it must only be regarded as a rough measure of population variability (Sokal and Rohlf, 1981). From Table 4.1 it can be seen that most of the skull measurements exhibit reasonably low (< 4) CV's within a single sex / age class. Those measurements exhibiting high CVs (and therefore less useful than the other measurements) include tooth measurements (CV = 1,2--14,8), supraoccipital height (SOH: CV = 2,9--9,5) and postorbital constriction (POC: CV = 1,9--8,9). The lowest CV's (and therefore the most useful characters) were exhibited by occipital condyle width (CNW: CV = 0,9--3,1), width at bullae (WAB: CV = 1,7--4,0), condylo - basal length (CBL: CV = 1,2--4,2) and zygomatic width (ZYW: CV = 1,4--4,3).

TESTS OF NORMALITY (Table 4.2). The frequency distribution histogram of MTR was significantly ($\underline{P} < 0.01$) skewed to the right ($\underline{g1}$ = 1,14) and leptokurtic ($\underline{g2}$ = 3,17), but an examination of the raw data showed this to be the result of a single individual having a disproportionately long mandibular tooth row (the individual was remeasured and a similar measurement for MTR was obtained). This demonstrates the sensitivity of the parameters $\underline{g1}$ and $\underline{g2}$ to the influence of aberrant individuals, or to possible large errors in measurement. Only BUL showed significant departure from normality ($\underline{P} < 0,05$) as indicated by Kolmorov-Smirnov $\underline{D}$

Table 4.1

Means (Y), two standard errors ($2S_Y$), coefficients of variation (CV) and sample sizes (N) in five age classes of male and female C. penicillata from Wesselsbron. Abbreviations of measurements are explained in APPENDIX I

Sex	Age class (N)		Measurements CBL	BCW	MRH	SOH	MTR	ICD	WAB	CNW	POC	IOW	ZYW	LP4	BUL	WP4
M	I(2)	Y	60,0	27,6	15,4	12,0	20,4	8,40	27,2	15,7	16,8	12,2	34,4	3,66	16,3	5,21
A		$2S_Y$	1,90	0,49	1,60	0,49	0,49	1,00	0,79	0,60	1,10	1,10	1,40	0,76	0,59	0,35
L		$C\bar{V}$	2,2	1,3	7,3	2,9	1,7	8,4	2,1	2,7	4,6	6,4	2,9	14,8	2,6	4,8
E																
S	II(12)	Y	64,1	28,3	16,8	12,3	21,1	7,81	27,6	15,7	17,0	14,4	37,2	5,92	16,8	5,26
		S_Y	1,54	0,38	0,42	0,36	0,40	0,22	0,70	0,38	0,70	0,40	0,92	0,26	0,58	0,20
		$C\bar{V}$	4,2	2,4	4,4	7,8	3,3	5,1	4,4	4,2	7,1	4,9	4,3	7,7	5,9	6,4
	III(33)	Y	65,2	28,5	17,6	12,4	21,3	8,07	28,0	16,0	16,1	14,7	38,6	6,04	17,2	5,32
		$2S_Y$	0,72	0,24	0,34	0,28	0,24	0,10	0,28	0,20	0,40	0,20	0,46	0,08	0,20	0,12
		$C\bar{V}$	3,1	2,5	5,6	6,4	3,1	3,9	2,8	3,6	7,4	4,1	3,5	4,1	3,2	6,4
	IV(36)	Y	66,3	28,4	18,0	12,6	21,4	8,48	28,2	16,0	15,6	15,2	39,7	6,06	17,2	5,29
		$2S_Y$	0,58	0,22	0,18	0,32	0,22	0,12	0,28	0,18	0,34	0,22	0,34	0,08	0,20	0,10
		$C\bar{V}$	2,6	2,3	2,9	7,5	3,1	4,2	3,0	3,5	6,7	4,2	2,6	3,5	3,6	5,4
	V(20)	Y	66,6	28,6	18,1	12,8	21,2	8,84	28,7	16,1	15,2	15,8	40,7	6,06	17,2	5,29
		$2S_Y$	0,48	0,40	0,36	0,36	0,20	0,20	0,36	0,28	0,60	0,32	0,32	0,12	0,18	0,12
		$C\bar{V}$	1,6	3,1	4,4	6,3	2,1	5,2	2,9	3,8	8,9	4,6	1,8	4,7	2,4	5,2
F	I(4)	Y	53,6	28,4	13,1	11,6	11,3	6,98	25,6	15,6	18,6	12,4	32,8	3,42	15,4	4,88
E		$2S_Y$	0,85	0,25	0,29	0,46	0,74	0,17	0,64	0,22	0,35	0,53	0,46	0,04	0,29	0,31
M		$C\bar{V}$	1,6	0,9	2,2	4,0	6,5	2,4	2,5	1,4	1,9	4,3	1,4	1,2	1,9	6,4
A																
L	II(10)	Y	62,6	28,2	16,5	11,9	21,0	7,82	27,5	15,7	16,7	13,8	36,3	6,00	16,8	5,11
E		$2S_Y$	1,54	0,52	0,50	0,72	0,38	0,26	0,68	0,50	0,72	0,52	0,98	0,12	0,46	0,20
S		$C\bar{V}$	3,9	2,9	4,8	9,5	2,8	5,2	4,0	5,0	6,7	6,0	4,3	3,4	4,4	6,1
	III(23)	Y	65,2	28,5	17,3	12,0	21,4	8,11	27,9	16,0	16,6	14,8	38,2	6,15	17,2	5,36
		$2S_Y$	0,76	0,34	0,32	0,30	0,28	0,18	0,38	0,30	0,48	0,32	0,52	0,12	0,26	0,16
		$C\bar{V}$	2,8	2,9	4,4	6,1	3,2	5,5	3,3	4,4	7,0	5,2	3,3	5,1	3,7	7,0
	IV(33)	Y	66,7	28,7	17,7	12,5	21,5	8,42	28,5	16,0	15,8	15,5	40,1	6,05	17,4	5,25
		$2S_Y$	0,60	0,16	0,28	0,22	0,26	0,10	0,22	0,20	0,48	0,18	0,30	0,12	0,18	0,10
		$C\bar{V}$	2,6	1,7	4,4	5,2	3,4	3,6	2,3	3,6	8,9	3,3	2,1	5,5	3,0	5,9
	V(9)	Y	66,7	28,5	17,8	13,1	21,7	8,90	28,7	16,2	14,9	15,7	40,4	6,18	17,4	5,37
		$2S_Y$	0,52	0,40	0,36	0,42	0,20	0,28	0,32	0,40	0,70	0,44	0,70	0,16	0,30	0,12
		$C\bar{V}$	1,2	2,2	3,1	4,8	1,4	4,7	1,7	3,6	7,0	4,3	2,6	3,7	2,6	3,1

Table 4.2

Measures of skewness (G1), kurtosis (G2), t tests of their significance, and Kolmorov-Smirnov (D) tests of normality for 14 skull measurements in a sample of 36 male, age class 4 *C. penicillata* from Wesselsbron. Significant t and D values are indicated by * ($P < 0,05$) or ** ($P < 0,01$). Abbreviations of measurements are explained in APPENDIX I.

Variable	G1	t value	G2	t value	D
CBL	0,353	0,898	-0,420	-0,547	0,091
BCW	-0,431	-1,097	0,081	0,105	0,085
MRH	-0,379	-0,964	-0,123	-0,160	0,112
SOH	0,505	1,285	-0,724	-0,943	0,127
MTR	1,143	2,908**	3,170	4,128**	0,101
ICD	-0,496	-1,262	0,499	0,650	0,104
WAB	0,514	1,308	0,338	0,505	0,092
CNW	0,525	1,336	0,648	0,844	0,100
POC	0,623	1,585	0,247	0,322	0,120
IOW	0,016	0,041	-0,703	-0,915	0,089
ZYW	-0,013	-0,033	-0,775	-1,009	0,071
LP4	0,705	1,794	0,043	0,056	0,120
BUL	-0,030	-0,076	1,625	2,116*	0,160*
WP4	-0,137	-0,349	0,132	0,172	0,098

values (Table 4.2).

ANALYSIS OF VARIANCE (Table 4.3). The results obtained from F - values (2 - way ANOVA) and from %SS's are congruent over the 14 skull measurements (Table 4.3), in spite of the statistical problems associated with the use of F - values in 2-way ANOVA's when subgroup sample sizes are unequal (see METHODS AND MATERIALS). For most of the measurements, significant ($P < 0,01$) F - values were obtained for age but not for sex. Similarly age gave much higher %SS's (%SS = 1,0--49,7) than did sex (%SS = 0,0--2,7). These results contradict Straney's (1978) generalisation, based on two species, that marked sexual dimorphism is typical of carnivores. Only one measurement (MRH) showed significant sexual dimorphism ($F = 6,05$; $P = 0,05$; Table 4.3), males having a greater mandible ramus height than females (Table 4.2). There were no consistent mean differences between sexes in any of the other measurements (Table 4.2). No measurements showed significant interaction between age and sex (Table 4.3).

Measurements involving the posterior part of the cranium (BCW, CNW) and certain toothrow measurements (MTR, LP^4, WP^4) did not demonstrate significant differences between age classes (Table 4.3). These measurements also gave relatively low %SS's for age and correspondingly high %SS's for error (i.e. individual variability). The absence of significant

age variation in BCW and CNW is probably due to the early cessation of growth in the braincase and occipital region of the skull. In support of this hypothesis, comparitive studies of mammalian craniology have demonstrated the existence of two typical patterns of skull growth: neural growth (braincase and associated elements) which occurs mainly during prenatal and early postnatal development, and somatic growth (facial skeleton) which follows a more protracted growth trajectory throughout postnatal development (Moore 1981: 283). In contrast to the other measurements, postorbital constriction (POC) shows a marked negative correlation with age (Tables 4.1 and 4.4). In terms of functional cranial analysis this is a consequence of the separation of the orbital and neural functional matrices as the skull elongates during growth (Moss and Young 1970).

MULTIPLE RANGE TESTS (Table 4.4) Of the nine measurements which showed significant age variation, three (CBL, MRH, WAB) grouped age classes 4 and 5 into a non-significant ($\underline{P} > 0.05$) subset (Table 4.4). The other age - dependent measurements tended to separate all of the age classes (IOW, ZYW, ICD) or to group age classes 2 and 3 (POC), 3--5 (BUL) or 2--4 (SOH).

MULTIVARIATE ANALYSIS OF VARIANCE (MANOVA: Table 4.7). The results of eight separate MANOVA tests (Table 4.7) showed that, in both males and females, age class subsets (2--5),

(3--5) and (3, 4) showed significant differences among age class mean centroids at the 1% level, while in the subset (4, 5) mean centroids were different at the 5% level. Since, from multiple range tests, the majority of individual measurements either did not discriminate between age classes or formed non - significant subsets comprising age classes 4 and 5, it was decided, for the purpose of subsequent geographic analyses, to pool data from age classes 4 and 5. This results in an unfortunate loss of data from specimens in age classes 1--3. In the Wesselsbron sample ($\underline{N}$ = 182), 84 specimens, or 46% of the total sample, belonged to age classes 1--3.

MANOVA of males and females in age class 4 indicated no significant secondary sexual differences in multivariate space (Table 4.7), and both sexes could be pooled for the purpose of subsequent geographic analyses.

MULTIGROUP PRINCIPAL COMPONENTS ANALYSIS (Tables 4.5, 4.6). In male and female Cynictis a general size component (component 1, having high positive loadings for most variables) explained 36,3% and 39,4% respectively of the total within - group variation, but only 17,7% and 16,8% respectively of the total between - group variation (Tables 4.5, 4.6). More important than size in discriminating between age groups was a shape component contrasting posterior and anterior skull widths, which accounted for 39%

Table 4.3

Results of 2-way ANOVA of four age classes (2--5) of male and female *C. penicillata* from Wesselsbron: *F* values and % Sum of Squares (%SS) of each source of variation. Significant differences are shown by * ($P < 0,05$) and ** ($P < 0,01$). Abbreviations of measurements are explained in APPENDIX I.

Variable	*F* values			%SS			
	Sex(S)	Age(A)	SxA	Sex(S)	Age(A)	SxA	Error
CBL	O,O5	18,80**	1,35	0,0	24,7	1,8	73,5
BCW	0,71	0,98	0,62	0,4	1,7	1,1	96,8
MRH	6,05*	16,66**	0,07	2,7	22,3	0,1	74,9
SOH	1,68	5,40**	1,33	0,9	8,5	2,1	88,5
MTR	0,94	2,31	1,02	0,5	3,9	1,7	93,9
ICD	0,38	40,70**	0,35	0,1	41,9	0,4	57,6
WAB	0,08	8,68**	0,89	0,0	13,2	1,4	85,4
CNW	0,00	1,63	0,10	0,0	2,8	0,2	97,0
POC	1,98	11,65**	0,86	1,0	16,8	1,2	81,0
IOW	0,00	33,26**	2,44	0,0	36,3	2,7	61,0
ZYW	1,09	57,78**	2,09	0,3	49,7	1,8	48,2
LP4	1,49	1,23	0,60	0,8	2,1	1,0	96,0
BUL	1,42	3,41*	0,38	0,8	5,6	0,6	92,9
WP4	0,31	1,58	0,54	0,2	2,7	0,9	96,2

Table 4.4

Multiple range tests (Student-Newman-Keuls: SNK) of age class means (sexes combined; age class 1 excluded) from 14 skull measurements, in C. penicillata from Wesselsbron (Vertical lines connect the means of maximum non-significant subsets at the 5% level). Abbreviations of measurements are explained in APPENDIX I. NS = No significant differences between means; AS = All means significantly different from each other.

Variable	Age class	Means (ordered)	SNK	Variable	Age class	Means (ordered)	SNK
CBL	2	63,4		CNW	2	15,7	
	3	65,2			4	16,0	NS
	4	66,5	|		3	16,0	
	5	66,6	|		5	16,1	
BCW	2	28,2		POC	5	15,1	
	3	28,5	NS		4	15,7	
	4	28,5			3	16,3	|
	5	28,6			2	16,9	|
MRH	2	16,6		IOW	2	14,1	
	3	17,5			3	14,7	AS
	4	17,9	|		4	15,4	
	5	18,0	|		5	15,7	
SOH	2	12,1	|	ZYW	2	36,8	
	3	12,3	|		3	38,4	AS
	4	12,5	|		4	39,9	
	5	12,9			5	40,6	
MTR	2	21,0		TL4	2	5,95	
	5	21,3	NS		4	6,06	NS
	3	21,3			3	6,08	
	4	21,4			5	6,10	
ICD	2	7,81		BUL	2	16,8	
	3	8,09	AS		3	17,2	|
	4	8,45			4	17,2	|
	5	8,86			5	17,3	|
WAB	2	27,5		TW4	2	5,19	
	3	28,0			4	5,27	NS
	4	28,3	|		3	5,34	
	5	28,7	|		5	5,36	

Table 4.5

Variation within (% variance, calculated from eigenvalues) and between (ANOVA: F values and percentage of variation explained by group effect (%SS)) four age classes (2--5) in 14 components (PCs) from a 14 variable multigroup principal components analysis of 101 male C. penicillata from Wesselsbron. Significance of F values indicated as NS (non - significant); * (P < 0,05); and ** (P < 0,01).

PC	% variance	ANOVA			Description
		F	P	%SS	
1	36,3	9,3	**	17,7	General size
2	14,5	1,5	NS	2,8	Skull width v.teeth
3	9,4	1,6	NS	3,1	POC & teeth v. SOH
4	7,0	20,5	**	39,0	Post. v. ant.widths
5	5,2	0,1	NS	0,2	SOH v. POC
6	5,1	0,4	NS	0,7	MRH v. BUL
7	4,4	4,6	**	8,8	MRH v. PWC
8	4,1	1,8	NS	3,3	SOH v. IOW
9	3,5	2,2	NS	4,2	ZYW v. ICD
10	2,7	3,2	*	6,0	CNW v. LP4
11	2,7	2,0	NS	3,8	MTR v. WP4
12	2,1	1,6	NS	3,1	ZYW v. CBL
13	1,6	1,5	NS	2,8	BCW v. WAB
14	1,3	2,3	NS	4,4	MTR v. CBL

Table 4.6

Variation within (% variance, calculated from eigenvalues) and between (ANOVA: F values and percentages of variation explained by group effect (%SS)) four age classes (2--5) in 14 components (PCs) from a 14 variable multigroup principal components analysis of 75 female C. penicillata from Wesselsbron. Significance of F values indicated as NS (non - significant); * ($P < 0,05$); and ** ($P < 0,01$).

PC	% variance	ANOVA			Description
		F	P	%SS	
1	39,4	10,1	**	16,8	General size
2	13,7	2,6	NS	4,3	Skull width v. teeth
3	9,2	7,2	**	12,0	Post. v. ant. widths
4	8,0	1,4	NS	2,3	Teeth & frontal v. skull & bulla lengths
5	6,1	5,5	**	9,1	IOW v. WAB
6	5,1	9,7	**	16,1	ICD v. MRH
7	4,0	2,0	NS	3,3	MRH & SOH v. BUL
8	3,2	8,9	**	14,8	ICD v. ZYW
9	2,8	0,8	NS	1,3	IOW & CNW v. BUL
10	2,4	4,3	**	7,1	MTR v. WP4
11	2,0	1,0	NS	1,7	WAB v. CNW
12	1,8	1,4	NS	2,4	LP4 v. WP4
13	1,5	1,0	NS	1,6	BCW v. LP4
14	0,8	4,3	**	7,2	MTR v. CBL

Table 4.7

Results of separate 14 - variable multivariate analyses of variance (MANOVA) of nine samples comprising different subsets of sex and relative age classes of C. penicillata from Wesselsbron. Significance of multivariate F values indicated as in Table 4.6. Sample sizes of individual sex and age classes given in Table 1. N indicates total sample size.

Sex	Age class(es)	F	P	N
Male	(2, 3, 4, 5)	3,31	**	101
	(3, 4, 5)	3,46	**	89
	(3, 4)	3,43	**	69
	(4, 5)	2,14	*	56
Female	(2, 3, 4, 5)	3,78	**	75
	(3, 4, 5)	3,75	**	65
	(3, 4)	4,91	**	56
	(4, 5)	2,36	*	42
(Male + female)	(4)	1,43	NS	69

(component 4 in males: Table 4.5) and 21,1% (components 3, 5 in females; Table 4.6) of between - group variation. This component represents the distinction between the major neural and facial growth trajectories of the mammal skull (discussed above), the latter following a more protracted course during postnatal growth.

The present results emphasize the point made by Thorpe (1988) that there is no necessary correlation between the percentage variation reflected by the within - group components and their contribution to between - group discrimination. In Cynictis individual variation (within age groups) is due primarily to isometric size, whereas age variation is dominated by allometric size whereby an increase in size with growth is associated with an increase in the ratio of facial width to braincase width. However, size still accounts for significant differences between age classes (Table 4.5: $F = 9,3$; Table 4.6: $F = 10,1$; $P < 0,01$).

The greater number of components demonstrating significant ($P < 0,05$) age variation in females (Table 4.6: seven components) compared with males (Table 4.5: four components) may be due to a more prolonged growth phase in females, or to greater individual variability in male skulls which masks age differences in certain minor components of skull shape.

DISCRIMINANT FUNCTIONS ANALYSIS (Fig. 4.1). Fig. 4.1 shows

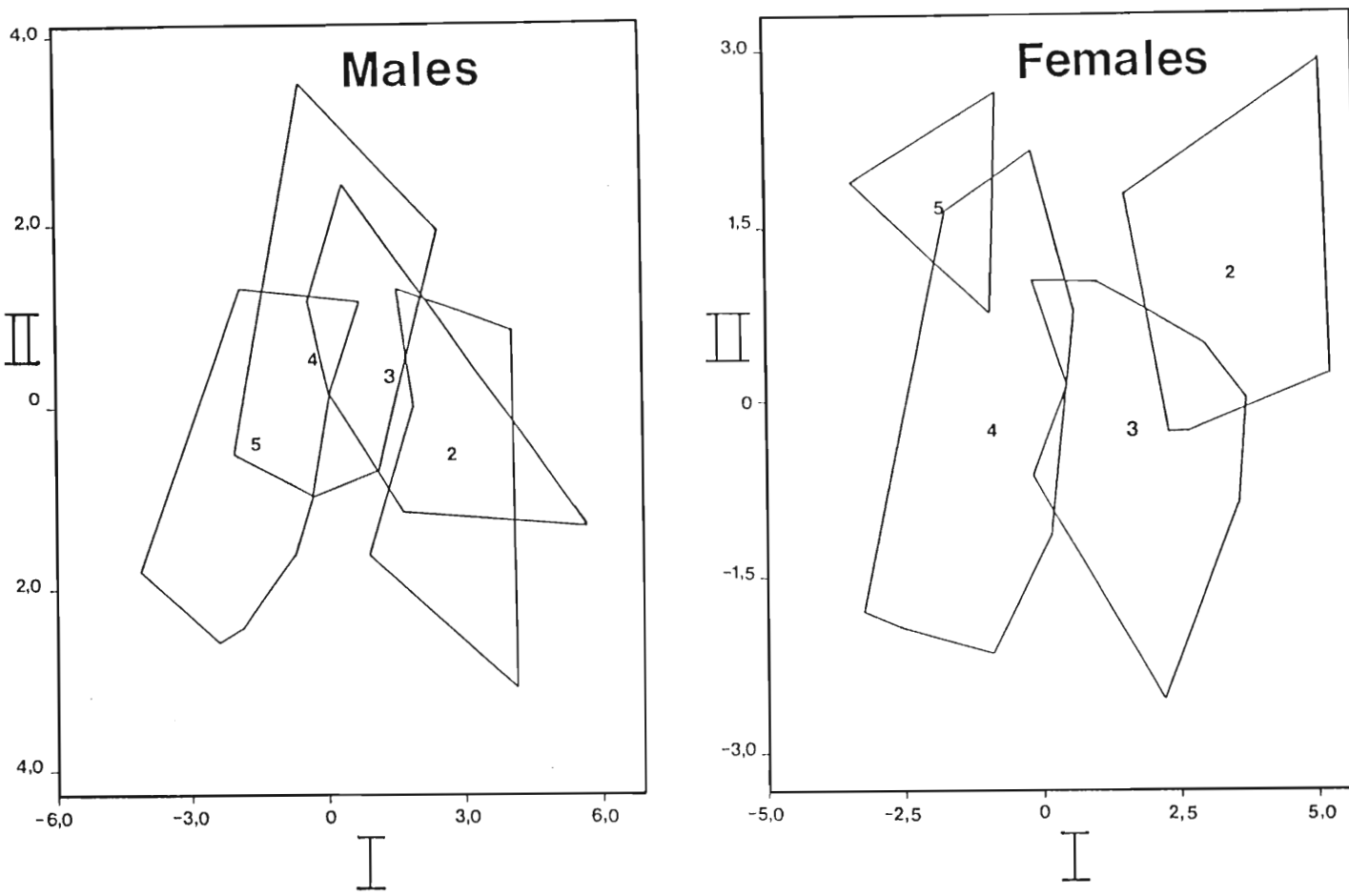


Fig. 4.1 Comparison of the first two canonical axes from discriminant functions analyses of male and female Cynictis penicillata from Wesselsbron, northern Orange Free State. Numbers 2 to 5 represent mean centroids of respective relative age classes based on cranial and dental criteria. Polygons enclose all individuals of a particular age class.

the distribution of age classes on the first two canonical vectors of a four - group discriminant functions analysis. Much less overlap between age classes occurs in females compared to males. This may be due to: 1) greater individual variability in males; or 2) differences in the patterns of cranial growth in males and females. For 10 out of 14 measurements, coefficients of variation (mean within - group values, excluding age class 1; taken from Table 4.1) were higher in males than in females suggesting that greater individual variability occurs in males. There is some evidence for slight differences in patterns of growth between males and females. In most measurements (eg. CBL, MRH, MTR, ICD, WAB, IOW, ZYW) males are larger than females in age classes 1 and 2, but females are generally larger in age classes 3, 4, and 5 (Table 4.1). This suggests that growth in males is faster, and flattens off earlier, than in females which reach a slightly larger final size. That these possible differences in male and female growth rates are not statistically significant is clearly indicated by the statistical non - significance of the sex - age interaction term in 2 - way ANOVA of individual measurements (Table 4.3). However, the above discussion raises an important point: even where there is no apparent sexual dimorphism in individual measurements, significant differences in growth patterns between males and females may result in non - significant subsets being formed from different subsets of age classes for males and females. In such cases

indiscriminate pooling of the sexes may result in unacceptable biases in forming samples for inter - OTU analyses.

Geographic variation

Qualitative tooth characters

Fewer individuals had missing first premolars (i.e. no trace of tooth or alveolus) in the top jaw, compared with the lower jaw, as shown in Table 4.8. There does not appear to be any apparent geographic pattern in Table 4.8 in the presence of first premolars in C. penicillata. The OTUs having the highest percentages of individuals with one or both P_1s missing were OTU 18 (northern Botswana) and OTU 33 (central Karroo). There did not appear to be any correlation between the percentage of individuals having broken or accidentally lost P1s (i.e. with the alveolus present, with or without the root of the tooth remaining) and the percentage of individuals having missing P1s, suggesting that the absence of P1s is a genetic character and not simply the consequence of accidental tooth loss or breakage. The finding of juveniles with missing P1s supports this conclusion.

In the mongooses, Smithers (1983) reported that the first premolar may be absent altogether (Suricata suricatta,

Table 4.8

Table showing percentages of individuals having 0, 1 or 2 first premolars present in the upper and lower jaws, in 39 OTUs in *C. penicillata*.

OTU	N	No.of first premolars						% indvs. having broken teeth
		Upper jaw			Lower jaw			
		0	1	2	0	1	2	
1	12	0	0	100	0	17	83	17
2	61	0	3	97	8	8	84	15
3	45	0	4	96	9	4	87	27
4	8	0	0	100	12	0	88	50
5	13	0	0	100	8	8	84	0
6	23	0	4	96	4	4	92	43
7	11	0	0	100	0	0	100	9
8	11	0	0	100	9	0	91	27
9	5	0	0	100	20	0	80	40
10	7	0	0	100	14	14	71	57
11	10	0	10	90	0	0	100	20
12	21	5	5	90	14	14	71	14
13	9	0	0	100	22	11	67	22
14	6	0	0	100	17	17	66	50
15	11	0	0	100	27	18	55	9
16	7	0	14	86	14	0	86	43
17	12	0	8	92	8	17	75	25
18	7	0	0	100	44	28	28	0
19	11	0	0	100	9	9	82	9
20	10	0	10	90	10	30	60	40
21	9	0	0	100	0	11	89	33
22	7	0	0	100	14	14	72	0
23	8	0	0	100	0	13	87	0
24	5	0	0	100	0	0	100	0
25	10	0	0	100	20	10	70	60
26	19	0	0	100	16	0	84	16
27	16	0	0	100	6	13	81	19
28	8	0	0	100	0	13	87	12
29	8	0	0	100	0	13	87	25
30	11	0	0	100	9	0	99	0
31	27	0	0	100	7	11	82	26
32	8	0	0	100	0	0	100	12
33	5	0	0	100	40	40	20	0
34	15	7	0	93	20	7	73	7
35	7	0	0	100	14	0	86	14
36	23	0	0	100	13	13	74	22
37	9	0	0	100	0	0	100	22
38	17	6	0	94	18	12	70	12
39	17	6	6	88	6	18	76	29

Helogale parvula, Mungos mungo), absent in the lower jaw (Galerella spp.) or always present in both jaws (most species of mongooses). In Galerella sanguinea the number of first premolars in the upper jaw is variable. In Atilax paludinosus the first premolars are usually absent in both jaws, but may occasionally be present. The significance of this variation in the presence of the first premolar is not clear, although absence of this tooth is associated with relatively small - skulled species of mongooses such as Suricata and Helogale, and partial absence with intermediate - sized species such as Cynictis and Galerella. Its loss or partial loss in certain mongoose species suggests that it has become vestigial, as is evidenced by its minute size and simple, apparently non - functional character.

Multivariate analyses

In this section ordination, clustering and discriminant procedures were carried out on 39 OTU (pooled localities; Fig. 4.2) means, to illustrate craniometric relationships among OTUs, and a further discriminant analysis was carried out on specimens to evaluate the extent of intergradation between craniometrically - defined phena / taxa. Means of nine craniometric characters in 15 geographic regions (see MATERIALS AND METHODS) were analysed by cladistic (distance Wagner) analysis in an attempt to reconstruct the historical

pattern of range expansion in Cynictis.

CLUSTER ANALYSES (Figs. 4.3, 4.4, 4.5). A distance (average taxonomic distance: ATD) phenogram of 39 OTUs, based on means of 14 cranial measurements, showed the existence of two distinct geographic groups (phena), separated by an ATD of 2,6 (i.e. A and B in Fig. 4.3). Phenon A includes southern localities (from southern Cape, Orange Free State, southern Transvaal), while phenon B comprises OTUs from northern localities (northern Transvaal, Namibia, Botswana and northern Cape). Further subdivisions of these major groups can be distinguished at an ATD phenon level of approximately 1,4--1,5 (i.e. C, D, E and F in Fig. 4.3). In the southern phenon OTUs from the central, southern and eastern Cape (D: Fig. 4.3) are separated from other OTUs (C: Fig. 4.3). As populations from the western Cape (OTUs 30--32) are similar craniometrically to populations from the Orange Free State and Transvaal, but are separated geographically by craniometrically dissimilar populations in the central, southern and eastern Cape, homomorphism is implicated (see also Owen and Qumsiyeh, 1987). In cases of homomorphism (the occurrence of geographically separate but phenotypically similar populations), formal recognition of subspecies is not appropriate. In the northern phenon two geographically contiguous sub - groups are present: OTUs from central and northern Botswana, northern Transvaal and northern Namibia (E: Fig. 4.3) are separated from northern

Fig. 4.2 Map showing distribution of Cynictis penicillata based on museum records, and geographic extent of 39 OTUs (indicated by circled groups of localities). Locality samples include specimens which were not analysed morphometrically because they belonged to 'non - adult' relative age classes (1--3). See under Material examined, in Taxonomy section, for a list of localities grouped under each OTU, and for locality sample sizes of morphometrically analysed and additional individuals.

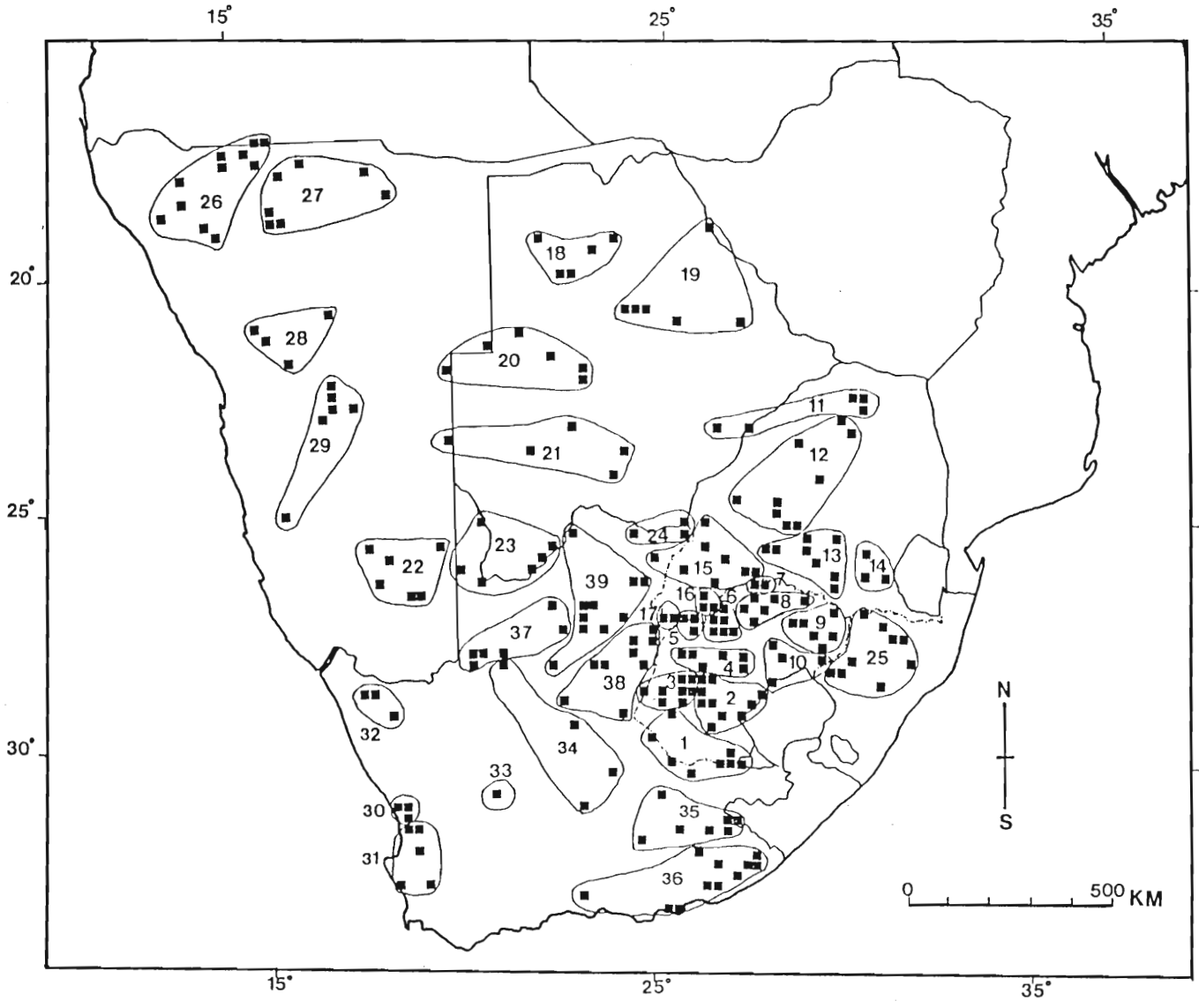

15°
25°
35°
20°
25°
30°
26
27
18
19
28
20
29
11
21
12
22
23
24
15
13
14
39
16
7
8
17
6
9
37
5
10
25
38
4
3
2
32
1
34
33
30
35
31
36
N
S
0
500 KM

Fig. 4.3 Distance phenogram (average taxonomic distance) from a UPGMA (unweighted pair group method with averages) 14 - variable cluster analysis of 39 OTU means in C. penicillata. The cophenetic correlation coefficient = 0,800. Numbered codes correspond with OTU codes in Fig. 4.2. Letters represent geographic regions as follows: OF = Orange Free State; SC = Southern Cape; ST = Southern Transvaal; NT = Northern Transvaal; NA = Natal; SW = Namibia; NC = Northern Cape; BT = Botswana.

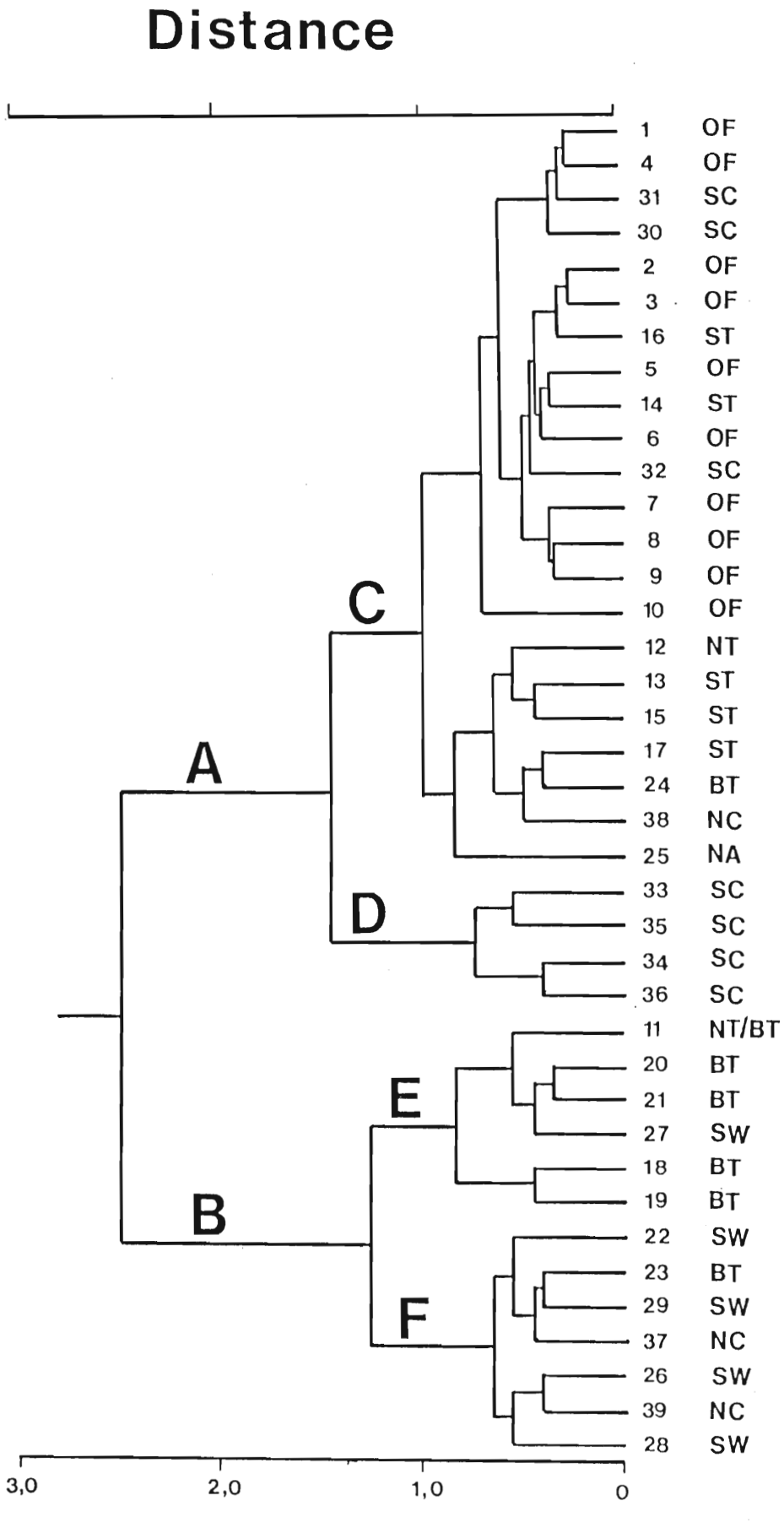

Distance
1 OF
4 OF
31 SC
30 SC
2 OF
3 OF
16 ST
5 OF
14 ST
6 OF
32 SC
7 OF
8 OF
9 OF
10 OF
12 NT
13 ST
15 ST
17 ST
24 BT
38 NC
25 NA
33 SC
35 SC
34 SC
36 SC
11 NT/BT
20 BT
21 BT
27 SW
18 BT
19 BT
22 SW
23 BT
29 SW
37 NC
26 SW
39 NC
28 SW
A
B
C
D
E
F
3,0
2,0
1,0
0

Fig. 4.4 Correlation phenogram from a UPGMA (unweighted pair group method with averages) 14 - variable cluster analysis of 39 OTU means in C. penicillata. The cophenetic correlation coefficient = 0,745. Numbered codes correspond with OTU codes in Fig. 4.2.

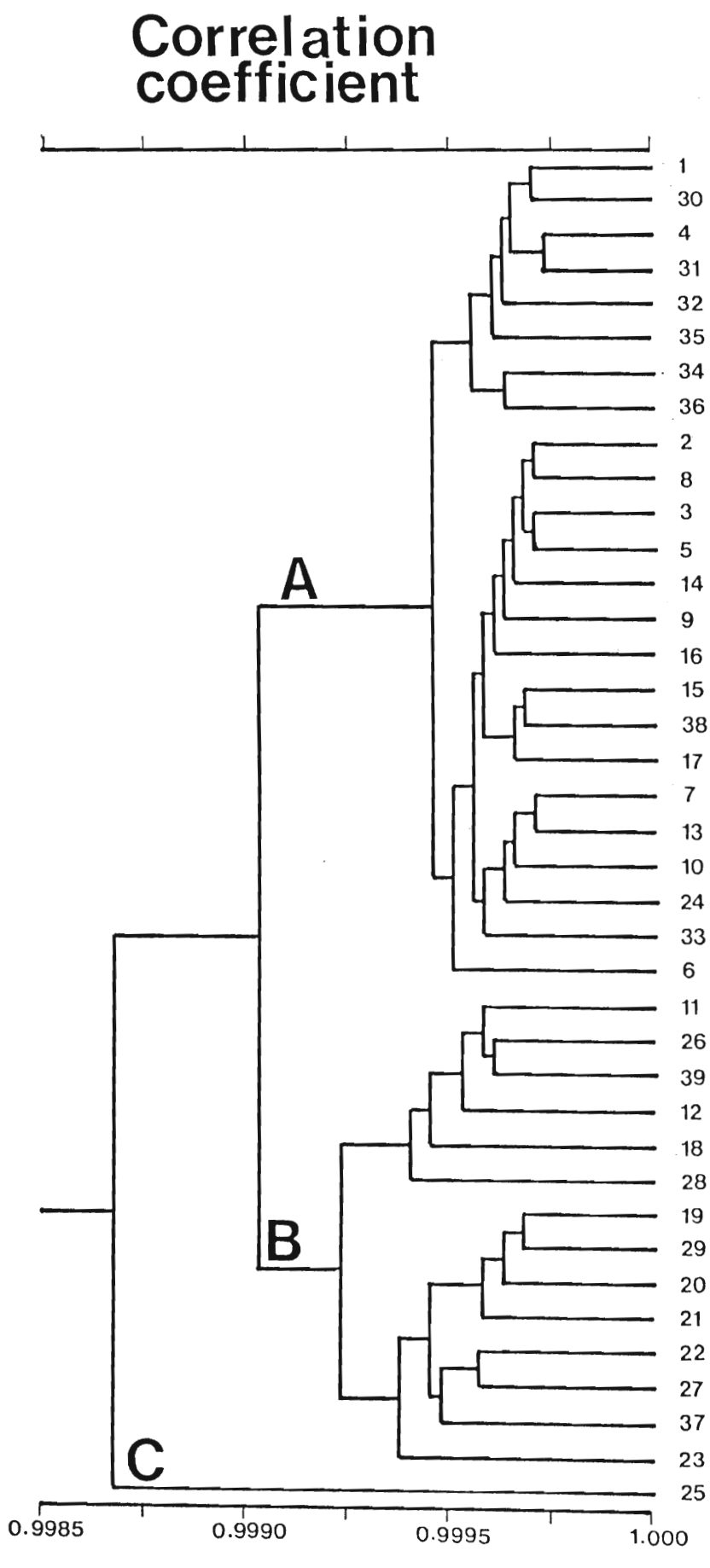
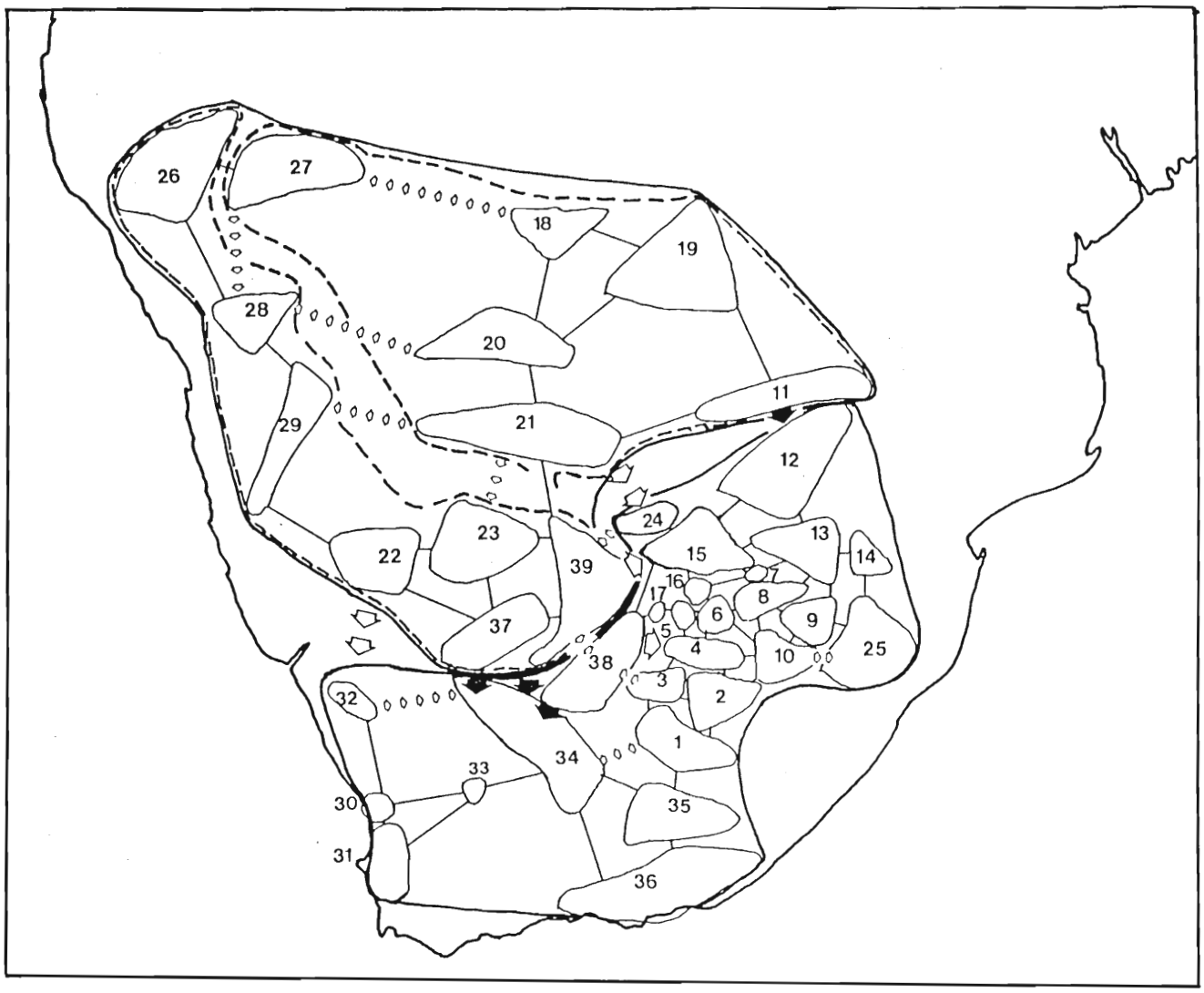

Correlation coefficient
1
30
4
31
32
35
34
36
2
8
3
5
14
9
16
15
38
17
7
13
10
24
33
6
11
26
39
12
18
28
19
29
20
21
22
27
37
23
25
A
B
C
0.9985
0.9990
0.9995
1.000

Fig. 4.5 Map showing geographical pattern of phenetic differentiation in C. penicillata. OTU codes correspond with those in Fig. 4.2. Solid lines connecting adjacent OTUs indicate average taxonomic distances (ATDs) < 1,0; small open arrows indicate ATDs between 1,0 and 1,5; large open arrows indicate ATDs between 1,5 and 2,0; closed arrows indicate ATDs > 2,0. Direction of arrows indicate direction of increase in overall skull size. Solid, thick lines enclose OTUs belonging to the northern and southern phena shown in Fig. 4.3; dashed lines enclose OTUs belonging to eastern and western subgroups of the northern phenon in Fig. 4.3.


26
27
18
19
28
20
11
29
21
12
24
23
13
14
22
39
15
16
17
8
6
9
37
5
4
10
25
38
3
2
32
1
34
33
30
35
31
36

Cape and southern and central Namibia (F: Fig. 4.3).

The correlation phenogram in Fig. 4.4 illustrates three major phena (A, B, C). Two of these (A and B) correspond exactly with the two major phena in the distance phenogram in Fig. 4.3. The third phenon in the correlation phenogram (C: Fig. 4.4) comprises a single OTU (25) which includes all specimens analysed from Natal. The geographical sub - groups present in the two phena in the distance phenogram (i.e. C, D, E and F: Fig. 4.3) cannot be discriminated on the correlation phenogram. This indicates that the two major phena described above can be distinguished on the basis of both skull size and skull shape, while geographical sub - groups of these phena are recognisable only on the grounds of skull size. Specimens from Natal are distinct from all other OTUs in skull shape, but not in skull size.

Figure 4.5 illustrates the geographic extent of the two major phena defined from the distance phenogram, and of the geographically contiguous subgroups present in the northern phenon. The extent of phenetic differentiation (ATDs) between adjacent localities, as shown by solid lines, small open, large open, and closed arrows indicating increasing values of ATD, illustrates the position and intensity of transition zones (stepped clines) separating northern and southern, and western and eastern groups (Fig. 4.5). The cline separating northern and southern populations tends to

be steeper (higher ATDs separating adjacent OTUs) than the one between western and eastern sub - populations of the northern population, although the gradient of the former varies quite considerably along its length. The north - south cline is steepest when it corresponds with biogeographic barriers such as the middle and lower Orange River basin and the Soutpansberg Mountains in northern Transvaal (Fig. 4.6), suggesting that geographic barriers (whether complete or partial) are important in reducing inter - population gene flow (see later discussion).

PRINCIPAL COMPONENTS ANALYSIS (Fig. 4.7). While cluster analysis (CA) illustrates overall differences among OTUs based on all 14 cranial measurements, principal components analysis (PCA) allows the influence of different variables on observed patterns of variation to be explored. A plot of principal component scores on the first two principal components of a PCA based on 39 OTU means and 14 variables, is shown in Fig. 4.7. A minimum spanning tree has been superimposed on the scattergram. The first component, a general size component with eigenvector loadings of similar sign (negative) and relative magnitude (Table 4.9), accounted for 93,0% of the variation. The second component, a shape vector contrasting skull length (positive eigenvalues) and width (negative eigenvalues: Table 4.9), accounted for 3,6% of the variation, while the third component, which was mainly influenced by the single

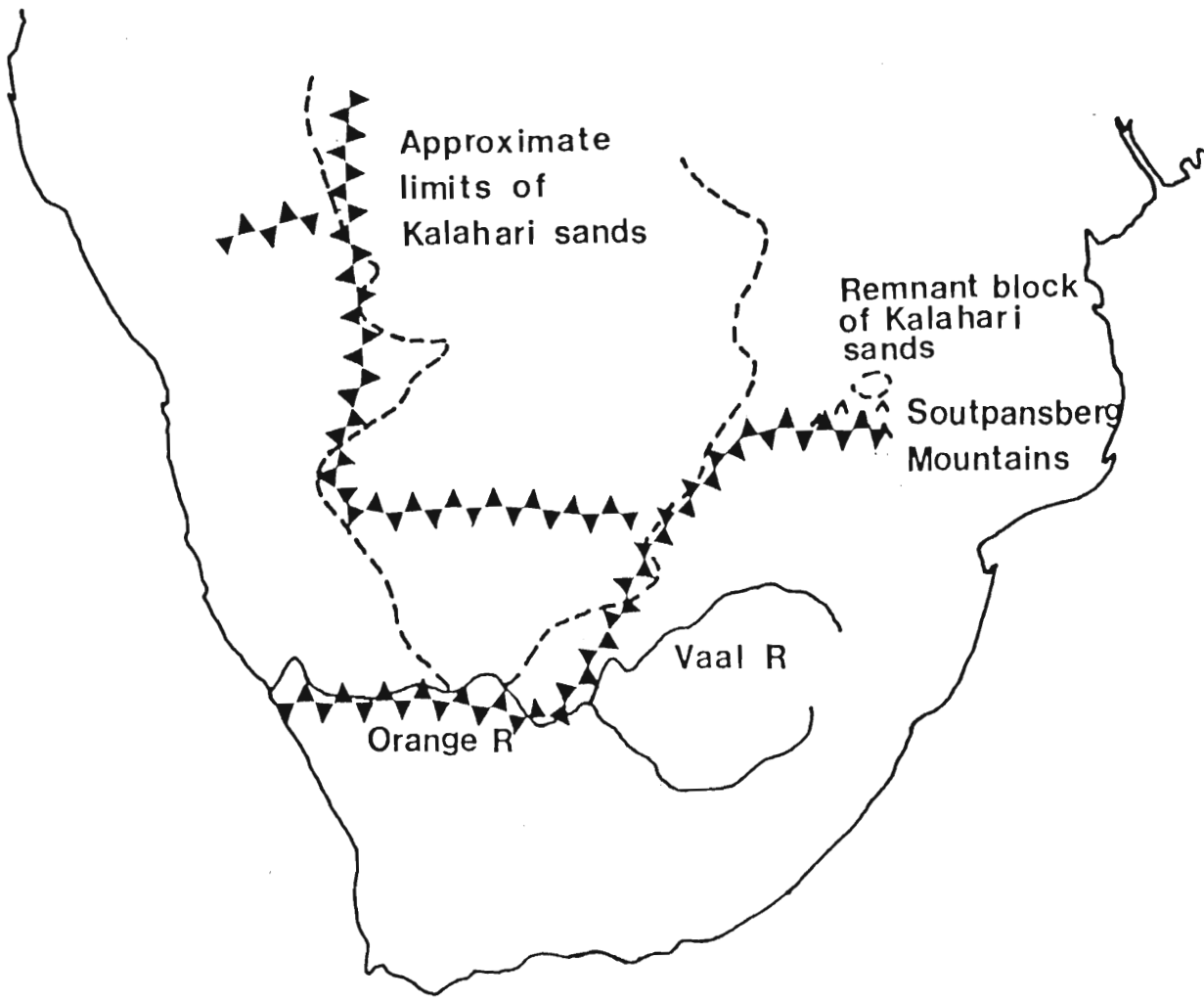


Fig. 4.6 Map showing certain biogeographical features in relation to approximate position of morphometric transition zones in Cynictis. Position of transition zones (indicated by double row of triangles) determined from geographic pattern of phenetic distances between adjacent OTUs (see Fig. 4.5).

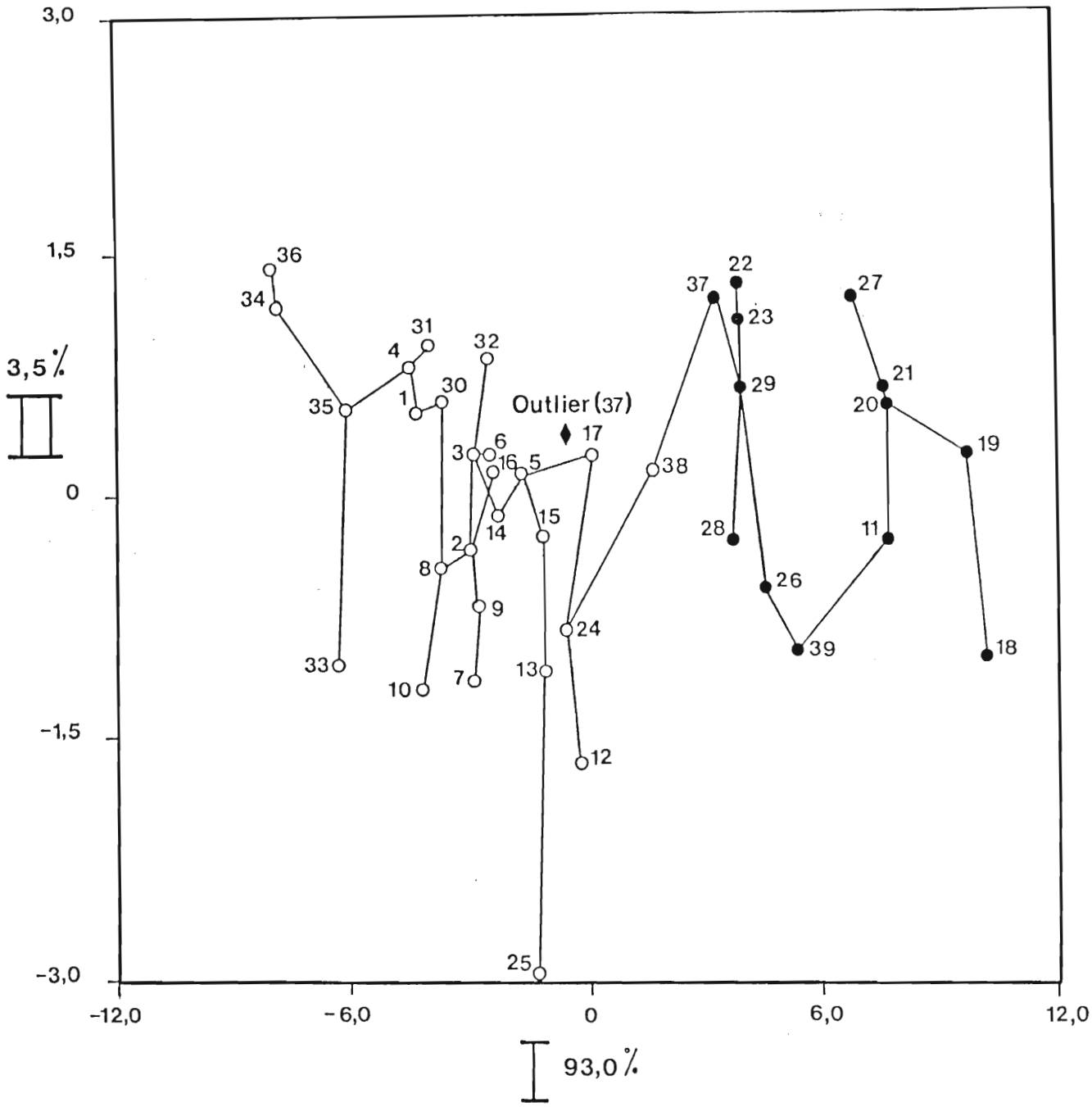


Fig. 4.7 Scattergram of first two components from a 14 - variable principal components analysis of 39 OTU means. A minimum spanning tree is superimposed. OTUs are defined in Fig. 4.2. Open circles represent OTUs from the southern phenon in Fig. 4.3, and closed circles represent the northern phenon. The closed diamond symbol represents a phenetic outlier from OTU 37 (see text for full explanation).

Table 4.9

Factor matrix from a 14 - variable principal components analysis of 39 OTUs of *C. penicillata*

Measurements		Factors (loadings x 1000)		
		I	II	III
Condylo - basal length	CBL	-674	608	200
Brain case width	BCW	-231	-317	108
Mandibular ramus height	MRH	-231	-317	108
Supraoccipital height	SOH	-107	-51	-93
Mandibular tooth row	MTR	-280	75	-28
Inter - canine distance	ICD	-103	-19	-76
Width at bullae	WAB	-297	-368	-328
Occipital condyle width	CNW	-124	-13	-6
Postorbital constriction	POC	-14	-337	873
Least interorbital width	IOW	-168	-239	-5
Zygomatic width	ZYW	-446	-456	-180
Length of P^4	LP4	-82	56	-17
Bulla length	BUL	-101	63	14
Width of P^4	WP4	-81	-9	-23
% Variance		93,0	3,6	1,1

variable, POC (very high, positive eigenvector loading on the third component: Table 4.9), only accounted for 1,1% of the variation. These results indicate that craniometric variation in C. penicillata is dominated by overall skull size.

The results in Fig. 4.7 and Table 4.9 were obtained by PCA of the covariance matrix. When PCA was repeated using the correlation matrix rather than the covariance matrix, the pattern of variation in the second component from the covariance matrix was lost (included in the first component), and the second component resembled the third component from the covariance matrix, in reflecting the importance of the variable POC. Since it was felt that the second component from the covariance matrix has biological reality, and since the pattern of variation on the 'POC - influenced' component did not produce a meaningful pattern of variation among OTUs, the results from the covariance matrix were considered to be superior, and only these results were presented in this study.

The two major phena distinguished from CA (Figs. 4.3, 4.4) are also evident in the PCA scattergram in Fig. 4.7, separated mainly on the basis of size (i.e. the first component). Since eigenvector loadings for the first component were negative, high negative scores on the first component represent larger - skulled individuals and vice

versa. The southern phenon (open circles in Fig. 4.7) is larger in skull size than the northern phenon (closed circles in Fig. 4.7). The position on the scatterplot of a single individual which was found to be an outlier of OTU 37, has been plotted using the method described in Dippenaar and Rautenbach (1986) for plotting an 'unknown' specimen on an existing scatterplot. This specimen was removed from the sample prior to calculation of means for CA and PCA, as it was observed to have a CBL of 67,0mm which was conspicuously higher than the highest CBL (64,3mm) recorded for other specimens from OTU 37. The position of this specimen on the scattergram confirms that it is a craniometric outlier, more typical of the southern phenon than the northern phenon in which it occurred.

Subgroups of the two major groups, corresponding with subclusters on the ATD phenogram (Fig. 4.3), can be distinguished on the basis of overall size (i.e. first component: Fig. 4.7). Variation within groups and subgroups is primarily along the second component (a shape vector; see above), with high positive scores indicating long, narrow skulls and high negative scores indicating shorter, wider skulls. By way of contrast variation between groups and sub - groups is primarily along the first component with high negative scores indicating larger skulls and high positive scores indicating smaller skulls. This trend is emphasized by the position of minimum spanning tree connections on the

scattergram which show greater phenetic similarity between individuals within a group (i.e. along the second component) than between adjacent individuals from different groups (along the first component). The existence of independent components of craniometric variation within and between subgroups and groups of OTUs is an indication that recognition of groups is based, not on arbitrary subdivisions of a simple cline in size, but rather on the existence of separate, or partly separate, gene pools which merit some form of taxonomic recognition.

The distinctiveness in shape of Natal specimens, indicated from the correlation phenogram (Fig. 4.4), is reflected in the position of OTU 25 as an outlier on the second principal component in Fig. 4.7. The large negative value of OTU 25 on the second principal component indicates that it represents a relatively short and wide (i.e. squat) skull shape compared to populations from the rest of the species' range.

DISCRIMINANT FUNCTIONS ANALYSIS OF OTUs (DFA: Fig. 4.8). In order to test the hypothesis that the two major groups of OTUs can be distinguished on statistical grounds a two - group DFA was carried out, using the major clusters defined from the distance phenogram (Fig. 4.3) as *a priori* groups. Fig. 4.8 shows the distribution of discriminant scores to be totally bimodal. OTUs were assigned to their correct *a priori* groups with 97% accuracy. Only OTU 38 was

misclassified (as belonging to the northern rather than the southern group). The phenetic intermediacy of OTU 38 is also indicated in its position midway between the distribution plots of the two groups in Fig. 4.8 as well as in its intermediate position on the PCA scattergram (Fig. 4.7). This result suggests that OTU 38 may be a zone of hybridisation (between two species), or intergradation (between two subspecies). The bimodal distribution of discriminant scores for specimens from the northern phenon (Fig. 4.8) reflects the occurrence of two sub - groups (with some overlap between them) within this phenon.

DFA OF INDIVIDUALS (Fig. 4.9). According to the biological species concept, species are 'groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups' (Mayr, 1942). The taxonomic and evolutionary reality of the parapatric phena described above depends therefore on evidence of interbreeding, or lack of interbreeding, between them. Using DFA of individuals, Genoways and Choate (1972) and George, Choate and Genoways (1981) provided indirect evidence that negligible interbreeding (as inferred from non - overlap of discriminant scores from craniometric data) occurred between three parapatric shrew phena (previously recognised as a single species Blarina brevicauda) from the southern United States. This approach, which assumes morphological intermediacy of hybrids, has been used to

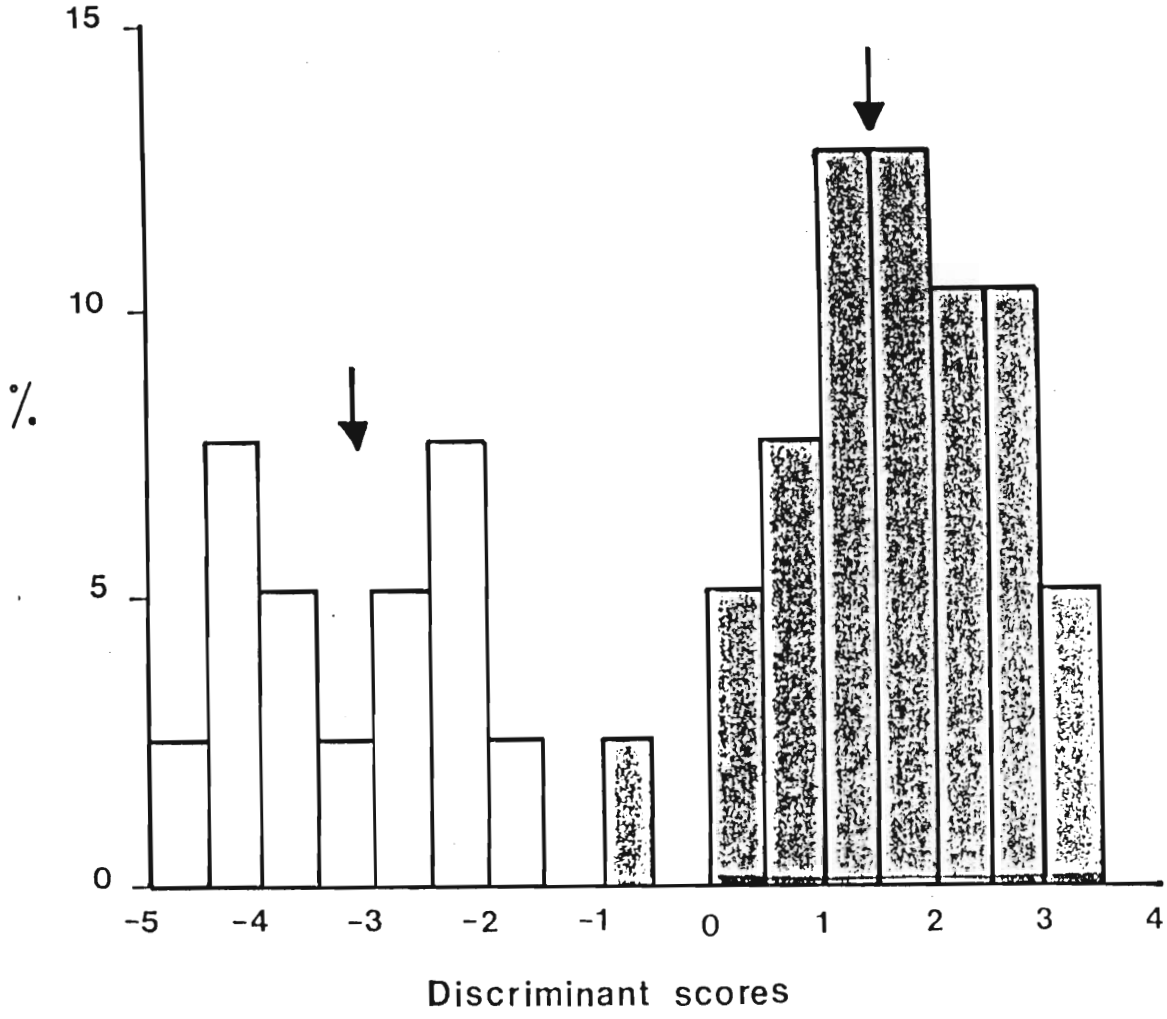


Fig. 4.8 Histogram of linear discriminant scores from a two - group discriminant functions analysis of 39 OTU means in C. penicillata. Arrows indicate positions of mean discriminant scores. Open bars indicate OTUs from the northern phenon in Fig. 4.3; closed bars indicate the southern phenon.

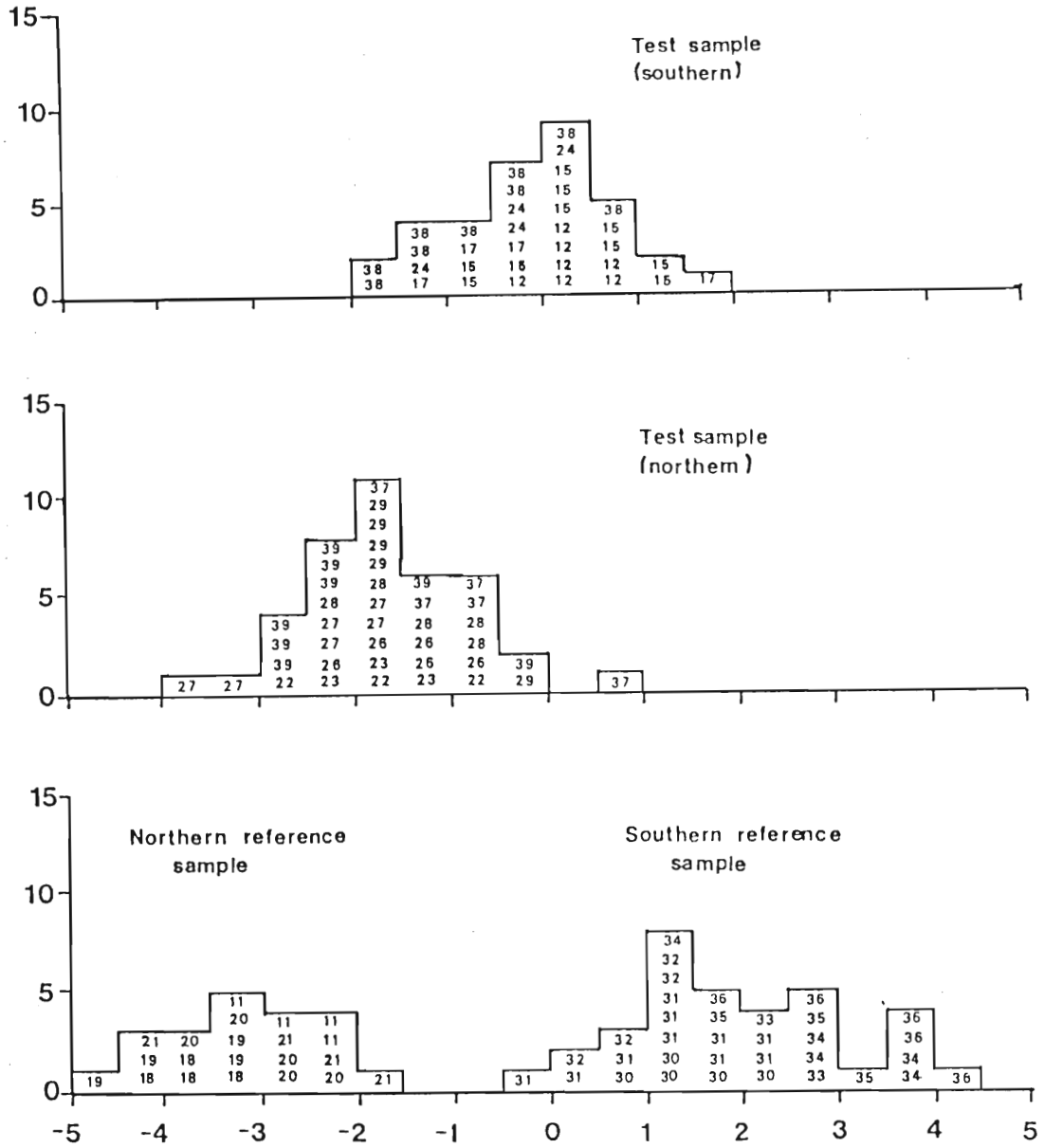


Fig. 4.9 Histogram of linear discriminant scores for C. penicillata individuals. Discriminant scores are indicated along the horizontal axes, and frequency of individuals is indicated along the vertical axes. Northern and southern reference samples are indicated in the lower histogram, test specimens referred to the southern phenon are indicated in the top histogram, test specimens referred to the northern phenon are indicated in the middle histogram. Codes within histograms indicate OTU assignment of individuals.

detect natural hybrids in a number of studies (Genoways and Choate, 1972, and refs. within; Dowling, Smith and Brown, 1989, and refs. within). Caution needs to be exercised as Neff and Smith (1978) have demonstrated that the degree of intermediacy of (known) hybrids may vary, and the amount of variability in hybrids and their parents may preclude the identification of all hybrid individuals. Neff and Smith (op. cit.) advocate the use of PCA rather than DFA for detecting natural hybrids, as the former is freer of computational assumptions. However, in the present case, it was decided that DFA was the appropriate technique for assessing the assignment of 'unknown' (in this case intermediately sized, potential hybrids) individuals to a priori groups. A priori groups were defined objectively by means of a previous CA and PCA of OTU means (Figs 4.3, 4.4, 4.7).

The lower histogram in Fig. 4.9 shows the non - overlap in discriminant scores between individuals from reference samples of the two major phena described above (Figs. 4.3, 4.4, 4.7). OTUs making up the two reference samples are indicated in Fig. 4.9. The test sample, comprising specimens from OTUs intermediate in skull size and geographical position between the two reference samples, was sub - divided into samples comprising OTUs referred to the southern (top histogram: Fig. 4.9) and northern (middle phenogram: Fig. 4.9) phena. These two test samples fall

north and south of the major transition zone separating the southern and northern phena (Fig. 4.5).

With the exception of the outlying individual from OTU 37 (discussed above), no overlap in discriminant scores occurs between adjacent OTUs in the northern test and southern reference samples in spite of an extensive zone of parapatry along the lower and middle Orange River (compare lower and middle histograms in Fig. 4.9). On the other hand a zone of intergradation between the northern and southern phena is indicated by the degree of overlap between histograms of the southern and northern test samples (upper and middle histograms in Fig. 4.9), involving OTUs in the northeastern Cape (24 (in part), 37--39) and southeastern Transvaal (14, 15, 24 (in part)).

Extensive intergradation is also indicated by the degree of overlap between the northern reference and northern test samples (middle and lower histograms: Fig. 4.9) which lie east and west respectively of the transition zone separating sub - groups of the northern phenon (see Fig. 4.5).

Univariate analyses

Summary statistics (means, standard deviations, ranges and coefficients of variation) for 14 cranial and two external measurements in 39 OTUs are given in Table 4.10. F values

from analysis of variance (ANOVA) of OTU means are given for each measurement in Table 4.10, and SS-STP diagrams are presented for six selected cranial measurements in Table 4.11. Apart from POC, which showed significant differences among OTUs only at the 5% level, all measurements showed significant differences among OTUs at the 0,1% level (Fig. 4.10). The high number of non - significant ($\underline{P} < 0,001$) subsets in SS-STP diagrams for most measurements (Fig. 4.11) is an indication of the extent of geographic variation in most measurements. External measurements tended to follow the same geographical trend as cranial measurements, with individuals having the smallest head and body (H&B) and tail (TL) lengths occurring in the northern Transvaal and Botswana (OTUs 11, 18--21, Table 4.10: H&B = 278--310; TL = 150--225) and the largest individuals occurring in the southern and eastern Cape (OTUs 33--36, Table 4.10: H&B = 304--390; TL = 230--290).

The order of ranked means is similar in all measurements, as indicated in the SS-STP diagrams of the six selected measurements (Fig. 4.11), with larger values in southern OTUs, intermediate values in the northern Cape, southern Botswana and Namibia, and small values in Botswana, northern Namibia and northern Transvaal. SS-STP diagrams of individual measurements show some degree of overlap between phena distinguished from multivariate analyses (Figs. 4.3, 4.4, 4.7). This is because the presence of a few

Table 4.10

Summary statistics of two external and fourteen cranial measurements in 39 pooled localities (OTUs) of *C. penicillata*, and *F* statistics from ANOVA of OTU means. *P* = significance probability of *F* values; *Y* = mean; *N* = sample size; S.D. = standard deviation; C.V. = coefficient of variation.

OTU	Head & body length				Tail length				CBL			
	Y(N)	S.D.	Range	C.V.	Y(N)	S.D.	Range	C.V.	Y(N)	S.D.	Range	C.V.
	F = 4,76; P << 0,001				F = 5,60; P << 0,001				F = 24,35; P << 0,001			
1	373 (6)	54,0	320-460	14,5	234 (6)	13,9	220-250	6,0	68,2 (9)	1,46	65,7-70,0	2,14
2	339 (30)	23,8	308-428	7,0	231 (30)	16,1	190-273	7,0	66,8 (36)	1,88	62,8-70,3	2,82
3	340 (27)	20,4	318-410	6,0	233 (27)	16,2	200-266	7,0	67,0 (27)	1,58	64,8-70,1	2,35
4	384 (4)	28,0	348-415	7,3	224 (4)	22,4	200-249	10,0	68,6 (5)	1,39	66,5-70,0	2,02
5	325 (10)	28,4	300-377	8,7	229 (10)	12,7	210-250	5,6	66,0 (10)	1,18	64,1-68,1	1,79
6	332 (7)	17,8	302-360	5,4	219 (7)	11,3	200-233	5,1	66,8 (11)	1,10	65,0-68,2	1,65
7	353 (5)	42,2	340-390	6,0	230 (5)	20,5	205-248	8,9	66,1 (5)	2,51	63,7-69,8	3,79
8	365 (8)	18,6	340-390	5,1	207 (8)	14,6	190-230	7,0	67,1 (8)	1,75	65,0-69,5	2,62
9	354 (4)	30,4	314-385	8,6	194 (4)	30,5	165-232	15,7	66,3 (4)	2,03	64,1-69,0	3,06
10	333 (4)	28,3	310-368	8,5	215 (4)	15,1	195-230	7,0	67,3 (5)	0,97	66,3-68,4	1,44
11	299 (4)	15,1	278-310	5,0	209 (4)	13,1	195-220	6,3	59,6 (4)	1,20	58,1-60,6	2,01
12	314 (7)	20,8	285-350	6,6	208 (7)	24,7	180-239	11,9	64,3 (9)	1,34	62,2-66,8	2,08
13	324 (6)	16,9	301-346	5,2	215 (6)	16,3	200-240	7,6	64,9 (6)	0,74	63,9-66,1	1,13
14	319 (5)	23,3	284-345	7,3	213 (5)	12,4	196-225	5,8	66,4 (5)	1,39	64,0-67,6	2,09
15	346 (10)	16,0	314-362	4,6	219 (10)	12,4	193-238	5,7	65,6 (10)	1,24	63,4-67,4	1,89
16	322 (3)	12,6	310-335	3,9	233 (3)	25,6	205-255	11,0	66,5 (4)	2,48	63,7-69,6	3,73
17	334 (4)	21,4	310-360	6,4	224 (4)	18,0	200-240	8,0	64,9 (4)	2,10	63,0-67,7	3,24
18	279 (3)	3,5	275-281	1,2	194 (3)	14,1	185-210	7,3	57,4 (4)	1,53	56,3-59,6	2,66
19	289 (4)	5,8	281-295	2,0	200 (4)	11,2	190-215	5,6	58,5 (5)	1,87	56,2-60,9	3,20
20	305 (5)	4,8	300-310	1,6	204 (4)	19,8	183-229	9,7	60,0 (6)	0,53	59,6-61,0	0,89
21	300 (4)	6,4	294-306	2,1	196 (4)	30,5	150-215	15,6	60,2 (4)	1,53	58,1-61,6	2,54
22	322 (4)	11,9	310-335	3,7	261 (4)	13,1	250-280	5,0	63,0 (4)	2,51	60,8-65,8	3,98
23	324 (2)	305-343			226 (2)	218-235			63,3 (3)	0,90	62,4-64,2	1,43
24	339 (4)	9,4	327-350	2,8	237 (4)	11,0	226-250	4,6	63,9 (4)	1,26	62,9-65,7	1,96
25	338 (5)	18,4	307-355	5,4	222 (5)	17,0	201-246	7,7	64,0 (4)	2,15	61,4-66,6	3,36
26	305 (4)	21,7	274-325	7,1	224 (4)	14,3	215-245	6,4	61,8 (5)	1,69	58,8-63,0	2,74
27	311 (5)	13,0	290-325	4,2	228 (5)	13,3	210-245	5,8	60,9 (6)	2,24	56,7-62,9	3,68
28	304 (2)	303-306			217 (2)	214-220			62,4 (4)	1,64	60,0-63,6	2,63
29	329 (6)	15,2	310-350	4,6	229 (6)	8,3	220-241	3,6	63,0 (6)	1,11	60,9-64,1	1,77
30	324 (4)	13,8	310-340	4,2	251 (4)	22,5	225-280	9,0	67,7 (5)	2,61	63,8-70,6	3,85
31	335 (4)	49,2	265-380	14,7	242 (4)	42,7	190-290	17.6	68,1 (12)	1,82	64,6-70,7	2,68
32	344 (4)	11,3	328-355	3,3	267 (4)	4,0	263-272	1,5	67,1 (4)	1,22	65,4-68,2	1,82
33	359 (4)	11,1	345-370	3,1	282 (4)	9,6	268-290	3,4	68,5 (3)	0,82	67,8-69,4	1,19
34	344 (3)	35,6	304-373	10,4	268 (3)	5,7	262-273	2,1	70,9 (5)	1,97	67,5-72,3	2,78
35	364 (3)	5,5	359-370	1,5	254 (3)	31,9	230-290	12,6	69,5 (5)	1,61	66,8-70,8	2,31
36	367 (3)	20,8	350-390	5,7	252 (3)	22,5	230-275	9,0	71,4 (6)	1,80	68,9-73,7	2,53
37	306 (5)	15,2	290-330	5,0	247 (5)	9,6	235-260	3,9	63,6 (5)	0,70	62,6-64,3	1,10
38	325 (6)	26,3	290-370	8,1	226 (6)	10,3	210-240	4,6	63,8 (10)	1,50	61,8-66,0	2,36
39	328 (7)	28,0	310-390	8,5	220 (7)	33,9	190-292	15,4	60,9 (11)	1,21	59,2-63,2	1,98

Table 4.10 (Continued)

	BCW				MRH				MTR			
	F = 14,71; P << 0,001				F = 10,73; P << 0,001				F = 24,37; P << 0,001			
1	28,7 (9)	0,82	27,2-29,8	2,85	18,7 (9)	0,70	17,6-19,8	3,74	21,8 (9)	0,69	20,7-22,6	3,16
2	28,5 (36)	0,72	27,1-30,3	2,54	18,0 (36)	0,70	17,0-19,6	3,90	21,6 (36)	0,65	20,2-22,9	2,99
3	28,3 (27)	0,67	27,0-30,0	2,37	18,0 (27)	0,94	16,6-20,6	5,22	21,7 (27)	1,01	17,4-23,0	4,66
4	28,9 (5)	0,90	27,6-29,8	3,12	18,6 (15)	1,29	17,2-20,6	6,96	21,7 (5)	0,70	21,0-22,8	3,26
5	28,2 (10)	0,64	27,4-29,5	2,25	17,7 (10)	0,86	16,2-18,8	4,85	21,4 (10)	0,73	20,0-22,3	3,41
6	28,2 (11)	0,80	26,9-29,1	2,84	17,9 (11)	0,67	16,9-19,1	3,76	21,1 (11)	0,65	19,9-22,1	3,10
7	28,7 (5)	0,15	28,5-28,9	0,51	18,6 (5)	0,71	17,4-19,3	3,84	21,4 (5)	0,66	20,6-22,0	3,10
8	29,0 (8)	0,54	27,7-29,3	1,87	18,4 (8)	0,75	17,6-19,7	4,10	21,8 (8)	0,24	21,3-22,0	1,12
9	28,7 (4)	0,64	28,0-29,5	2,23	18,2 (4)	0,60	17,4-18,7	3,31	22,0 (4)	0,73	21,1-22,7	3,34
10	29,3 (5)	0,79	28,4-30,5	2,69	18,4 (5)	0,37	18,2-19,1	2,01	21,7 (5)	0,42	21,1-22,1	1,94
11	25,8 (4)	0,76	25,1-26,9	2,94	16,1 (4)	0,28	15,8-16,4	1,71	18,4 (4)	0,39	18,0-18,9	2,10
12	28,5 (9)	0,58	27,5-29,6	2,02	17,6 (9)	0,64	16,2-18,6	3,66	20,6 (8)	0,67	19,7-21,8	3,24
13	28,3 (6)	0,56	27,2-28,8	1,99	18,1 (6)	0,69	17,0-18,8	3,83	21,1 (6)	0,29	20,7-21,4	1,40
14	28,3 (5)	0,73	27,4-29,3	2,58	17,8 (5)	0,50	17,4-18,7	2,82	21,5 (5)	0,40	21,1-22,1	1,84
15	28,7 (11)	0,60	27,9-29,7	2,08	17,5 (11)	0,57	16,9-18,7	3,28	21,1 (11)	0,44	20,3-21,8	2,08
16	28,2 (4)	0,79	27,0-28,8	2,82	18,0 (4)	0,81	17,4-19,2	4,47	21,7 (4)	1,16	20,1-22,8	5,33
17	27,8 (4)	0,70	27,2-28,6	2,53	17,4 (4)	0,50	17,0-18,0	2,90	20,6 (4)	0,29	20,4-21,0	1,39
18	26,1 (3)	0,38	25,8-26,5	1,45	16,0 (4)	0,49	15,4-16,5	3,09	18,0 (4)	0,81	16,9-18,6	4,50
19	25,6 (5)	0,80	24,8-26,6	3,11	16,1 (4)	0,57	15,5-16,7	3,52	18,1 (5)	0,60	17,5-19,1	3,29
20	26,3 (6)	0,55	25,6-27,0	2,09	16,1 (6)	0,49	15,3-16,6	3,03	19,0 (6)	0,53	18,3-19,8	2,78
21	25,9 (4)	0,29	25,6-26,3	1,14	16,6 (4)	1,01	16,0-18,1	6,08	18,8 (4)	0,90	18,0-19,7	4,81
22	26,8 (4)	0,17	26,5-26,9	0,65	17,3 (4)	0,79	16,6-18,4	4,55	19,8 (4)	0,24	19,5-20,1	1,24
23	26,7 (3)	0,58	26,3-27,4	2,19	16,9 (3)	0,38	16,5-17,2	2,23	19,9 (3)	0,36	19,5-20,2	1,81
24	28,0 (3)	0,96	27,1-29,0	3,44	17,7 (4)	0,99	16,6-19,0	5,61	20,5 (4)	0,36	20,0-20,8	1,74
25	29,3 (5)	1,20	27,3-30,3	4,09	18,4 (5)	0,88	17,1-19,2	4,77	20,8 (5)	0,62	20,2-21,8	2,97
26	26,9 (5)	0,43	26,5-27,6	1,59	16,4 (5)	0,44	16,1-17,2	2,67	19,1 (5)	0,69	18,4-20,1	3,61
27	25,8 (6)	0,45	25,5-26,7	1,74	16,7 (6)	0,73	15,6-17,4	4,36	18,8 (5)	0,68	18,2-19,9	3,59
28	26,8 (4)	0,53	26,2-27,4	1,98	17,7 (4)	0,52	17,1-18,3	2,92	18,9 (4)	0,96	17,8-20,1	5,07
29	26,9 (6)	0,70	25,8-27,7	2,59	17,0 (6)	0,52	16,3-17,6	3,04	19,2 (5)	0,53	18,5-19,8	2,74
30	28,3 (5)	0,57	27,8-29,2	2,03	18,7 (5)	1,02	17,6-20,1	5,44	21,7 (5)	0,56	20,8-22,2	2,59
31	28,7 (12)	0,74	27,8-30,2	2,56	18,9 (12)	0,74	17,7-20,2	3,92	21,8 (12)	0,77	20,9-23,2	3,52
32	28,2 (4)	0,52	27,8-29,0	1,86	18,0 (4)	0,95	16,9-19,0	5,29	21,6 (4)	0,51	21,1-22,3	2,36
33	29,8 (3)	0,85	29,0-30,7	2,85	19,4 (4)	0,99	18,0-20,1	5,10	22,4 (4)	0,51	22,0-23,1	2,27
34	29,3 (5)	1,07	28,2-30,6	3,66	19,2 (5)	1,10	17,4-20,1	5,75	23,0 (5)	0,60	22,0-23,5	2,61
35	29,3 (5)	0,51	28,6-29,9	1,75	19,2 (4)	0,21	18,9-19,4	1,08	22,8 (4)	0,29	22,4-23,0	1,26
36	29,4 (7)	1,08	27,9-30,9	3,68	19,8 (9)	0,78	18,2-20,8	3,92	23,1 (8)	0,62	22,2-24,1	2,69
37	26,4 (5)	0,87	25,2-27,4	3,29	16,6 (5)	0,76	15,9-17,8	4,56	20,1 (5)	0,63	19,2-20,9	3,13
38	27,6 (11)	0,60	26,7-28,6	2,17	17,1 (11)	0,63	15,8-17,7	3,67	20,5 (9)	0,40	19,9-21,1	1,97
39	27,2 (10)	0,80	26,3-28,4	2,95	16,4 (10)	0,66	15,2-17,2	4,02	19,3 (10)	0,51	18,4-20,1	2,65

Table 4.10 (Continued)

	ICD				WAB				CNW			
	F = 12,64; P << 0,001				F = 19,20; P << 0,001				F = 6,01; P << 0,001			
1	8,46 (9)	0,09	8,35-8,68	1,08	28,5 (9)	0,95	27,0-30,2	3,35	16,0 (9)	0,86	14,4-17,2	5,37
2	8,55 (36)	0,32	7,92-9,14	3,76	28,6 (36)	0,82	27,1-30,1	2,87	16,1 (36)	0,57	15,0-17,5	3,54
3	8,50 (27)	0,28	7,87-9,00	3,27	28,6 (27)	0,93	27,1-31,2	3,24	15,9 (27)	0,66	14,1-16,8	4,16
4	8,27 (5)	0,58	7,64-8,95	7,02	28,7 (5)	1,00	26,9-29,3	3,48	16,4 (5)	0,45	15,8-17,0	2,74
5	8,39 (10)	0,23	8,05-8,76	2,72	28,4 (10)	0,83	26,7-29,7	2,93	15,9 (10)	0,69	14,7-17,1	4,33
6	8,62 (11)	0,27	8,07-9,04	3,10	29,0 (11)	0,56	28,0-30,0	1,92	16,2 (11)	0,43	15,5-17,0	2,68
7	8,46 (5)	0,26	8,27-8,90	3,11	29,2 (5)	0,56	28,5-29,8	1,91	16,4 (5)	1,13	15,2-17,8	6,85
8	8,55 (8)	0,37	7,69-8,87	4,37	28,8 (8)	0,71	27,7-29,6	2,48	16,4 (8)	0,45	15,7-17,0	2,76
9	8,66 (4)	0,18	8,45-8,89	2,09	29,0 (4)	1,41	27,4-30,3	4,85	16,3 (4)	0,80	15,5-17,2	4,94
10	8,74 (5)	0,20	8,52-9,06	2,62	29,4 (5)	0,69	28,8-30,4	2,36	16,3 (5)	0,46	15,9-16,8	2,79
11	7,16 (4)	0,17	6,92-7,31	2,37	25,5 (4)	0,35	25,1-25,9	1,37	15,2 (4)	0,55	14,6-15,8	3,60
12	8,28 (9)	0,49	7,47-8,95	5,96	28,1 (9)	0,68	27,2-29,4	2,42	16,1 (9)	0,51	15,6-17,0	3,16
13	8,18 (6)	0,33	7,57-8,44	4,03	28,3 (6)	0,70	27,5-29,5	2,47	15,9 (6)	0,53	15,3-16,6	3,34
14	8,44 (5)	0,28	8,00-8,77	3,37	28,7 (5)	0,84	28,0-29,8	2,94	15,7 (5)	0,46	15,2-16,3	2,97
15	8,24 (11)	0,37	7,40-8,71	4,52	28,3 (11)	0,84	26,7-29,3	2,98	16,2 (10)	0,48	15,2-17,0	2,93
16	8,73 (4)	0,26	8,55-9,12	3,01	27,8 (4)	0,95	26,8-28,9	3,43	16,1 (4)	1,20	14,4-17,2	7,49
17	8,28 (4)	0,63	7,81-9,20	7,58	27,8 (4)	0,97	27,2-29,3	3,50	16,2 (4)	0,52	15,7-16,6	3,22
18	7,08 (4)	0,28	6,81-7,44	4,00	24,8 (4)	0,68	24,3-25,9	2,75	14,2 (4)	0,43	13,8-14,8	3,06
19	6,98 (5)	0,42	6,61-7,47	6,07	24,9 (5)	0,72	24,1-26,0	2,88	14,6 (4)	0,41	14,1-14,9	2,83
20	7,36 (6)	0,48	6.87-8,04	6,50	25,0 (6)	0,78	23,9-26,3	3,13	14,8 (6)	0,31	14,3-15,0	2,07
21	7,32 (4)	0,24	7,14-7,67	3,32	24,9 (4)	0,67	24,4-25,8	2,69	15,2 (4)	0,46	14,7-15,8	3,01
22	7,66 (4)	0,61	6,96-8,30	8,02	26,4 (4)	0,66	25,8-27,3	2,49	15,3 (4)	0,99	13,9-16,1	6,49
23	7,70 (3)	0,20	7,49-7,89	2,60	25,6 (3)	0,80	24,8-26,4	3,13	15,1 (3)	0,10	15,0-15,2	0,66
24	7,92 (4)	0,19	7,69-8,11	2,36	27,8 (4)	0,57	27,0-28,3	2,06	16,1 (4)	0,36	15,8-16,6	2,23
25	8,10 (4)	0,38	7,53-8,36	4,76	29,1 (5)	0,53	28,2-29,6	1,82	15,7 (4)	0,72	14,8-16,5	4,62
26	7,74 (5)	0,72	7,04-8,68	9,27	26,5 (5)	0,57	25,9-27,4	2,16	15,5 (4)	0,79	14,3-16,0	5,10
27	7,49 (6)	0,26	7,06-7,80	3,42	25,3 (6)	0,58	24,3-25,8	2,28	14,9 (6)	0,40	14,4-15,5	2,70
28	7,86 (4)	0,48	7,31-8,28	6,08	26,1 (4)	0,68	25,2-26,8	2,62	15,5 (4)	0,74	14,8-16,4	4,77
29	7,64 (5)	0,64	6,92-8,40	8,45	26,2 (6)	0,48	25,8-27,1	1,84	15,4 (6)	0,45	14,7-16,0	2,90
30	8,63 (5)	0,20	8,40-8,94	2,37	28,0 (5)	0,98	26,4-28,9	3,51	16,4 (5)	0,52	15,7-17,0	3,15
31	8,52 (12)	0,30	8,15-9,03	3,52	28,4 (11)	0,84	26,8-29,8	2,95	16,4 (11)	0,47	15,4-17,1	2,88
32	8,12 (4)	0,44	7,70-8,60	5,45	28,1 (4)	0,60	27,7-29,0	2,15	16,3 (4)	0,31	15,9-16,6	1,90
33	8,61 (4)	0,50	7,86-8,89	5,81	29,5 (3)	0,82	28,8-30,4	2,77	17,0 (3)	0,80	16,2-17,8	4,71
34	9,00 (5)	0,34	8,57-9,50	3,82	29,6 (5)	0,88	28,3-30,6	2,97	17,1 (5)	0,60	16,5-17,9	3,53
35	8,57 (5)	0,20	8,30-8,84	2,37	29,1 (4)	1,22	27,9-30,2	4,19	16,5 (5)	0,61	15,8-17,4	3,67
36	8,63 (6)	0,27	8,26-9,03	3,16	29,2 (7)	1,12	27,8-30,9	3,82	16,5 (6)	0,58	15,8-17,3	3,53
37	7,80 (5)	0,28	7,53-8,25	3,59	26,1 (5)	0,69	25,1-26,8	2,64	15,5 (5)	0,60	14,6-16,2	3,85
38	8,04 (11)	0,40	7,36-8,58	4,98	27,1 (10)	0,70	26,0-27,9	2,57	15,5 (11)	0,59	14,9-17,0	3,84
39	7,48 (10)	0,48	6,87-8,53	6,36	26,2 (9)	0,96	25,5-28,2	3,65	15,1 (11)	0,51	14,5-16,2	3,34

Table 4.10 (Continued)

	POC				IOW				ZYW			
	F = 1,47; P > 0,01				F = 8,42; P << 0,001				F = 17,90; P << 0,001			
1	14,9 (9)	1,49	12,9-17,0	10,00	15,6 (9)	0,88	13,8-16,8	5,63	40,7 (9)	1,38	38,2-42,0	3,40
2	15,2 (36)	1,46	12,9-19,4	9,67	15,5 (36)	0,66	14,3-17,7	4,25	40,4 (36)	1,18	38,0-44,2	2,91
3	14,8 (27)	1,02	12,9-17,0	6,88	15,4 (27)	0,71	13,8-16,8	4,60	39,9 (27)	1,35	36,6-42,1	3,38
4	15,0 (5)	0,84	13,9-16,0	5,61	15,4 (5)	0,72	14,6-16,4	4,71	40,3 (5)	1,26	38,9-42,1	3,12
5	14,6 (10)	1,20	13,0-16,5	8,16	15,1 (10)	0,71	14,3-16,8	4,68	39,4 (10)	0,99	38,0-40,8	2,52
6	14,2 (11)	1,29	12,1-15,9	9,02	15,5 (11)	0,50	14,7-16,5	3,26	39,8 (11)	0,88	38,4-41,4	2,21
7	15,5 (5)	1.10	14,1-16,8	7,12	15,8 (5)	0,49	15,0-16,2	3,11	40,3 (4)	0,72	39,4-41,0	1,78
8	15,3 (8)	1,25	14,2-17,9	8,16	15,8 (8)	0,90	14,7-17,1	5,73	40,4 (8)	1,08	39,1-42,2	2,67
9	15,4 (4)	0,88	14,7-16,6	5,71	15,4 (4)	1,28	13,9-16,9	8,32	40,0 (4)	0,85	38,8-40,8	2,13
10	16,0 (5)	1,93	13,2-17,6	12,06	16,5 (5)	1,14	15,2-18,2	6,89	40,7 (5)	0,88	39,5-41,9	2,16
11	14,5 (4)	0,36	14,2-15,0	2,48	14,1 (4)	0,58	13,6-14,7	4,10	35,8 (4)	0,33	35,4-36,1	0,92
12	16,4 (9)	0,94	14,8-17,6	5,76	15,5 (9)	0,50	14,9-16,2	3,20	39,4 (9)	0,99	37,8-41,1	2,51
13	15,3 (6)	1,21	13,1-16,6	7,89	15,3 (6)	0,30	15,0-15,8	1,97	39,8 (6)	0,31	39,3-40,2	0,79
14	14,7 (5)	0,21	14,4-14,9	1,41	15,9 (5)	0,55	15,0-16,4	3,49	39,7 (5)	1,41	37,6-41,2	3,55
15	15,1 (11)	1,61	12,7-17,2	10,66	15,1 (11)	0,58	14,1-15,8	3,87	39,0 (11)	1,39	36,3-40,9	3,56
16	14,8 (4)	1,42	13,2-16,6	9,64	15,1 (4)	1,08	13,8-16,4	7,17	40,3 (4)	1,11	39,5-41,9	2,77
17	14,7 (4)	0,98	13,5-15,9	6,69	14,8 (4)	0,66	14,2-15,6	4,45	38,4 (4)	1,84	36,7-41,0	4,78
18	15,2 (4)	1,10	13,6-16,0	7,20	13,4 (4)	0,50	12,8-14,0	3,78	34,6 (4)	0,60	34,0-35,4	1,75
19	14,7 (5)	0,83	13,6-15,8	5,67	13,4 (5)	0,74	12,6-14,2	5,54	34,0 (4)	0,92	33,2-34,9	2,72
20	14,6 (6)	0,88	13,3-15,4	6,03	13,5 (5)	0,59	12,6-14,0	4,38	35,0 (5)	1,30	33,4-36,7	3,70
21	14,9 (4)	0,39	14,5-15,4	2,60	13,0 (4)	0,24	12,7-13,2	1,82	35,3 (4)	1,36	33,5-36,8	3,86
22	14,4 (4)	1,25	13,0-16,0	8,71	13,7 (3)	0,50	13,2-14,3	3,66	36,0 (3)	1,70	34,0-37,0	4,74
23	16,3 (3)	0,79	15,4-16,9	4,87	14,1 (3)	0,66	13,5-14,8	4,65	36,0 (3)	2,06	33,6-37,3	5,71
24	15,5 (4)	0,46	14,9-16,0	3,02	14,9 (4)	0,88	13,7-15,6	5,92	38,7 (4)	1,78	37,3-41,1	4,61
25	16,2 (5)	1,37	14,8-18,3	8,46	15,7 (5)	0,81	14,6-16,5	5,18	40,7 (5)	1,28	38,7-42,2	3,15
26	15,8 (5)	0,46	15,1-16,3	2,88	14,2 (5)	0,30	13,8-14,6	2,08	37,0 (5)	1,12	36,0-38,9	3,02
27	14,1 (6)	1,30	12,8-16,2	9,21	13,6 (6)	0,72	12,7-14,7	5,26	35,2 (6)	1,10	33,8-36,8	3,11
28	15,5 (4)	0,96	14,8-16,9	6,23	14,7 (4)	0,55	14,1-15,4	3,73	37,4 (4)	0,37	36,9-37,7	0,99
29	15,5 (6)	1,34	14,0-17,4	8,63	14,4 (6)	0,79	13,8-15,9	5,44	36,2 (5)	1,51	34,9-38,8	4,18
30	15.0 (5)	1,73	13,6-17,9	11,54	15,4 (5)	0,67	14,4-16,1	4,35	40,6 (5)	0,75	39,4-41,4	1,86
31	14,8 (12)	1,10	13,2-17,7	7,43	15,4 (12)	0,60	14,2-16,4	3,87	39,9 (10)	1,12	38,1-41,7	2,82
32	14,3 (4)	1,10	13,3-15,6	7,55	15,5 (4)	0,21	15,2-15,7	1,33	39,6 (4)	0,70	38,9-40,5	1,77
33	15,8 (4)	1,05	14,4-16,6	6,68	16,4 (4)	0,44	16,0-17,0	2,71	42,0 (3)	0,06	41,9-42,0	0,14
34	14,8 (5)	0,61	14,3-15,8	4,15	16,2 (5)	0,52	15,4-16,8	3,22	41,5 (5)	1,26	40,1-43,0	3,05
35	15,8 (5)	0,70	14,7-16,6	4,46	15,7 (5)	0,58	14,9-16,3	3,70	40,9 (4)	1,98	38,9-43,1	4,84
36	15,2 (7)	0,77	14,3-16,5	5,08	15,9 (7)	0,76	14,8-16,7	4,79	41,5 (6)	1,67	39,8-43,6	4,02
37	15,2 (5)	0,86	13,8-16,0	5,68	14,6 (5)	0,57	13,6-15,0	3,89	36,6 (5)	1,20	35,4-38,0	3,27
38	14,8 (11)	0,52	14,0-15,8	3,54	14,8 (10)	0,72	13,9-16,1	4,90	37,7 (11)	1,39	35,6-40,9	3,68
39	15,6 (11)	1,25	14,1-17,5	8,01	14,6 (11)	0,76	13,6-15,9	5,20	36,6 (10)	1,22	35,3-39,2	3,32

Table 4.10 (Continued)

	BUL				WP4				SOH			
	F = 5,50; P << 0,001				F = 10,48; P << 0,001				F = 3,90; P << 0,001			
1	17,6 (9)	0,67	16,3-18,4	3,80	5,40 (9)	0,29	4,91-5,75	5,44	12,8 (9)	0,60	12,0-13,8	4,70
2	17,2 (36)	0,69	15,6-18,8	4,02	5,39 (36)	0,30	4,91-6,11	4,91	13,0 (36)	0,79	11,5-15,6	6,10
3	17,0 (27)	0,60	15,8-18,1	3,54	5,45 (27)	0,26	4,93-5,96	4,83	13,0 (27)	0,63	11,8-14,5	4,81
4	17,6 (5)	0,36	17,3-18,1	2,03	5,33 (5)	0,26	4,95-5,65	4,82	12,6 (5)	0,92	11,4-13,7	7,31
5	17,3 (10)	0,43	16,8-17,9	2,47	5,42 (10)	0,31	4,93-5,99	5,72	12,9 (10)	0,64	12,1-14,3	4,97
6	17,4 (11)	0,55	16,4-18,2	3,15	5,29 (11)	0,23	4,75-5,61	4,38	13,1 (11)	0,70	12,0-14,2	5,36
7	17,6 (5)	0,35	17,1-18,0	2,01	5,62 (5)	0,35	5,32-6,00	6,20	13,1 (5)	0,72	12,0-13,9	5,55
8	17,3 (8)	0,64	16,0-18,3	3,72	5,62 (8)	0,16	5,38-5,90	2,94	13,0 (8)	0,40	12,2-13,4	3,08
9	16,9 (4)	0,50	16,3-17,4	2,94	5,64 (4)	0,20	5,40-5,90	3,65	12,6 (4)	0,91	12,0-14,0	7,20
10	17,8 (5)	0,57	17,1-18,3	3,20	5,81 (5)	0,18	5,50-5,99	3,20	13,5 (5)	0,52	13,1-14,2	3,86
11	16,0 (4)	0,13	15,8-16,1	0,81	4,50 (4)	0,29	4,10-4,77	6,36	11,2 (4)	0,64	10,7-12,1	5,72
12	17,0 (9)	0,33	16,5-17,4	1,95	5,12 (9)	0,25	4,70-5,56	4,97	12,0 (9)	1,30	10,0-14,0	10,80
13	16,9 (6)	0,45	16,2-17,6	2,67	5,18 (6)	0,28	4,91-5,63	5,37	13,0 (6)	0,92	11,7-14,0	7,04
14	17,1 (5)	0,41	16,6-17,7	2,38	5,44 (5)	0,18	5,20-5,65	3,40	12,5 (5)	0,27	12,3-13,0	2,15
15	17,1 (11)	0,36	16,7-17,7	2,08	5,28 (11)	0,21	4,90-5,60	3,92	12,3 (10)	0,56	11,5-13,0	4,52
16	17,0 (4)	0,78	16,2-18,0	4,57	5,37 (4)	0,54	4,56-5,73	10,14	13,1 (4)	0,42	12,8-13,7	3,24
17	17,4 (4)	0,44	17,2-18,1	2,50	5,18 (4)	0,33	4,75-5,49	6,45	12,4 (4)	0,46	11,9-13,0	3,74
18	15,8 (4)	0,39	15,4-16,2	2,45	4,33 (4)	0,34	4,01-4,70	7,90	11,6 (4)	0,57	11,0-12,2	4,88
19	15,9 (5)	0,40	15,3-16,3	2,50	4,61 (5)	0,28	4,40-4,95	6,00	11,5 (4)	0,43	10,9-11,9	3,77
20	16,4 (6)	0,47	15,7-17,0	2,86	4,71 (5)	0,20	4,49-4,92	4,17	11,4 (6)	0,72	10,5-12,4	6,32
21	16,0 (4)	0,66	15,0-16,5	4,11	4,55 (4)	0,24	4,29-4,83	5,21	11,8 (4)	0,79	11,0-12,9	6,71
22	16,8 (4)	0,26	16,6-17,1	1,56	4,95 (4)	0,32	4,64-5,40	6,52	12,4 (4)	0,50	11,8-13,0	4,00
23	16,6 (3)	0,50	16,1-17,1	3,04	4,92 (3)	0,28	4,60-5,14	5,80	12,0 (3)	0,53	11,6-12,6	4,41
24	17,1 (4)	0,16	16,9-17,3	0,96	5,38 (4)	0,32	5,07-5,83	5,97	12,4 (4)	0,33	12,1-12,8	2,68
25	17,1 (5)	0,45	16,5-17,7	2,63	5,39 (5)	0,45	4,87-6,02	8,33	12,9 (4)	0,41	12,5-13,3	3,16
26	16,9 (5)	0,65	15,9-17,5	3,86	4,90 (5)	0,19	4,69-5,20	3,81	11,9 (4)	0,69	10,9-12,4	5,78
27	17,1 (5)	0,36	16,7-17,5	2,10	4,76 (5)	0,19	4,47-4,95	4,06	11,6 (6)	1,37	10,2-13,5	11,84
28	16,8 (4)	0,87	15,9-18,0	5,17	4,72 (4)	0,39	4,33-5,09	8,22	12,3 (4)	0,72	11,3-13,0	5,86
29	16,9 (6)	0,68	15,7-17,5	4,05	4,86 (6)	0,48	4,36-5,65	9,84	12,0 (6)	0,71	11,0-13,1	5,96
30	17,6 (5)	0,85	16,4-18,8	4,84	5,39 (5)	0,19	5,07-5,53	3,46	12,7 (5)	0,91	11,2-13,6	7,17
31	17,6 (12)	0,51	16,8-18,7	2,91	5,45 (12)	0,38	4,76-5,92	6,97	12,7 (8)	1,11	10,8-14,0	8,72
32	17,6 (4)	0,45	17,0-18,0	2,55	5,73 (4)	0,26	5,40-6,00	4,46	12,2 (3)	0,72	11,4-12,8	5,91
33	18,0 (3)	0,15	17,8-18,1	0,83	5,75 (4)	0,50	5,29-6,46	8,75	12,8 (3)	0,60	12,2-13,4	4,72
34	18,0 (5)	0,62	17,2-18,7	3,47	6,07 (5)	0,29	5,60-6,40	4,85	13,4 (5)	0,90	12,4-14,8	6,73
35	17,5 (4)	0,12	17,4-17,6	0,68	5,68 (5)	0,46	5,21-6,36	8,10	12,6 (4)	0,57	11,9-13,2	4,53
36	17,6 (7)	0,36	17,2-18,2	2,04	5,84 (9)	0,30	5,50-6,40	5,07	13,6 (5)	0,81	12,6-14,8	5,95
37	17,2 (5)	0,55	16,3-17,7	3,22	5,01 (5)	0,15	4,88-5,24	2,94	12,1 (5)	0,36	11,7-12,5	3,02
38	16,8 (11)	0,43	15,9-17,7	2,59	5,06 (10)	0,28	4,68-5,39	5,52	12,5 (11)	0,38	11,9-13,1	3,07
39	16,3 (11)	0,58	15,1-17,2	3,57	4,83 (11)	0,26	4,39-5,32	5,30	12,0 (10)	0,82	11,2-14,0	6,80

Table 4.10 (Continued)
LP4

	F = 13,76; P << 0,001			
1	6,24 (9)	0,25	5,93-6,67	4,00
2	6,11 (36)	0,20	5,68-6,48	3,31
3	6,23 (27)	0,26	5,60-6,77	4,13
4	6,20 (5)	0,35	5,93-6,75	5,68
5	6,23 (10)	0,23	5,93-6,73	3,67
6	5,94 (11)	0,25	5,46-6,21	4,23
7	6,11 (5)	0,19	5,95-6,33	3,11
8	6,38 (8)	0,24	6,02-6,90	3,82
9	6,24 (4)	0,27	6,01-6,54	4,31
10	6,34 (5)	0,40	5,80-6,89	6,27
11	5,37 (4)	0,21	5,20-5,66	3,88
12	5,83 (9)	0,34	5,40-6,35	5,92
13	5,77 (6)	0,30	5,42-6,30	5,28
14	6,04 (5)	0,19	5,88-6,35	3,10
15	6,02 (11)	0,27	5,52-6,51	4,53
16	6,22 (4)	0,60	5,33-6,61	9,62
17	5,85 (4)	0,19	5,61-6,01	3,22
18	5,13 (4)	0,32	4,84-5,47	6,19
19	5,22 (5)	0,38	4,75-5,79	7,31
20	5,41 (6)	0,14	5,16-5,55	2,50
21	5,28 (4)	0,22	5,08-5,57	4,08
22	5,85 (4)	0,23	5,60-6,05	3,96
23	5,76 (3)	0,25	5,55-6,03	4,29
24	6,11 (4)	0,21	5,92-6,40	3,35
25	5,95 (5)	0,27	5,61-6,21	4,59
26	5,60 (5)	0,28	5,16-5,92	4,96
27	5,52 (6)	0,24	5,20-5,92	4,43
28	5,43 (4)	0,39	4,88-5,77	7,27
29	5,36 (6)	0,19	5,12-5,66	3,62
30	6,48 (5)	0,34	5,92-6,84	5,33
31	6,47 (12)	0,31	6,00-6,85	4,79
32	6,46 (4)	0,23	6,25-6,79	3,58
33	6,53 (4)	0,24	6,30-6,87	3,76
34	6,79 (5)	0,29	6,57-7,30	4,31
35	6,36 (5)	0,34	5,99-6,93	5,44
36	6,68 (9)	0,24	6,33-7,05	3,52
37	5,94 (5)	0,43	5,57-6,56	7,24
38	5,85 (10)	0,26	4,51-6,31	4,46
39	5,64 (11)	0,32	5,20-6,12	5,67

Table 4.11

Results of SS-STP analyses of selected cranial measurements of Cynictis penicillata in Southern Africa. Non - significant subsets ($P < 0,001$) are indicated by vertical lines to the right of each array of means. OTU codes correspond to those in Fig. 4.2 and Table 4.11).

CBL			MRH		
OTU	Mean	Subsets	OTU	Mean	Subsets
36	71,37		36	19,84	
34	70,90		33	19,42	
35	69,50		34	19,22	
4	68,58		35	19,18	
33	68,50		31	18,88	
1	68,24		1	18,73	
31	68,11		30	18,74	
30	67,72		7	18,6	
10	67,32		4	18,56	
32	67,08		10	18,44	
8	67,06		25	18,44	
3	67,02		8	18,39	
6	66,81		9	18,18	
2	66,78		13	18,10	
16	66,52		16	18,05	
14	66,38		32	18,02	
9	66,28		2	18,01	
7	66,08		3	17,97	
5	65,97		6	17,91	
15	65,57		14	17,84	
13	64,88		28	17,70	
17	64,88		24	17,68	
12	64,27		5	17,68	
25	64,02		12	17,57	
24	63,92		15	17,49	
38	63,81		17	17,42	
37	63,60		22	17,30	
23	63,30		38	17,07	
29	63,02		29	17,00	
22	63,02		23	16,93	
28	62,42		27	16,68	
26	61,78		21	16,60	
39	60,92		37	16,58	
27	60,90		26	16,44	
21	60,25		39	16,38	
20	60,00		20	16,13	
11	59,58		11	16,12	
19	58,54		19	16,12	
18	57,35		18	15,95	

Table 4.11 (Continued)

MTR		IOW	
36	23,10	10	16,54
34	23,02	33	16,35
35	22,78	34	16,24
33	22,35	14	15,88
9	21,95	36	15,87
1	21,81	7	15,84
31	21,78	8	15,79
8	21,76	25	15,72
3	21,72	35	15,68
30	21,72	1	15,57
16	21,70	2	15,52
10	21,68	12	15,51
4	21,66	6	15,48
2	21,60	32	15,48
32	21,60	31	15,41
14	21,48	30	15,38
7	21,42	9	15,38
5	21,38	3	15,36
15	21,14	4	15,36
6	21,08	13	15,27
13	21,07	5	15,14
25	20,82	16	15,08
12	20,62	15	15,07
17	20,62	24	14,88
38	20,51	17	14,85
24	20,50	38	14,79
37	20,12	28	14,70
23	19,90	39	14,59
24	19,80	37	14,58
39	19,34	29	14,45
29	19,22	26	14,24
26	19,14	11	14,15
20	18,97	23	14,10
28	18,88	22	13,73
27	18,82	27	13,60
21	18,78	20	13,50
11	18,38	19	13,42
19	18,10	18	13,38
18	17,98	21	13,05

Table 4.11 (Continued)

	ZYW		SOH
33	41,97	36	13,58
36	41,47	10	13,54
34	41,46	34	13,38
35	40,90	6	13,12
25	40,70	16	13,10
1	40,68	7	13,08
10	40,66	13	13,03
30	40,56	3	13,02
2	40,45	2	13,00
8	40,44	8	12,96
4	40,34	5	12,93
7	40,28	25	12,90
16	40,28	1	12,80
9	39,98	33	12,77
31	39,92	31	12,69
3	39,91	30	12,69
6	39,80	9	12,65
13	39,77	4	12,64
14	39,72	35	12,55
32	39,58	14	12,54
5	39,42	38	12,46
12	39,37	17	12,45
15	38,95	22	12,40
24	38,72	24	12,35
17	38,45	28	12,32
38	37,74	15	12,31
28	37,45	32	12,20
26	37,02	37	12,06
39	36,62	12	12,03
37	36,62	39	12,02
29	36,18	23	12,00
22	36,97	29	11,95
23	36,97	26	11,92
11	35,78	21	11,82
21	35,32	18	11,62
27	35,22	27	11,57
20	35,02	19	11,52
18	34,60	20	11,45
19	34,05	11	11,18

intermediate - sized OTUs (which are not necessarily geographically centrally placed) allows the formation of numerous, overlapping non - significant subsets between southern and northern populations. Also SS-STP seems to be more conservative in categorising groups than do multivariate clustering and ordination methods. Willig and Owen (1986, 1987) have pointed out that univariate results do not necessarily emulate the results of multivariate analyses, and that the latter are generally more suitable than the former.

GENERAL DISCUSSION

Pattern and mode of speciation in *Cynictis*

Referring to studies of stable hybrid zones, Dowling *et al.* (1989) state that 'the study of speciation involves analysis of the causes of restriction of gene flow between incipient species. Such analysis is especially informative in situations where hybridisation occurs and reproductive isolation is incomplete'. This comment can be applied to zones of intergradation between subspecies, since it is mechanisms operating within these zones that determine the possible outcome (speciation or extinction) of subspecies. For the purpose of this discussion subspecies are regarded as units of evolution, and not arbitrary constructs of convenience. The subspecies definition of Lidicker (1962) is

adopted, whereby a subspecies is '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 geographic area, is usually partially isolated, and may intergrade gradually, although over a fairly narrow zone, with adjacent subspecies'. As discussed below, the parapatric phena of Cynictis can best be recognised provisionally as subspecies.

The causes of restriction of gene flow depend on the mode of speciation implicated in a particular case (see Bush, 1975 for a reveiw of the different modes of speciation). Two alternative modes of speciation (allopatric or parapatric) may explain the geographic pattern of divergence in skull size described above. Both modes are discussed below with respect to the evidence obtained from the various multivariate analyses of Cynictis populations, and this is followed by a discussion of the proposed pattern of 'subspeciation' in the species, based on cladistic analysis of geographic regions and palaeoclimatic and biogeographic evidence.

Parapatric speciation

Based on computer simulation studies, Endler (1977) proposed a model of parapatric speciation whereby steep, stable

clines in gene frequencies may form in response to selection acting in environmental gradients or ecotones, in spite of continuing gene flow. Modifiers within the cline favour assortative mating of like genotypes due to heterozygote disadvantage (selection will favour any system that reduces the cost of wasted reproductive effort resulting from the production of hybrids of reduced viability). According to this model parapatric populations become genetically differentiated and may eventually acquire reproductive isolation and become full species. Barriers, or partial barriers, tend to increase the steepness of clines and to 'attract' clines (formed across an existing ecotone) towards them. In a review of vertebrate hybrid zones in nature, Moore (1977) found that most hybrid zones coincided with ecotones, suggesting the importance of selection in preventing widespread introgression between incipient species or subspecies.

There is a clear correlation between transition zones in Cynictis and the ecotone marked by the limit of Kalahari sands in Southern Africa (Fig. 4.6). While biogeographical barriers, such as the middle and lower Orange River valley and the Soutpansberg Mountains, are also associated with the north - south transition zone, they are themselves partly correlated with the limits of Kalahari sands (Fig. 4.6). Cynictis populations occur in relatively low densities in the middle and lower Orange River valley (H. Erasmus pers.

comm.), possibly due to the extreme aridity of this region (much of which receives less than 100mm rainfall annually), suggesting that this region may act as a partial barrier to gene flow.

The increased steepness of transition zones when they are associated with biogeographical barriers, rather than with ecotones in the absence of barriers (Fig. 4.5, 4.6 and previous discussion), is in accord with the predictions of Endler's (op. cit.) computer models. This provides indirect evidence that restriction of gene flow between phena in Cynictis may be due to selection gradients (ecotones) and / or partial barriers, i.e. in situ parapatric speciation (sensu Endler).

Allopatric speciation

According to Mayr (1982) most cases of parapatric speciation are more easily explained as secondary contact zones of previously isolated populations. Mayr (1978) has criticised the parapatric model of speciation for failing to take into account past and present vegetational barriers. Vrba (1985a) has also argued that vegetational or climatic changes may be just as formidable obstacles as gross topographical barriers.

The importance of past environmental changes as mediators of

allopatric speciation has been emphasized recently (Brain, 1985; Vrba, 1985a, b; Taylor, Campbell, Meester, Willan and van Dyk, 1989). According to Vrba's (1985a, b) turnover - pulse hypothesis, owing to evolutionary conservatism and habitat - specificity of species, climatic (or tectonic) changes may result in fragmentation of the species range, followed by extinction, intra - specific evolution or speciation.

The turnover - pulse hypothesis predicts that Pleistocene palaeoenvironmental changes would provide clues to the pattern and mode of speciation in Cynictis. Much information on palaeoenvironments in Southern Africa has been gathered in recent years, mostly in relation to the late Quaternary (see Klein, 1984 and Deacon and Lancaster, 1988 for recent reveiws). The presence of fossil drainage lines points to a much wetter previous climate in the Kalahari. In the Karroo - Namaqualian ecozone, generally wetter conditions prevailed between 30 000 BP and 13 000 BP, while in the Kalahari the last major wet phase lasted from about 32 000 BP to 22 000 BP. Conversely, the existence of fixed dune systems throughout the Kalahari (occurring in regions receiving up to 800 mm annual rainfall) is compelling evidence for a former, much drier period. The dunes in the south west Kalahari were last active about 20 000 BP to 17 000 BP (Deacon and Lancaster, 1988).

Since Cynictis is absent from unvegetated dunes in the Namib, the occurrence of such conditions in a belt across the southern Kalahari would have constituted an effective barrier between Karroo and Kalahari populations of Cynictis during the late Pleistocene. Similarly, the postulated widespread occurrence of humid conditions in the Karro - Namaqualian and Kalahari ecozones during the late Pleistocene would have had profound effects on the distribution of vegetation types (as implied by Cooke, 1962, and evidenced from palynological (pollen) data in Southern Africa generally: Van Zinderen Bakker, 1962). Under very humid conditions, semi arid habitats (Karroo scrub, Kalahari thornveld) would have contracted, at the expense of more mesic habitats, such as savanna woodland, and Afro - montane forest. As Cynictis is absent from mesic savannas, being restricted to the Semi - Arid Biome (Davis, 1962), this sequence of events would almost certainly have led to fragmentation and compression of the species' range. These conditions would have promoted genetic and phenetic differentiation in isolated refugia. The alternating contraction and expansion of Kalahari sands during dry and wet phases (see also Broadley, 1978) may have accounted for the present morphometric transition zones between Namibia and Botswana and between the northern and southern phena (Fig. 4.5) which correspond with the present day extent of Kalahari sands.

Pattern of subspeciation

Vrba (1985a) states that cladistic and biogeographic analyses of extant taxa may provide valuable, indirect tests of the turnover - pulse hypothesis. Phylogenetic analysis of geographic regions, following the approach of Thorpe (1986a, b), was used to attempt to infer the historical pattern of range expansion in Cynictis. According to Thorpe (1986a) such an approach can discriminate between transition zones which have originated in parapatry and those which have resulted from secondary contact of previously isolated populations. Phylogenetic analysis of intra - specific populations (preferably combined with a knowledge of biogeography and palaeoenvironments) may therefore prove to be a useful tool in distinguishing between parapatric and allopatric speciation at the intra - specific level (i.e. while speciation is still occurring).

The two Wagner trees in Fig. 4.10 were obtained from: 1) construction of a distance Wagner tree, taking the southern - most geographic region (E Cape) as the hypothetical ancestor; 2) midpoint - rooting of a distance Wagner network. Both trees were based on a matrix of nine gap - coded characters in 15 geographic regions (Table 4.10). Five geographic regions (Central Transvaal, S Transvaal, OFS, Natal, W Cape) were identical in character states for all nine characters and were treated as a single group 'SOUTH'

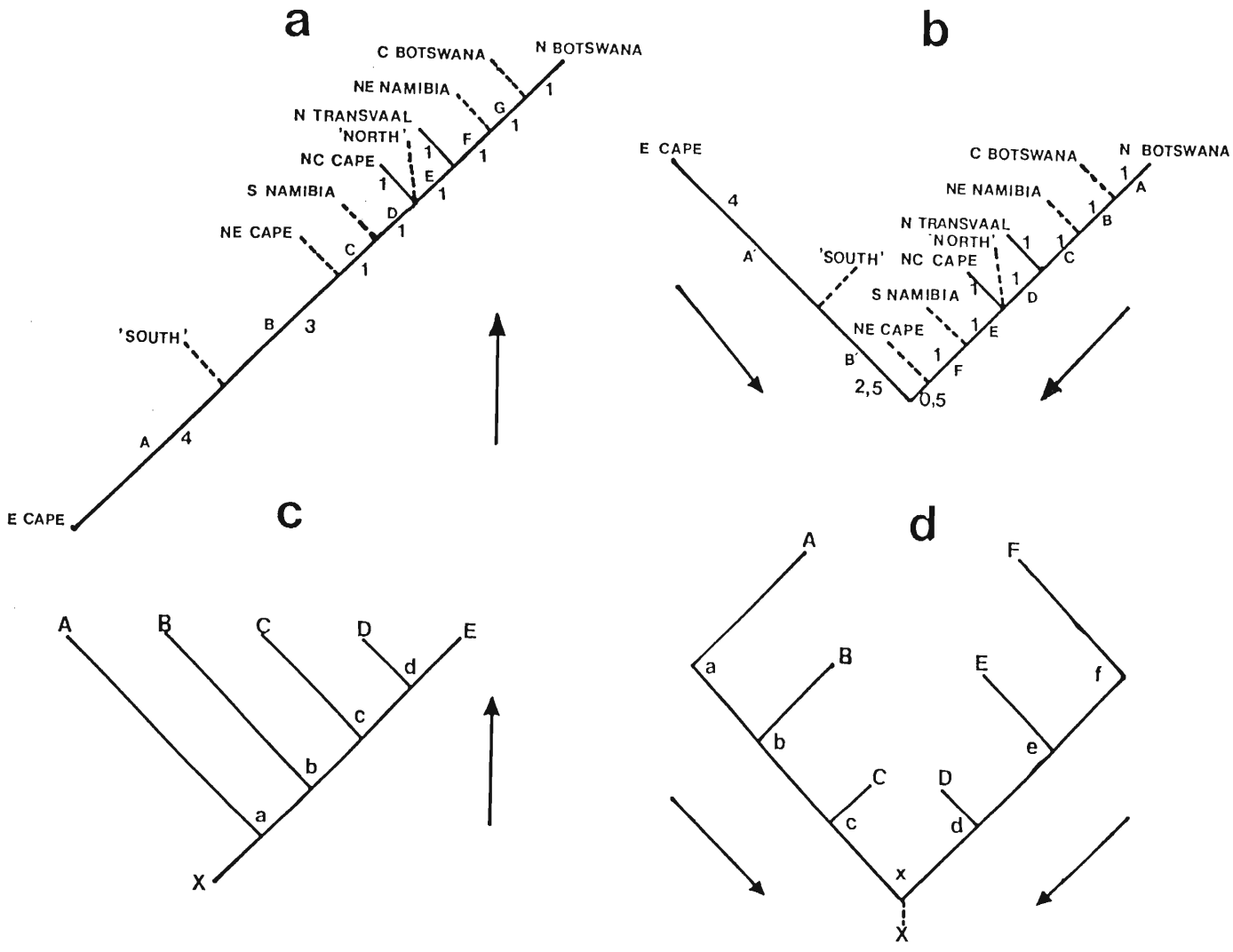
Table 4.12

Gap - coded character states of nine craniometric variables in 15 geographic regions in C. penicillata. Explanation of variable abbreviations given in Appendix I. Explanation of geographic regions and gap - coding procedure given in text.

	Variables								
Regions	CBL	BCW	MRH	MTR	WAB	IOW	ZYW	BUL	WP4
1 NE Namibia	1	1	1	2	3	1	1	0	1
2 NW Namibia	1	1	1	2	2	0	1	0	1
3 Central Namibia	1	1	1	2	2	0	1	0	1
4 S Namibia	1	1	1	1	2	0	1	0	1
5 Central Botswana	1	1	1	2	3	1	1	1	1
6 N central Cape	1	1	1	2	2	0	1	1	1
7 NE Cape	1	1	1	1	1	0	1	0	1
8 N Botswana	2	1	1	2	3	1	1	1	1
9 N Transvaal	1	1	1	2	3	0	1	1	1
10 C Transvaal	1	0	1	1	0	0	0	0	1
11 S Transvaal	1	0	1	1	0	0	0	0	1
12 OFS	1	0	1	1	0	0	0	0	1
13 Natal	1	0	1	1	0	0	0	0	1
14 W Cape	1	0	1	1	0	0	0	0	1
15 E Cape	0	0	0	0	0	0	0	0	0

Fig. 4.10 **Fig. 4.10a** and **b**: Phylogeny of populations of C. penicillata. Distance Wagner trees were derived from a Manhattan distance matrix from a data matrix of nine 'gap - coded' characters based on original variable means for 15 regional populations. Wagner networks were rooted by: **a**) ancestor rooting (taking E Cape as the ancestral population) and; **b**) midpoint rooting. Nodes at each branch represent hypothetical ancestors of populations represented by their corresponding branches. Numbers indicate units of anagenic change. Dotted lines indicate populations in which no anagenic change has occurred, i.e. populations which are identical to their hypothesized ancestral populations. Arrows indicate proposed direction of evolution. Patterns of range expansion involved in phylogenetic steps A to G (Fig 4.10a) and sublineages A' to B' and A to F (Fig. 4.10b) are plotted in Fig. 4.11.

Fig. 4.10c and **d**: Hypothetical examples of Wagner trees (modified from Thorpe 1984a) indicating the existence of clear directional evolution. Upper case letters represent terminal taxa and lower case letters hypothetical ancestors. Arrows represent direction of evolution. **Fig. 4.10c.** Pattern of anagenesis showing a clear direction of evolution away from the outgroup (X), with a greater degree of anagenesis occurring in taxa closer to the outgroup. **Fig. 4.10d.** Pattern of anagenesis showing reticulate evolution between sublineage A, B, C and sublineage D, E, F. Each sublineage resembles the tree in Fig. 4.10c, although the direction of evolution in the two sublineages is toward (rather than away from) the outgroup 'root' x. Thus x cannot be taken as the root of these sublineages and the midpoint roots a (for sublineage A, B, C) and f (for sublineage D, E, F) are appropriate.


a
C BOTSWANA
N BOTSWANA
NE NAMIBIA
N TRANSVAAL
'NORTH'
NC CAPE
S NAMIBIA
NE CAPE
'SOUTH'
E CAPE
b
E CAPE
C BOTSWANA
N BOTSWANA
NE NAMIBIA
N TRANSVAAL
'NORTH'
'SOUTH'
NC CAPE
S NAMIBIA
NE CAPE
2,5
0,5
c
A
B
C
D
E
X
d
A
F
B
E
C
D
X

on the Wagner trees (Fig. 4.10). Similarly NW Namibia and Central Namibia ('NORTH' in Fig. 4.10) were identical.

Absence of anagenic change characterises most of the geographic regions (NE Namiibia, 'NORTH', S Namibia, Central Botswana, NE Cape, 'SOUTH': Fig. 4.10). However, considerable anagenic change has occurred in the 'ancestral' region (E Cape: four distance units), and between the hypothetical ancestors of 'SOUTH' and all the northern regions (three distance units), while some anagenic change (one distance unit) has occurred in NC Cape, N Botswana and N Transvaal (Fig. 4.10a, b)

Thorpe (1986a) proposed that, where phylogeny rather than current ecology is responsible for observed patterns of geographic variation, the degree of anagenesis should be greatest in older (more primitive) taxa and progressively less in more recent (advanced) taxa (Fig. 4.10c). In the ancestor - rooted Wagner tree (Fig. 4.10a) the pattern of anagenesis conforms to the pattern predicted due to phylogeny, with the greatest degree of anagenic change occurring in the oldest (i.e. ancestral) region (E Cape), and reduced anagenic change occurring in the more recently evolved northern regions. The recent origin of the northern region is also suggested by their higher degree of cladogenesis (splitting) compared with the southern regions (gene flow between the 'older' southern regions may have

obscured previous synapomorphies).

The position of the 'root' in the midpoint - rooted Wagner tree (Fig. 4.10b) suggests that two convergent lineages, a southern and a northern, may be involved. Thorpe (1986a) describes a case where two separate lineages of house snakes (Natrix natrix), which originated independently in North Africa and southern Italy (after being isolated by glaciation), expanded their ranges to meet in France, Holland and Germany, resulting in what he termed 'reticulate evolution' (see Fig. 4.10d). The midpoint - rooted Wagner tree in Fig 4.10b may represent a similar situation, but this cannot be verified from the pattern of anagenesis. In the case of reticulate evolution greater anagenic change should occur at the northern and southern extremes of the species range (this is true for E Cape but not for N Botswana), and reduced anagenic change should occur in regions closest to the midpoint 'root' (Fig, 4.10d). The pattern of anagenesis in the midpoint - rooted tree for Cynictis populations (Fig. 4.10b) does not follow this predicted pattern.

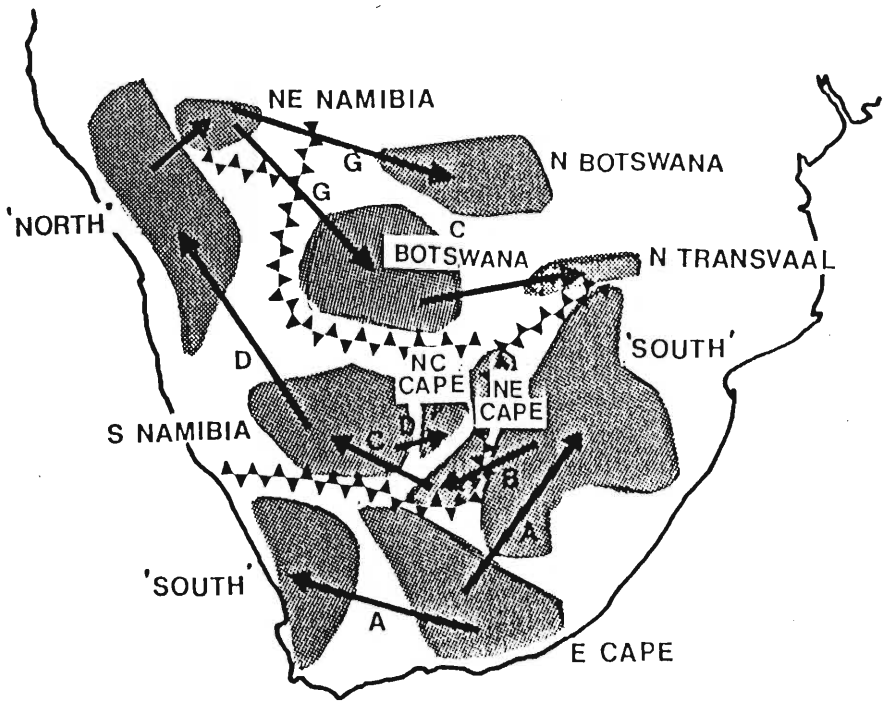
The two trees presented in Fig. 4.10 therefore represent alternative hypotheses concerning the historical pattern of range expansion in Cynictis. This becomes clearer when the different cladograms are superimposed on the geographic range of the species (Fig. 4.11).

Based on the alternative models of range expansion in Cynictis (Fig. 4.11a, b), and postulated palaeoenvironmental changes, two alternative hypotheses can be put forward to explain the pattern of (sub)speciation in the species:

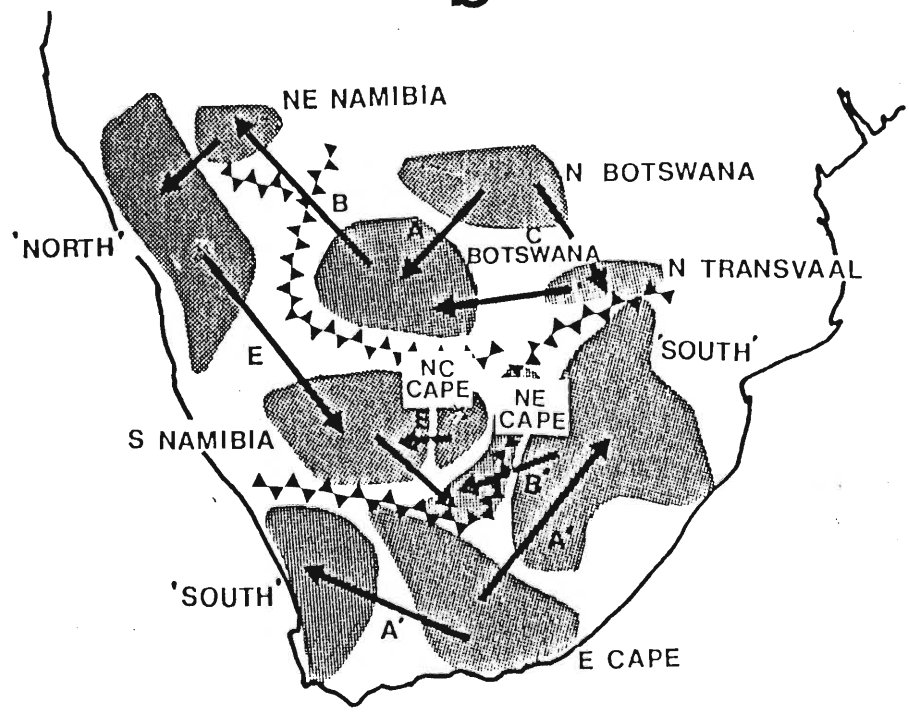
1) According to the ancestor - rooted Wagner tree, the larger - sized hypothetical ancestral population originated in the central and eastern Karroo (E Cape: Fig. 4.11a). Based on a phenetic analysis of morphological and behavioral characters, Baker (1987) suggests that Cynictis may have evolved either from Ichneumia or Galerella. Cynictis also bears a superficial resemblance to Paracynictis (which was not included in Baker's study), and Sclater (1900) recognised the latter as a synonym of the former. If Cynictis evolved in the Karroo (i.e. E Cape in Figs 4.10, 4.11) as suggested here, its most likely sister group is Galerella pulverulenta, as none of the other species mentioned above occur in the southern Cape. However it is also conceivable that C. penicillata, and later G. pulverulenta, evolved as peripheral isolates from a G. sanguinea - like ancestor, as the present distribution of the latter species extends as far as the borders of the Karroo in the Orange Free State and the Cape Province (Smithers, 1983). The ancestors of G. pulverulenta and C. penicillata exploited different niches in the Karroo ecosystem, G. pulverulenta being slightly more carnivorous

Fig. 4.11 Range expansion in C. penicillata as indicated by distance Wagner analyses (Fig. 4.10), employing ancestor - rooting (**a**) and midpoint rooting (**b**) methods. Transition zones between phena are indicated by double rows of triangles. Arrows indicate phylogenetic steps between hypothesized ancestors (Fig. 4.10). The two proposed patterns of range expansion in the species are not fully concordant with the two Wagner trees in Fig. 4.10. Phylogenetic steps E and F (Fig. 4.10a: from 'NORTH' to N. Transvaal to NE. Namibia), and steps C and D (Fig. 10b: from NE. Namibia to N. Transvaal to 'NORTH') have been omitted from **Fig. 4.11a** and **Fig. 4.11b** respectively as they appear unlikely in terms of the historical pattern of range expansion in the species. Simpler steps (between 'NORTH' and NE. Namibia, and between N. Transvaal and central Botswana) have been plotted to allow for more plausible hypotheses of range expansion in the species.

a


NE NAMIBIA
N BOTSWANA
G
G
'NORTH'
C
BOTSWANA
N TRANSVAAL
'SOUTH'
D
NC CAPE
NE CAPE
S NAMIBIA
C
D
B
A
'SOUTH'
A
E CAPE

b


NE NAMIBIA
N BOTSWANA
B
A
C
'NORTH'
BOTSWANA
N TRANSVAAL
E
'SOUTH'
NC CAPE
NE CAPE
S NAMIBIA
B
A'
'SOUTH'
A'
E CAPE

than C. penicillata, and having a more solitary behavior.

From the Karroo, the species' range expanded into favourable open grassland and semi arid habitats in the western Cape, Orange Free State and southern Transvaal ('SOUTH' in Fig.4.11a). The lower and middle Orange River valley may have hindered the northwards expansion of the species at this stage. It is also conceivable that extremely humid conditions may have prevailed at the time (as they did, for example, between 32 000 BP and 22 000 BP), resulting in the possible existence of unfavourable mesic habitats in the northern Cape, Botswana, northern Transvaal and Namibia, which would have hindered the northwards migration of populations. Another possibility, if C. penicillata evolved from G. sanguinea, is that sympatry between the two species may have been prevented by competitive exlusion by G. sanguinea at an early stage in the speciation of C. penicillata when similarities in their niches prevented coexistence. This may explain why very little sympatry occurs at present between G. sanguinea and G. pulverulenta (Smithers, 1983).

From the southern Transvaal the species expanded into the northern Cape, southern and then northern Namibia (Fig. 4.11a). Presumably, conditions at this stage favoured colonisation of Namibia but not Botswana. It may have been that Kalahari sandveld habitats, having contracted somewhat

during the previous wet phase, were still separated from semi - arid habitats in Namibia by a belt of mesic savanna habitats (as predicted for a wet phase by Cooke, 1962), preventing the colonisation of Botswana. Subsequent expansion occurred from northern Namibia into central Botswana and northern Botswana and thence to northern Transvaal (Fig. 4.11a). These latter colonisation events may have been facilitated by the expansion of Kalahari sands to their approximate present - day limits and beyond. Kalahari sands expanded eastwards to include most of the Transvaal and Zimbabwe (see also Broadley, 1978), as evidenced by the occurrence of Cynictis populations (resembling Botswana Kalahari populations in skull size and coloration) on relic pockets of Kalahari sands in the northern Transvaal. Clearly the northern Transvaal population was isolated from Kalahari populations in Botswana during a subsequent wet phase when Kalahari sands contracted to their present limits.

According to this scenario, observed morphometric transition zones (see Fig. 4.5) between Transvaal and the northeastern Cape, and between Namibia and Botswana, are primary in nature, while the zones between populations north and south of the Soutpansberg and north and south of the middle and lower Orange River, are due to secondary 'contact' of populations (Fig. 4.11a). It is possible that after the species had reached its maximum range, a subsequent (less severe) wet phase occurred, leading to small - scale range

fragmentation resulting in three refugia (in South Africa, Namibia and Botswana), thus allowing genetic differences to occur in allopatry, giving rise to the observed transition zones when the ranges of the refugia later expanded. Thus, apparent 'primary' zones may be explained as secondary contact zones, induced by small scale climatic fluctuations, which are not detected by Thorpe's (1986b) method. 'Primary' zones are not therefore necessary indicators of parapatric speciation.

2) According to the midpoint - rooted tree, separate northern and southern populations may have existed in the past, and reticulate evolution may have occurred as these two populations expanded to meet each other. It is possible that the species initially spread throughout its current range, under climatic conditions similar to those operating at present, after which Pleistocene climatic and vegetational changes (eg. the widespread, humid phase referred to above) resulted in range fragmentation and compression, and isolation of northern and southern refugia populations. It is likely that the species may have initially exhited a gradual northerly decline in skull size in accordance with Bergmann's Rule. During the hypothesized fragmentation of the species' range the intermediate - sized populations may have become extinct leaving populations in the northern and southern refugia having extreme size differences. With the return of more favourable conditions,

ranges of the small - sized, northern and large - sized, southern populations may have expanded to meet each other (Fig. 4.11b) to produce the present - day transition zones. In this case the entire length of the steeper north - south transition zone is secondary in nature, while the more gradual east - west transition zone is primary in nature. A similar explanation was suggested to account for the occurrence of parapatric species in the shrew genus Blarina in the southern Great Plains of the United States (Genoways and Choate, 1972).

Of the two hypotheses discussed above, the former is more plausible as it is based on the ancestor rooted tree. As pointed out above, the ancestor rooted tree (and not the midpoint rooted tree) is consistent with a phylogenetic rather than a current ecological interpretation as it shows a discernible pattern of anagenesis, indicating greatest anagenic change in the hyothesized ancestral E. Cape population.

While past environmental changes can plausibly account for the allopatric origin of genetic differences between phena, it is not immediately clear what forces are acting to maintain transition zones between phena. Where transition zones are associated with potential barriers (Orange River and Soutpansberg Mountains), there appears to be no hybridisation between populations north and south of the

transition zone (see Fig. 4.9, and earlier discussion on DFA of individuals), suggesting that present barriers (or partial barriers) are effective in restricting gene flow. On the other hand, where transition zones are associated with ecotones marked by the limit of Kalahari sands, there is indirect evidence for hybridisation between phena (i.e. in northeastern Cape and southwestern Transvaal, and in northeastern and eastern Namibia: see Fig. 4.9).

Moore (1977) puts forward three alternative hypotheses to explain the persistence of narrow hybrid zones in vertebrates: 1) the ephemeral - zone hypothesis (equivalent to Dobzhansky's (1937) hypothesis of speciation by reinforcement); 2) the dynamic - equilibrium hypothesis; and 3) the hybrid - superiority hypothesis. The ephemeral - zone hypothesis is no longer widely accepted (Moore, 1977, Paterson, 1985; Dowling *at. al.*, 1989) since many examples of stable zones have been documented in nature (Moore, 1977). The dynamic - zone hypothesis maintains that hybrids (which have reduced viability relative to their parents) are confined to a small area by steep selection gradients, and that the origin of anti-hybridisation mechanisms in hybrid zones is prevented by the immigration of 'naive' parents. According to Moore (1977) the dynamic - zone hypothesis only applies in the case of very narrow hybrid zones. According to the hybrid - superiority hypothesis, hybrid zones persist as a result of hybrids being better adapted than their

parents in restricted (eg. ecotonal) conditions. According to Moore, the fact that hybrid zones are often associated with ecotones is evidence in support of the hybrid - superiority hypothesis. In Cynictis hybrid zones do not appear to be particularly narrow (as required by the dynamic - zone hypothesis), and they do appear to be correlated with ecotones (as predicted by the hybrid - superiority hypothesis) so that the hybrid - superiority hypothesis seems to be most applicable.

Speciation in Cynictis therefore appears to be 'alloparapatric' in mode. Past climatic changes in the late Pleistocene of Southern Africa may adequately account for the origin of phenetic differences in allopatry during the postulated history of range expansion of the species, as discussed above. However, the existence of zones of intergradation between phena which are associated with the ecotone marked by the limits of Kalahari sands, provides indirect evidence that widespread introgression is being prevented by steep selection gradients, as suggested by proponents of parapatric speciation. However, without knowing the antiquity and stability of the observed hybrid zones one cannot discount the possibility that they are ephemeral in nature and therefore in the process of either being eliminated or forming effective postmating and premating isolating mechanisms by the process of reinforcement.

Taxonomic conclusions

The above results demonstrate the existence of two distinct, parapatric phena in C. penicillata, with a sharp stepped cline between them (Figs. 4.3, 4.4, 4.5, 4.7). Sub - phena are present within each phenon (Figs. 4.3, 4.7), but only in the northern phenon do these comprise meaningful geographical groups, separated by a transition zone (Fig. 4.5, and earlier discussion). Indirect evidence, from DFA of individuals, suggests that intergradation does not occur between the northern and southern phena over most of the zone of parapatry, being restricted to a limited area in the north - eastern Cape. Since the transition zone coincides with potential geographic barriers or partial barriers (mid and lower Orange River valley and Soutpansberg Mountains) over most of its length, but not in the zone of intergradation, it is possible that that the two phena are geographically but not reproductively isolated.

Since reproductive isolation (the main criterion of the biological species concept: Mayr, 1942) cannot be unequivically proven (there was morphometric evidence for introgression between northern and southern phena), it was decided, conservatively, to recognise northern and southern phena as separate subspecies. Genetic distances between these phena, based on electrophoretic analysis (Taylor,

Campbell, van Dyk, Watson, Pallett and Erasmus, in press) were very low (0,008--0,063), suggesting that the two phena are certainly not well - established species (although this does not discount the possibility of their being incipient, or recently evolved, species).

The two divergent sub - phena within the northern phenon can also be recognised as subspecies, having a definite transition zone between them (Fig. 4.5), although some degree of overlap occurs between them (see ranges of discriminant scores for northern and southern 'test' OTUs in Fig. 4.9).

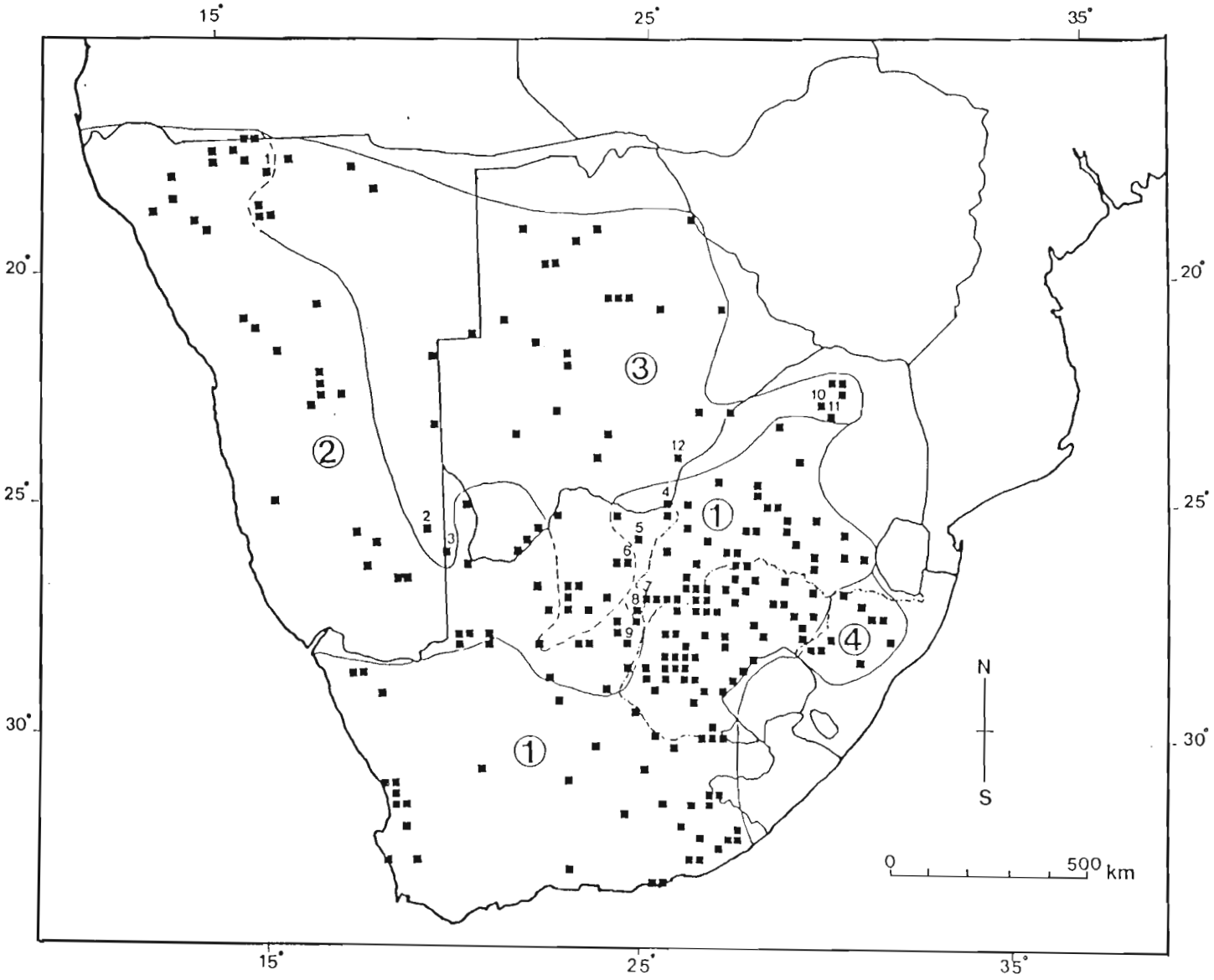
Analysis of colorimetric data (using Munsell charts and a tristimulus colorimeter: Taylor, Meester and Rautenbach in press) supports the craniometric results, with populations south of the Orange River, and south of the Soutpansberg, being distinctly redder and richer in colour (higher values for dominant wavelength (DOM) and excitatory purity (PUR)) than northern populations, and specimens from Botswana having extremely low DOM and PUR values (very yellow and faded) compared to intermediate DOM and PUR values in Namibia. The direction of anagenic change in subspecies is therefore perfectly concordant in size and colour, with extremely high values of skull size, DOM ('redness') and PUR (colour intensity) in the south, intermediate values in Namibia and extremely low values in Botswana and northern

Transvaal. This concordance between two sets of independent character suites provides additional evidence for genetic differentiation between these three subspecies.

The distinctive skull shape (short and wide) of Natal specimens (Figs. 4.4, 4.7), and the fact that Natal populations are separated by the Drakensberg Mountain range from populations to the west, merits the formal recognition of a fourth subspecies, from Natal. Four subspecies are henceforth designated for C. penicillata.

The distributions of the four subspecies are given in Fig 4.12. For the most part distribution of subspecies was based on the grouping of OTUs into phena as illustrated in Figs. 4.3 and 4.4. However, based on a geographic plot of canonical scores of individuals (using the data depicted in Fig. 4.9), certain OTUs (38 and 39) and individual localities (1, 2, 3, 8, 10, 11 in Fig. 12) were relocated to obtain a more accurate representation of subspecies borders, as shown in Fig. 4.12. In some regions subspecies borders could be not be accurately described as certain individual locality samples (localities 4, 5, 7, 9 in Fig. 4.12) comprised individuals having skull measurements typical of both northern and southern phena. It is interesting to note that these localities are positioned close to the boundaries between subspecies, indicated that intergradation between subspecies is limited to a fairly narrow zone. Localities

Fig. 4.12 Map showing geographic extent of four subspecies of Cynictis penicillata in Southern Africa based on craniometric anaysis: 1 = C. p. penicillata; 2 = C. p. bradfieldi; 3 = C. p. coombsii; 4 = C. p. natalensis. Dashed lines indicate areas of introgression where subspecies borders cannot be clearly demarcated. Numbered localities are referred to in the text.


15°
25°
35°
20°
25°
30°
1
2
3
4
5
6
7
8
9
10
11
12
①
②
③
④
N
S
0
500 km

10, 11 and 12 in Fig. 4.12 are represented only by 'non - adult' (i.e. age class 2 and 3) or badly broken skulls and were tentatively assigned to the C. p. coombsii on the basis of external (locality 12) and cranial (localities 10 and 11) measurements.

ACCOUNTS OF SUBSPECIES

Cynictis penicillata penicillata (G. Cuvier, 1829)

Herpestes penicillatus G. Cuvier, Le Regne animal 2nd edn 1: 158. April 1829. Cape of Good Hope; Uitenhage, eastern Cape Province, fide Roberts (1951: 151).

Mangusta Le Vaillantii A. Smith, Zoological Journal 4: 437. May 1829. South Africa.

Cynictis steedmanni Ogilby, Proceedings of the Zoological Society, London: 49. 1833. Uitenhage, eastern Cape Province.

Cynictis ogilbyii A. Smith, South African Quarterly Journal 2: 117. 1834. Bushman Flat and northern parts of Graaff - Reinet district.

Cynictis lepturus A. Smith, Illustrations of the Zoology of South Africa, Mammals:pl. 17 and text. 1839. Arid plains towards the Tropic of Capricorn (= Marico district, fide Roberts, 1951: 154).

Cynictis penicillata pallidior Thomas and Schwann, Abstracts, Proceedings of the Zoological Society,

London 2: 5; Proceedings of the Zoological Society, London 1: 175. 1904. Klipfontein, north of Steinkopf, Little Namaqualand, northwestern Cape Province.

Cynictis penicillata intensa Schwann, Proceedings of the Zoological Society, London: 104. 1906. Deelfontein, north of Richmond, Cape Province.

Cynictis penicillata brachyura Roberts, Annals of the Transvaal Museum 10: 68. 1924. Boschkop, near Johannesburg, Transvaal.

HOLOTYPE. The holotype described by Cuvier was not examined, as it was not located in any of the institutes included in this study. The type locality is Uitenhage in the eastern Cape Province.

DISTRIBUTION (Fig. 4.12). Cape Province, south of the Orange River; Orange Free State; Transvaal north to Pietersburg district; intergrading with C. p. bradfieldi in northeastern Cape Province and southeastern Botswana.

DIAGNOSIS. Largest of the subspecies: head and body length almost always greater than 300mm (265--460mm: Table 4.13); condylobasal length of skull almost always greater than 64mm(62,2--73,7: Table 4.13). Colour tends to be a rich reddish orange in the southern Cape becoming slightly yellower in the Orange Free State and southern Transvaal and markedly paler in Namaqualand. On the whole colour is redder

Table 4.13

Morphometric and colorimetric measurement and ratio statistics for Cynictis penicillata penicillata specimens examined. Colorimetric variables, HUE, VALUE, CHROMA, DOM (dominant wavelength), BRT (brightness), PUR (excitatory purity) were obtained using Munsell charts and a tristimulus colorimeter and are explained in the text. Low values of HUE, and high values of DOM indicate a redder coloration; high values of VALUE and BRT indicate a paler coloration; high values of CHROMA and PUR indicate a more saturated coloration.

Character	N	Y	SD	Range
EXTERNAL MEASUREMENTS				
H&B	169	341	27,34	265--460
TAIL	169	230	23,35	165--290
CRANIAL MEASUREMENTS				
CBL	203	67,0	2,17	62,2--73,7
BCW	204	28,6	0,78	26,9--30,9
MRH	207	18,2	0,94	16,2--20,8
SOH	196	12,9	0,78	10,0--15,6
MTR	205	21,6	0,86	17,4--24,1
ICD	208	8,49	0,35	7,40--9,50
WAB	203	28,6	0,91	26,4--31,2
CNW	202	16,2	0,63	14,1--17,9
POC	206	15,1	1,24	12,1--19,4
IOW	205	15,5	0,73	13,7--18,2
ZYW	200	40,1	1,33	36,3--44,2
LP^4	208	6,21	0,34	5,33--7,30
BUL	204	17,3	0,59	15,6--18,8
WP^4	208	5,45	0,34	4,56--6,46
COLOUR MEASUREMENTS				
HUE	36	18,2	1,95	15,0--20,0
VALUE	36	5,8	1,12	4--8
CHROMA	36	6,8	1,49	1--8
DOM	36	583,4	1,87	580--587
BRT	36	14,4	4,89	8,1--27,0
PUR	36	51,0	8,42	18,4--60,9
RATIOS				
TAIL/H&Bx100	170	67,5	7,77	45,4--88,8
ZYW/CBLx100	197	59,9	1,95	54,2--65,2

and richer than in the other subspecies (higher values for DOM (580--587) and PUR (18,4--60,9): see Table 4.13).

SPECIMENS EXAMINED. OTU codes given below are as in Fig. 4.2. Numbers outside brackets indicate sample sizes of morphometrically analysed (age class 4 and 5) specimens from each locality; numbers inside brackets indicate sample sizes of additional (age class 1--3) specimens that were not morphometrically analysed.

OTU Pooled localities and sample sizes

1 ORANGE FREE STATE. Lemoenboord: NM, 1; Allermansdrift: NM, 1; Eendrag: NM, 1; Olifontsfontein: NM, 1 (2); Fauresmith: TM, 2; Melkspruit: NM, 1; Kraaifontein: NM, 1; Rouxville: TM, 1; Klipkraal: NM, (1); Hexrivier: NM, (1).

2 ORANGE FREE STATE. Goeie Hoop: NM, (1); Waaikraal: NM, 1; Voorspoed: NM, 1; Ventersburg: TM, (1); Sunnyside: TM, 1; Tussenrivier: TM, (2); Koppieskraal: NM, 1 (1); Leeukop: NM, 1; Middeldeel: NM, 1; Glen Agricultural College: NM, 4 (3), TM, 4 (1); Bishop's Glen: NM, 1 (2); Holmesdale: NM, 7 (5); Mimosa: NM, 9 (5); Merino: NM, 2 (3); Vereyannelkop: NM, 1; Alpha: NM, (1); Donkerhoek: NM, (1); Dewetsdorp: TM, 1.

3 ORANGE FREE STATE. Krugersdrift: NM, (1); Rooikraal: NM, 3 (8); Ietwater: NM, 2; Trutersdrift: NM, 10 (4); Paalkraal: NM, (1); Nielsview: NM, 2 (1); Barberspan: NM, 1; Bultfontein: NM, 3 (1); Abrahamskraal: NM, 2; Paardenkraal: NM, (1); Wonderkop: NM, 1 (1); Brand Valley: NM, 1; Tweerivier: NM, 1; Nooitgesein: NM, 1; Koppiesdam: NM, (1).

4 ORANGE FREE STATE. Beste Hoop: NM, (1); Bakenfontein: NM, 1; Winburg: TM, 1; Willem Pretorius Reserve: TM, 1; Soutpan: NM, (1); Eldorado District: NM, 1 (1); Veekraal: NM,1.

5 ORANGE FREE STATE. Bloemhof Dam: NM, 1; Glasgow: NM, 1; Leeukraal: NM, (1); Beestekraal: TM, 8 (2).

6 ORANGE FREE STATE. Graspan: NM, (1); Philip: TM, 2 (1); Odendaalsrus: TM, 8 (7); Dayaartsdam: NM, (1); Rooidam: TM, (1); Angra Pequina: TM, 1 (1).

7 ORANGE FREE STATE. Helena: NM, 1; Parma: TM, 3;

Vredefort Road: BM, 1 (7).

8 ORANGE FREE STATE. Erfdeel: NM, 1; Schurwepoort: NM, (1); Leeupoort: NM, 1; Alyna: NM, 1; Kroonstad: KM, 4 (2); Heuningspruit: KM, 1.

9 ORANGE FREE STATE. Sussanaskop: NM, 1; Helena: NM, 1; Eindelik: NM, 1; Toledo, (1); Vitulugt: NM, 1.

10 ORANGE FREE STATE. Harala: NM, 1; Summerslie: NM, (1); Gansfontein: TM, 1; Buckland Downs: TM, 1; 15m W Bethlehem: TM, 1; Harrismith: BM, 1 (1).

12 TRANSVAAL. Wilgekuil: TM, 1 (1); Zandspruit: TM, 1; Mosdene Private Nature Reserve: TM, 1; Jericho: TM, 1; Rietondale, Pretoria: TM, 2; Derdepoort Radio Station, Pretoria: TM, (1); Hatfield, Pretoria: TM, 1; Pietersburg: BM, 1 (2); Pretoria: BM, (1); Kaal Plaas: TM, 1 (2); Rhenosterfontein: TM, (4).

13 TRANSVAAL. Fountain Blue, Johannesburg: TM, 1; Tarlton: TM, 1; Hartebeesfontein: TM, (1); Delmas: TM, 1; Rolspruit: TM, 1 (1); Middelburg: TM, 1; Roodepoort: TM, 1; Goodehoop: TM, (1).

14 TRANSVAAL. Joshua Moolman Private Nature Reserve: TM, 2; Holbank: TM, (1); Carolina: TM, 1; Ermelo: KM, 1; Wakkerstroom: BM, 1 (2).

15 TRANSVAAL. Oorbietjiesfontein: TM, (2); Witpoort: TM, 1; Ratzegaiiskraal: TM, 2; 20m W Ventersdorp: TM, 1; Pretoria Zoo Farm: TM, 1 (1); Barberspan Private Nature Reserve: TM, 1; Boschop (type locality of C. p. brachyura): TM, 1; Marico District (type locality of C. p. leptura): BM, 1; CAPE. Duikerbult, MM, 3.

16 TRANSVAAL. Brandhoek: TM, 2 (1); Klipkuil: TM, 1 (2); Leeudoringstad : TM, 1.

17 TRANSVAAL. Welgedaan: TM, 3 (3); Panfontein: TM, (4); Bloemhof: TM, 1; S A Lombard Nature Reserve: TM, (2).

24 BOTSWANA. 10m W Ramathlabama: NMZ, 4; Gaberones (type locality for C. p. bechuanae): TM, (1). CAPE. 20m SW Mafeking: TM, (1); Cremona: MM, (1).

30 CAPE. Olifants R: TM, 1 (1); Klaver: TM, (4); Vredendal: TM, 4 (2).

31 CAPE. Graafwater: KM, 4 (5); Lamberts Bay: KM, 3 (9); Compagnies Drift: KM, 2 (1); Eendekuil: TM, (1); Welbedacht: TM, 1; Modder R: KM, 2.

32 CAPE. Kangnas: TM, (1); Eenriet: KM, 2 (2); Klipfontein (type locality for C. p. pallidior): BM, 2 (2).

33 CAPE. Gonna: KM, 4 (1).

34 CAPE. 12 km S, 105km W De Aar: KM, 1; Deelfontein (type locality for C. p. intensa): BM, 2 (3); Victoria West: DM, 2 (3); Keikamspoort: TM, (1); Louisvale: BM, (3).

35 CAPE. Mountain Zebra National Park: TM, 1 (1); Whittlesea: KM, 1; Middelburg: KM, 1 (1); Queenstown: KM, 2; Bolotwa: KM, (1); Tarkastad: KM, (1).

36 CAPE. Kleinpoort: TM, (1); Grahamstown: KM, 1, BM, 1 (3); King Williams Town: KM, 2; Kei Rd: KM, 1 (1); Peddie: KM, 1; Atherstone: KM, 1; Bedford: KM, 1 (2); Uitenhage (type locality for C. p. penicillata): BM, 1; Port Elizabeth: TM, (1); Mydrecht: KM, (1); Blaney: KM,

(1); Lk Kaboussie: KM (1); Fort Beaufort: KM, (1); 29km N, 41km E Uniondale: KM, (1); 2km N, 2,1km W King Williams Town: KM, (1).

38 CAPE. Uitsigskool: MM, 1.

Cynictis penicillata bradfieldi Roberts, 1924

Cynictis penicillata bradfieldi Roberts, Annals of the Transvaal Museum 10: 69. 1924. Quickborn, 96km north of Okahandja, Damaraland, Namibia.

Cynictis bradfieldi cinderella Thomas, Proceedings of the Zoological Society, London: 375. 1927. Ondongwa, 1074m (3525 ft), central Ovamboland, northern Namibia.

Cynictis penicillata karasensis Roberts, Annals of the Transvaal Museum 19: 235. 1938. Kochena, Great Karas Mountains, Great Karas Mountains.

HOLOTYPE. Transvaal Museum No. 3484. Skin and skull of adult (skull age class 5) male in good condition. Collected by R. D. Bradfield on 31 January 1923, from Farm Quickborn, Okahandja District, Namibia.

DISTRIBUTION (Fig. 4.12). Northern Cape; southern Botswana; southern, central and northwestern Namibia; intergrading with C. p. penicillata in northeastern Cape and southeastern Botswana, and with C. p. coombsii in northeastern and eastern Namibia and southern Botswana.

DIAGNOSIS. Intermediate - sized subspecies: head and body length 274--370; CBL 58,8--65,8 (Table 4.14). Colour intermediate in DOM (579--583: Table 4.14) and PUR (31,6--52,6: Table 4.14) between C. p. penicillata and C. p. coombsii, i.e. orange to yellowish in hue and moderately faded.

SPECIMENS EXAMINED. OTU codes given below are as in Fig. 4.2. Numbers outside brackets indicate sample sizes of morphometrically analysed (age class 4 and 5) specimens from each locality; numbers inside brackets indicate sample sizes of additional (age class 1--3) specimens.

OTU Pooled localities and sample sizes

22 NAMIBIA. Reinfels: SM, 1; Berseba: BM, 1 (1); Spitzkoppe: SM, 1; Kochena (type locality of C. p. karasensis): TM, (1); Warmfontein: SM, (1).

23 CAPE. Grootdrink: MM, 1 (2); Mata Mata, Kalahari Gemsbok National Park: TM, 1. BOTSWANA. Khuis: NMZ, 1; 4m NNW Bokspits: NMZ, (1); 5m N Tsabong: NMZ, (2).

26 NAMIBIA. Ukuambi: TM, 1 (1); Oshikanga: TM, 2 (5); Ombalantu: TM, 1; Tshandi: TM, (1); Elim: TM, (2); Ukuanyama: TM, (2); Hazeldene: TM, (2); Kovares: BM, 1 (1); Ombombo: BM, (1); S Kaokoveld: KM, (1).

27 NAMIBIA. Ondonga (type locality for C. p. cinderella): BM, 2, TM, (2);

28 NAMIBIA. 4km Okombake Reserve: TM, (1); Quickborn (type locality for C. p. bradfieldi): TM, 2; Erongo Plateau: KM, (3); Okavakonde: SM, 1; Westjolenhof: SM, 1.

29 NAMIBIA. Auachab: TM, 1; Autabib: SM, 1; Wortel: SM, 1; Leutsven St, Windhoek: SM, (1); Gorassis: SM, (1); Bellrode: BM, 2 (1).

37 CAPE. Blisfontein: TM, 1, KM, 1 (1); Cnydas: TM, 1 (1); Gosa: MM, 1; Franshoek: MM, 2; Augrabies: TM, (1); Riemvasmaak: MM, (1).

38 CAPE. Waterford: MM, 1 (2); Barclay West: MM, 3 (1); Witput: MM, 2; Sydney on Vaal: MM, 1; Naauwte: MM, 1; Bellsbank Estates: MM, 1 (1); Fourteen Streams: TM, 1; Hopefield Estates MM, (1); Cape Nature Conservation

Table 4.14

Morphometric and colorimetric measurement and ratio statistics for Cynictis penicillata bradfieldi holotype and specimens examined (includes holotype). Colorimetric variables, HUE, VALUE, CHROMA, DOM (dominant wavelength), BRT (brightness), PUR (excitatory purity) were obtained using Munsell charts and a tristimulus colorimeter and are explained in the text. Low values of HUE, and high values of DOM indicate a redder coloration; high values of VALUE and BRT indicate a paler coloration; high values of CHROMA and PUR indicate a more saturated coloration.

Character	Holotype	N	Y	SD	Range
EXTERNAL MEASUREMENTS					
H&B	13'(330mm)	31	318	19,29	274--370
TAIL	8,5'(215mm)	31	232	17,72	190--280
HF(S.U.)	2,75'(70mm)	-	-	-	-
CRANIAL MEASUREMENTS					
CBL	63,2	39	63,0	1,46	58,8--65,8
BCW	27,4	40	26,9	0,71	25,2--28,6
MRH	17,5	40	17,0	0,66	15,8--18,4
SOH	13,0	39	12,1	0,58	10,8--13,1
MTR	20,1	36	19,7	0,79	17,8--21,1
ICD	7,61	39	7,81	0,44	6,92--8,68
WAB	26,8	38	26,4	0,76	24,8--27,9
CNW	15,8	39	15,4	0,54	14,3--17,0
POC	15,0	40	15,3	1,06	13,0--17,5
IOW	14,1	38	14,5	0,59	13,5--15,9
ZYW	37,6	38	37,0	1,29	33,6--40,9
LP^4	5,77	39	5,68	0,35	4,88--6,56
BUL	16,7	40	16,8	0,54	15,7--18,0
WP^4	5,01	39	4,95	0,30	4,33--5,65
COLOUR MEASUREMENTS					
HUE	20,0	18	20,6	1,61	17,5--22,5
VALUE	5	18	6,0	1,00	5--7
CHROMA	8	18	5,5	1,69	4--8
DOM	582	18	581,4	1,42	579--583
BRT	13,2	18	17,1	4,08	11,3--26,4
PUR	50,7	18	44,2	5,21	31,6--52,6
RATIOS					
TAIL/H&Bx100	65,2	31	73,3	6,70	59,4--86,7
ZYW/CBLx100	59,5	37	58,6	2,29	52,3--62,6

Station, Hartswater, (1).

Cynictis penicillata coombsii Roberts, 1929

Cynictis penicillata coombsii Roberts, Annals of the Transvaal Museum 13: 90. 1929. Farm Swarthaak, Soutpansberg, northern Transvaal.

Cynictis penicillata kalaharica Roberts, Annals of the Transvaal Museum 15: 4. 1932. Kaotwe Pan, central Kalahari, Botswana.

Cynictis penicillata bechuanae Roberts, Annals of the Transvaal Museum 15: 4. 1932. Gaberones, southeastern Botswana.

HOLOTYPE. Transvaal Museum No. 4877. Skin and skull of adult (skull age class 5) male, collected by C. Coombs on 18 April 1927, at Farm Swarthaak, Soutpansberg, northern Transvaal. Skull shattered by shot.

DISTRIBUTION (Fig. 4.12). Soutpansberg district of Transvaal, north of the Soutpansberg Mountains (although two specimens were collected just south of the Soutpansberg at Blijdschap Private Nature Reserve); central and northern Botswana; intergrading with C. p. bradfieldi in northeastern and eastern Namibia and southern Botswana.

DIAGNOSIS. Smallest of the subspecies: head and body length

usually less than 300mm (275--390: Table 4.15); CBL almost always less than 61mm (56,2--62,9: Table 4.15). Colour extremely yellow and bleached, having a grizzled appearance due to contrasting, alternating black and yellow pigments in guard hairs. This subspecies exhibits the lowest colorimetric measurements of DOM (578--582: extremely yellow) and PUR (29,5--45,3: extremely bleached) in the species.

REMARKS. The type locality for C. p. coombsii was given incorrectly as Swarthoek (a farm on the southern slopes of the Soutpansberg Mountains) in the original description by Roberts, and in subsequent citations, and has been recently corrected (Taylor and Meester, 1989) to Swarthaak (a farm north of the Soutpansberg, previously owned by C. Coombs, the collector of the type specimen). There is evidence that this subspecies is extending its range southwards in Transvaal as specimens (albeit 'non - adults') were examined from two localities south of the Soutpansberg Mountains (localities 10 and 11 in Fig. 4.12) which had small skulls typical of this subspecies.

SPECIMENS EXAMINED. OTU codes given below are as in Fig. 4.2. Numbers outside brackets indicate sample sizes of morphometrically analysed (age class 4 and 5) specimens from each locality; numbers inside brackets indicate sample sizes of additional (age class 1--3) specimens.

Table 4.15

Morphometric and colorimetric measurement and ratio statistics for Cynictis penicillata coombsii holotype and specimens examined (includes holotype). Colorimetric variables, HUE, VALUE, CHROMA, DOM (dominant wavelength), BRT (brightness), PUR (excitatory purity) were obtained using Munsell charts and a tristimulus colorimeter and are explained in the text. Low values of HUE, and high values of DOM indicate a redder coloration; high values of VALUE and BRT indicate a paler coloration; high values of CHROMA and PUR indicate a more saturated coloration.

Character	Holotype	N	Ȳ	SD	Range
EXTERNAL MEASUREMENTS					
H&B	299	30	304	21,28	275--390
TAIL	230	29	210	24,80	150--292
HF(S.U.)	60	-	-	-	-
EAR	22	-	-	-	-
CRANIAL MEASUREMENTS					
CBL	-	37	59,7	1,74	56,2--62,9
BCW	-	35	26,2	0,84	24,8--28,4
MRH	-	35	16,3	0,63	15,2--18,1
SOH	-	35	11,7	0,86	10,2--14,0
MTR	18,3	36	18,7	0,74	16,9--20,1
ICD	-	36	7,26	0,39	6,61--8,53
WAB	-	36	25,3	0,87	23,9--28,2
CNW	-	36	14,8	0,54	13,8--16,2
POC	14,3	37	14,8	1,02	12,8--17,0
IOW	13,5	36	13,7	0,78	12,6--15,9
ZYW	-	35	35,2	1,27	33,2--39,2
LP^4	-	37	5,41	0,30	4,75--6,12
BUL	-	36	16,2	0,57	15,0--17,5
WP^4	-	35	4,63	0,28	4,01--5,32
COLOUR MEASUREMENTS					
HUE	20,0	9	20,6	1,10	20,0--22,5
VALUE	6	9	5,3	0,71	4--6
CHROMA	4	9	3,9	1,05	2--6
DOM	581	9	580,4	1,24	578--582
BRT	15,6	9	14,7	2,04	12,0--18,4
PUR	36,0	9	37,6	5,44	29,5--45,3
RATIOS					
TAIL/H&Bx100	76,9	30	68,6	6,12	50,8--81,0
ZYW/CBLx100	-	34	59,1	1,94	55,6--62,9

OTU Pooled localities and sample sizes

11 TRANSVAAL. Montrose Estates: TM, 1 (4); Blijdschap Private Nature Reserve: TM, (2); Junction of Crocodile and Matlabis R: TM, 1; Swarthaak Farm: TM, (1). BOTSWANA. Debeeti: NMZ, 2.

12 TRANSVAAL. Fort Klipdam: TM, (2); Amsterdam: KM, (1).

18 BOTSWANA. 77m E Maun: TM, (1); Xangwa: TM, 1; Lk Ngami: NMZ, 1; 14m W Sehitwa: NMZ, 1; Malopo R: NMZ, 1 (1); 15m N Nokaneng: NMZ, (1).

19 BOTSWANA. Bacops: TM, 1; Lk Dow: NMZ, 1; Toromoja: NMZ, (1); 7m from Nkomo on Bacops Rd: NMZ, 1; Tamafupi: NMZ, 1 (1); Damucheche Pan: NMZ, 1 (2); 45m SW Francistown: NMZ, (1); Nkomo Village: NMZ (1).

20 BOTSWANA. Damara Pan: TM, 1 (1), BM, (1); Gemsbok Pan: TM, 1; Kaotwe Pan (type locality of C. p. kalaharica): TM, 1 (1). NAMIBIA. Die Hoek: SM, 2; Sandfontein: KM, (1), BM, 1 (1).

21 BOTSWANA. Tshane: NMZ, 1 (2); Sekhuma Pan: KM, (1); Nakuntsi: NMZ, (1); Kang: NMZ, 2; 15m W Takatowan: NMZ, (1). NAMIBIA. Gunstelling: SM, 1.

22 NAMIBIA. Gaibis: SM, 1.

23 CAPE. Swartbasrivier: MM, (1).

27 NAMIBIA. Ondangua: TM, 2 (5); central Ovamboland: KM, (1); Ovamboland: SM, 1; Mangetti Quarantine Block: SM, (1); Okondera Flats, Etosha National Park: SM, (1); Wolfnes, Etosha National Park: SM (1).

39 CAPE. Marthavale: TM, 1; Vryburg: TM, 3; Duinval: MM, 1; Marthasdale: MM, 2 (2); Kansvat: MM, 1; Gathlose; MM, 1; Sishen: MM, 1; Griqualand West: MM, 1; Junction of Upington and Kuruman, W of Witdraaii: TM, (1); Kuruman: TM, (1); BM, (1); Piries: MM, (1); Grootfontein: MM, (1).

Cynictis penicillata natalensis, new subspecies

HOLOTYPE. Transvaal Museum No. 35538. Skin and skull of adult (age class 4) female, collected 19th August, 1982, by P. Milstein, at Farm Uitsicht (no. 501), Natal.

DISTRIBUTION (Fig. 4.12). This subspecies occurs in the northern and western parts of the province, and appears to be separated from the other subspecies by the Drakensberg

Range.

DIAGNOSIS. This Natal subspecies can be distinguished in having a comparitively short and wide skull shape (Fig. 4.7). The ratio of ZYW to CBL is an approximate measure of this character. Adults from Natal have skulls in which ZYW comprises 60,8--64,3% of CBL (Table 4.16). This ratio is usually less than 61% and hardly ever as high as 63% in other subspecies (three out of the four Natal adults had skulls with a ratio of 63% or greater compared with only 4% of specimens from other subspecies ($\underline{N}$ = 268)). As recognition of this subspecies is based on only a few specimens, it needs to be tested with a larger sample of Natal individuals.

SPECIMENS EXAMINED. OTU codes given below are as in Fig. 4.2. Numbers outside brackets indicate sample sizes of morphometrically analysed (age class 4 and 5) specimens from each locality; numbers inside brackets indicate sample sizes of additional (age class 1--3) specimens.

OTU Pooled localities and sample sizes

25 NATAL. Uitsicht: TM, 1; Bellevue: TM, 1; Kambula: NAM, 1 (1); Greytown: NAM, (1); Spring Grove: NAM, 2 (1); Bergville: NAM, (1); Newcastle: BM, (1); Geluk: NAM, (1).

ACKNOWLEDGEMENTS

Table 4.16

Morphometric and colorimetric measurement and ratio statistics for Cynictis penicillata natalensis holotype and specimens examined (includes holotype). Colorimetric variables, HUE, VALUE, CHROMA, DOM (dominant wavelength), BRT (brightness), PUR (excitatory purity) were obtained using Munsell charts and a tristimulus colorimeter and are explained in the text. Low values of HUE, and high values of DOM indicate a redder coloration; high values of VALUE and BRT indicate a paler coloration; high values of CHROMA and PUR indicate a more saturated coloration.

Character	Holotype	N	Y	SD	Range
EXTERNAL MEASUREMENTS					
H&B	346	5	338	18,38	307--355
TAIL	214	5	222	17,04	201--246
CRANIAL MEASUREMENTS					
CBL	61,4	4	64,0	2,15	61,4--66
BCW	27,3	5	29,3	1,20	27,3--30
MRH	17,1	5	18,4	0,88	17,1--19
SOH	12,5	4	12,9	0,41	12,5--13
MTR	20,5	5	20,8	0,62	20,2--21
ICD	7,53	4	8,10	0,38	7,53--8,
WAB	28,2	5	29,1	0,53	28,2--29
CNW	14,8	4	15,7	0,72	14,8--16
POC	15,3	5	16,2	1,37	14,8--18
IOW	14,6	5	15,7	0,81	14,6--16
ZYW	38,7	5	40,7	1,28	38,7--42
LP^4	5,61	5	5,95	0,27	5,61--6,
BUL	17,1	5	17,1	0,45	16,5--17
WP^4	5,09	5	5,39	0,45	4,87--6,
COLOUR MEASUREMENTS					
HUE	17,5	-	-	-	-
VALUE	5	-	-	-	-
CHROMA	8	-	-	-	-
DOM	584	-	-	-	-
BRT	13,0	-	-	-	-
PUR	46,3	-	-	-	-
RATIOS					
TAIL/H&Bx100	61,8	5	65,6	3,07	61,8--69
ZYW/CBLx100	63,0	4	63,0	1,56	60,8--64

The financial support of the Foundation for Research Development to I.L.R. and J.M. is gratefully acknowledged. The following institutions and curators kindly loaned us material or allowed us access to their collections: Mr L. R. Wingate (KM), Mr J. Watson (NMB), Dr B. R. Stuckenberg (NAM), Dr G. B. Corbet, Miss P. Jenkins, Miss J. Ingles, and Mr J. E. Hill (BM), Mr C. G. Coetzee (SM), Mr A. Kumirai (NMZ), Miss P. S. Linger and Mr H. Erasmus (MM). PJT is most grateful to the Director of the Transvaal Museum, Dr C. K. Brain, for access to the Museum's mammal collection, as well as library, computer and other facilities during 1986 and 1987. Dr N. J. Dippenaar is to be thanked most heartily for his assistance and advice in the fields of multivariate morphometric techniques and computer applications.

REFERENCES

ALLEN, G. M., 1939. A checklist of African mammals. Bulletin of the Museum of Comparative Zoology at Harvard College **83**: 1--763.

BAKER, C. M., 1987. Biology of the Water Mongoose (Atilax paludinosus). PhD thesis, University of Natal, Durban.

BARTON, N. H. and HEWITT, G. M., 1985. Analysis of hybrid zones. Annual review of ecology and systematics **16**: 113--148.

BEST, T. L., 1978. Variation in Kangaroo rats (Genus Dipodomys) of the heermanni group in Baja California,

Mexico. Journal of Mammalogy **59**(1): 160--175.

BLACKITH, R. E. and REYMENT, R. A., 1971. Multivariate morphometrics. Academic Press, London and New York.

BRAIN, C. K., 1985. Temperature - induced environmental changes in Africa as evolutionary stimuli. In: VRBA, E. S., ed., Species and speciation, pp. 45--52. Transvaal Museum Monograph No. 4. Transvaal Museum, Pretoria.

BROADLEY, D. G., 1978. A revision of the genus Platysaurus A Smith (Sauria: Cordylidae). Occasional Papers of the National Museums and Monuments of Rhodesia, Series B, **6**: 129--185.

BUSH, G. L., 1975. Modes of animal speciation. Annual review of ecology and systematics **6**: 339--364.

CHERRY, L. M., CASE, S. M., KUNKEL, J. G., WYLES, J. S. and WILSON, A. C., 1982. Body shape metrics and organismal evolution. Evolution **36**(5): 914--933.

CHEVERUD, J. M., 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. Evolution **36**(3): 499-516.

COOKE, H. B. S., 1962. The Pleistocene environment Southern Africa. Hypothetical vegetation in Southern Africa during the Pleistocene. Annals of the Cape Provincial Museums **2**: 11-15.

DAVIS, D. H. S., 1962. Distribution patterns of Southern African Muridae, with notes on some of their fossil antecedents. Annals of the Cape Provincial Museums **2**:

56--76.

DEACON, J. and LANCASTER, N., 1988. Late Quaternary palaeoenvironments of Southern Africa. Clarendon Press, Oxford.

DEBLASE, A. F. and MARTIN, R. E., 1981. A Manual of Mammalogy, 2nd ed. Wm. C. Brown Company Publishers, Dubuque, Iowa.

DIPPENAAR, N. J. and RAUTENBACH, I. L., 1986. Morphometrics and karyology of the Southern African species of the genus Acomys I. Geoffroy Saint-Hilaire, 1838 (Rodentia: Muridae). Annals of the Transvaal Museum **34**(6): 129--183.

DOBZHANSKY, T., 1937. Genetics and the origin of species. Columbia University Press, New York.

DOWLING, T. E., SMITH, G. R. and BROWN, W. M., 1989. Reproductive isolation and introgression between Notropis cornutus and Notropos chrysocephalus (Family Ciprinidae): comparison of morphology, allozymes, and mitochondrial DNA. Evolution **43**(3): 620--634.

ELLERMAN, J. R., MORRISON-SCOTT, T. C. S. and HAYMAN, R. W., 1953. Southern African mammals. 1758--1951: a reclassification. British Museum (Natural History), London.

ENDLER, J. A., 1977. Geographic variation, speciation and clines. Princeton University Press, Princeton New Jersey.

ERASMUS, B. H. (Personal communication). Cape Provincial

Administration: Nature Conservation, P. O. Box 456, Kimberley, 8300.

FARRIS, J. S., 1970. Methods for computing Wagner trees. Systematic Zoology **19**: 83--92.

GENOWAYS, H. H., 1973. Systematics and evolutionary relationships of spiny pocket mice, Genus Liomys. Special Publication No. 5, Texas Tech University.

GENOWAYS, H. H. and CHOATE, J. R., 1972. A multivariate analysis of systematic relationships among populations of the short - tailed shrew (Genus Blarina) in Nebraska. Systematic Zoology **21**: 106--116.

GEORGE, S. B., CHOATE, J. R. and GENOWAYS, H. H., 1981. Distribution and taxonomic status of Blarina hylophaga Elliot (Insectivora: Soricidae). Annals of Carnegie Museum **50**: 493--513.

JENSEN, R. J., 1981. Wagner networks and Wagner trees: a presentation of methods for estimating most parsimonious solutions. Taxon **30**(3): 576--590.

KLEIN, R. G., ed, 1984. Southern African prehistory and paleoenvironments. A.A. Balkema, Rotterdam, Boston.

KUNKEL, J. G., CHERRY, L. M., CASE, S. M. and WILSON, A. C., 1980. M - statistics and morphometric divergence. Science **208**: 1060--1061.

LEAMY, L., 1983. Variance partitioning and effects of sex and age on morphometric traits in randombred house mice. Journal of Mammalogy **64**(1): 55--61.

LIDICKER, W. Z., 1962. The nature of subspecies boundaries

in a desert rodent and its implications for subspecies taxonomy. Systematic Zoology **11**: 160--171.

LUNDHOLM, B. G., 1955. A taxonomic study of Cynictis penicillata (G. Cuvier). Annals of the Transvaal Museum **22**: 305--319.

MAYR, E., 1942. Systematics and the origin of species. Columbia University Press, New York.

MAYR, E., 1963. Animal species and evolution. Harvard University Press, Cambridge.

MAYR, E., 1978. Review of M. J. D. White, 1978: Modes of speciation. Systematic Zoology **27**(4): 478--482.

MAYR, E., 1982. Speciation and macroevolution. Evolution **36**(6): 1119--1132.

MEESTER, J. A. J., RAUTENBACH, I. L., DIPPENAAR, N. J. and BAKER, C. M., 1986. Classification of Southern African Mammals. Transvaal Museum Monograph No. 5. Transvaal Museum, Pretoria.

MOORE, W. S., 1977. An evaluation of narrow hybrid zones in vertebrates. The Quarterly Review of Biology **52**: 263--277.

MOORE, W. J., 1981. The mammalian skull. Cambridge University Press, Cambridge.

MOSS, M. L. and YOUNG, R. W., 1970. Functional approach to craniology. American Journal of Physical Anthropology **18**: 281--292.

NEFF, N. A. and MARCUS, L. F., 1980. A survey of multivariate methods for systematists. Privately

published, New York [Printed at the American Museum of Natural History].

NEFF, N. A. and SMITH, G. R., 1978. Multivariate analysis of hybrid fishes. Systematic Zoology **28**: 176--196.

OWEN, R. D. and QUMSIYEH, M. B., 1987. The subspecies problem in the Trident leaf - nosed bat, Asellia tridens: homomorphism in widely separated populations. Zeitschrift Säugetierkunde **52**: 329--337

OLSON, E. and MILLER, R., 1958. Morphological integration. University of Chicago Press, Chicago.

PATERSON, H. E. H., 1985. The recognition concept of species. In: VRBA, E. S., ed., Species and speciation., pp. 21--29. Transvaal Museum Monograph No. 4. Transvaal Museum, Pretoria.

PIMENTEL, R.. A., 1979. Morphometrics. The multivariate analysis of biological data. Kendall / Hunt Publishing Company, Dubuque, Iowa.

PIMENTEL, R. A. and SMITH, J. D., 1986a. BIOΣTAT I. A tutorial manual. Sigma Soft, Placentia, CA.

PIMENTEL, R. A. and SMITH, J. D., 1986b. BIOΣTAT II. A tutorial manual, 2nd ed. Sigma Soft, Placentia, CA.

POWER, D. M., 1971. Statistical analysis of character correlations in Brewers blackbirds. Systematic Zoology **20**: 186--203.

ROBERTS, A., 1951. The mammals of South Africa. Trustees of the 'Mammals of South Africa' Book Fund, Johannesburg.

ROHLF, F. J, 1986. NTSYS-pc. Numerical taxonomy system for

the IBM PC microcomputer (and compatibles). Ver. 1,01. Applied Biostatistics Inc., New York.

SCLATER, W. L., 1900. The mammals of South Africa(Volume I). Porter, London.

SHORTRIDGE, G. C., 1934. The mammals of South West Africa (Volume II). William Heinemann, London.

SMITHERS, R. H. N., 1983. The mammals of the southern African subregion. University of Pretoria, Pretoria.

SNEATH, P. H. A. and SOKAL, R. R., 1973. Numerical taxonomy. W. H. Freeman and Co, San Francisco.

SOKAL, R. R. and ROHLF, F. J., 1981. Biometry, 2nd ed. W. H. Freeman and Co, San Francisco.

STRANEY, D. O., 1978. Variance partitioning and non - geographic variation. Journal of Mammalogy **59**: 1--11.

TAYLOR, P. J., CAMPBELL, G. K., MEESTER, J., WILLAN, K. and VAN DYK, D., 1989. Genetic variation in the rodent subfamily Otomyinae (Muridae). 1. Allozyme divergence among four species. South African Journal of Science **85**: 257--262.

TAYLOR, P. J., MEESTER, J. and RAUTENBACH, I. L. A quantitative analysis of geographical colour variation in the Yellow Mongoose Cynictis penicillata Ogilbyi, 1833, in Southern Africa. Annals of the Transvaal Museum (In Press).

TAYLOR, P. J. and MEESTER, J. A. J., 1989. The type locality of Cynictis penicillata coombsii Roberts, 1929 and Gerbillus paeba coombsii Roberts, 1929. Zeitschrift

für Säugetierkunde **54**: 329--330.

THOMAS, P. A., 1968. Variation and covariation in characters of the rabbit tick, Haemaphysalis leporispalustris. University of Kansas Science Bulletin **47**: 787--828.

THORPE, R. S., 1976. Biometric analysis of geographic variation and racial affinities. Biological Reviews **51**: 407--452.

THORPE, R. S., 1984a. Primary and secondary transition zones in speciation and population differentiation: a phylogenetic analysis of range expansion. Evolution **38**(2): 233--243.

THORPE, R. S., 1984b. Coding morphometric characters for constructing distance Wagner networks. Evolution **38**(2): 244-255.

THORPE, R. S., 1988. Multiple group principal components analysis and population differentiation. Journal of Zoology, London **216**: 37--40.

VAN ZINDEREN BAKKER, E. M., 1962. Botanical evidence for Quaternary climates in Africa. Annals of the Cape Provincial Museums **2**: 16--31.

VRBA, E. S., 1985a. Environment and evolution: alternative causes of the temporal distribution of evolutionary events. South African Journal of Science **81**: 229--236.

VRBA, E. S., 1985b. Introductory comments on species and speciation. In: VRBA, E. S., ed., Species and speciation, pp. ix--xviii. Transvaal Museum Monograph No. 4. Transvaal Museum, Pretoria.

WARD, J., 1963. Hierarchical grouping to optimise an objective function. Journal of the American Statistical Association **58**: 236--243.

WATSON, J. P., and DIPPENAAR, N. J., 1987. The species limits of Galerella sanguinea (Ruppell, 1836), G. pulverulenta (Wagner, 1839) and G. nigrata (Thomas, 1928) in Southern Africa (Carnivora: Viverridae). Navorsinge van die Nasionale Museum Bloemfontein **5**(14): 356--413.

WHITE, M. J. D., 1978. Chain processes in chromosomal speciation. Systematic Zoology **27**: 285--298.

WIIG, O., 1985. Multivariate variation in feral American male mink (Mustela vison) from Southern Norway. Journal of Zoology, London **206**: 441--452.

WILLIG, M.. R., OWEN, R. D. and COLBERT, R. L., 1986. Assessment of morphometric variation in natural populations: The inadequacy of the univariate approach. Systematic Zoology **35**: 195--203.

WILLIG, M. R. and OWEN, R. D., 1987. Univariate analyses of morphometric variation do not emulate the results of multivariate analyses. Systematic Zoology **36**(4): 398--400.

ZUMPT, I. F., 1969. Factors influencing rabies outbreaks: the age and breeding cycle of the Yellow Mongoose, Cynictis penicillata (G. Cuvier). Journal of the South African Veterinary and Medical Association **40**(3): 319--322.

APPENDIX I

PROTOCOL FOR SELECTING MEANINGFUL, NON - REDUNDANT VARIABLES FOR A CRANIOMETRIC STUDY

The importance of excluding redundant (i.e. highly correlated) variables from a morphometric study is generally acknowledged (Blackith and Reyment, 1971; Sneath and Sokal, 1973; Thorpe, 1976), although hardly ever considered in practice (see Thomas, 1968; Best, 1978 for exceptions to this). To obtain a suitable sample of uncorrelated measurements of the skull and mandible in C. penicillata, a preliminary analysis was conducted prior to measuring the entire sample of skulls. Forty - eight measurements of the teeth, mandible and skull (modified from Roberts, 1951; Lundholm, 1955; de Blase and Martin, 1981; Watson and Dippenaar, 1987) were taken on a sample of 27 male skulls of the same age class, from Wesselsbron in the Orange Free State (Fig. 4.13). A correlation matrix was calculated for all pairs of measurements, and this was summarised by means of cluster analysis, using Ward's (1963) hierarchical method (see Cheverud, 1982 for the justification for using Ward's method rather than the usual UPGMA method (Sneath and Sokal, 1973) in this context). Representative variables were selected from each of 14 sub - clusters of variables on the correlation phenogram, on the basis of low coefficients of variability, previous use, and ease of measurement (ringed

numbers in Fig. 4.13 represent final set of measurements). The composition of the 14 sub - clusters of variables is given in Table 4.17, as well as their possible functional interpretations, as discussed below. The procedure outlined above follows the general approach suggested by Power (1971) and Thorpe (1976) for selecting non - covarying characters for a multivariate study.

Interpretation of correlations between measurements

Using a similar approach to that outlined above, Cheverud (1982) found that correlated subsets of measurements ('P - sets') corresponded almost exactly with functional sets of measurements ('F - sets') defined independently on the basis of functional cranial analysis (Moss and Young, 1970). This result appeared to confirm the main hypothesis of the concept of morphological integration (Olson and Miller, 1958), that developmentally and functionally related traits are highly morphologically integrated (highly correlated).

Table 4.17 indicates the assignment of measurements to the different correlated sub - clusters ('P - sets' of Cheverud) identified from the correlation phenogram. Despite the fact that many of the variables used in the present study could not easily be assigned independently to different functional divisions of the skulls ('mixed' measurements such as condylobasal length cross many of the functional units of

Fig. 4.13 Skull of Cynictis illustrating reference points of 48 measurements taken for preliminary correlation analysis in a sample of 27 male skulls of the same relative age class. Ringed numbers indicate 14 uncorrelated measurements selected for morphometric analysis. Anatomical terminology follows Thomas (1905) and deBlase and Martin (1981). 1 (GML) Greatest mandible length, from posterior surface of angular process to anterior edge of alveolus of first incisor. 2 (MTR) Mandibular tooth row, from anterior edge of P_2 alveolus to posterior edge of M_2 alveolus. 3 (MRH) Mandible ramus height, from dorsal edge of coronoid process to ventral edge of angular process. 4 (MCA) Mandibular condyle - angular distance, from dorsal edge of mandibular condyle to ventral edge of angular process. 5 (LMH) Least mandible height, taken at midpoint of P_4 alveolus. 6 (MCS) Mandibular condyle spread, taken between lateral edges of mandibular condyles. 7 (MWP) Mandible width taken on lingual surface of P_4 alveoli. 8 (MWC) Mandible width taken on lingual surface of canine alveoli. 9 (MCW) Mandibular condyle width. 10 (CBL) Condylo basal length of skull, from gnathion to condylion. 11 (PAL) Palatilar length, from hensilion to palation. 12 (LPF) Length of palatal foramen. 13 (IOE) Distance from infraorbital foramen to anterior edge of ear opening. 14 (IOP) Distance from infraorbital foramen to posterior edge of postorbital bar where it joins with zygomatic arch's dorsal extension. 15 (NPO) Distance from anterior edge of nasal to posterior edge of postorbital bar. 16 (CP^2) Distance from posterior edge of canine alveolus to anterior edge of P^2 alveolus. 17 (ROW) Rostrum width, taken on centre line of canines. 18 (ZYW) Greatest zygomatic width, taken between outer margins of zygomatic arches, perpendicular to skull axis. 19 (BCW) Brain case width at dorsal root of squamosals. 20 (ICD) Inter - canine width, taken at lingual surface of canine alveoli. 21 (VCW) Vidian canal width at foramena lateral to pterygoid processes. 22 (POC) Postorbital constriction. 23 (WAB) Width at bullae, taken on ear openings perpendicular to skull axis. 24 (CNW) Greatest occipital condyle width, taken perpendicular to skull axis. 25 (FJW) Least distance between foramena jugulare on posterior edge of bullae. 26 (MAW) Greatest maxillary width, taken where P^4 and M^1 meet. 27 (HOM) Height of maxilla, from dorsal edge of infraorbital foramen to point on maxilla where P^2 and P^3 meet. 28 (SOH) Supraoccipital height from junction of nuchal and sagittal crests to dorsal edge of foramen magnum. 29 (SHM) Skull height taken vertically from posterior M^2 alveolus. 30 (BCH) Brain case height from dorsal surface of sagittal crest to midventral surface of basioccipital between anterior bullae. 31 (BUL) Greatest bulla length taken parallel with skull axis. 32 (BUW) Greatest bulla width taken perpendicular to skull axis. 33 (CML) Canine - molar length, from anterior edge of canine alveolus to posterior edge of M^2 alveolus. 34 (LP_3) Length of P_3 taken along cingulum. 35 (LM_1) Length of M_1 taken along cingulum. 36 (LM_2) Length of M_2 taken along cingulum. 37 (WP_3) Greatest cross - sectional crown width of P_3. 38 (WM_1) Greatest cross - sectional crown width of M_1. 39 (WM_2) Greatest cross - sectional crown width of M_2. 40 (TLP^3) Length of P^3 taken along cingulum. 41 (LP^4) Length of P^4 taken along cingulum. 42 (LM^2) Length of M^2 taken along cingulum. 43 (WP^3) Greatest cross - sectional crown width of P^3. 44 (WP^4) Greatest cross - sectional crown width of P^4. 45 (WM^2) Greatest cross - sectional crown width of M^2. 46 (IOW) Least interorbital width. 47 (LM^1) Length of M^1 taken along cingulum. 48 (WM^1) Greatest cross - sectional crown width of M^1.

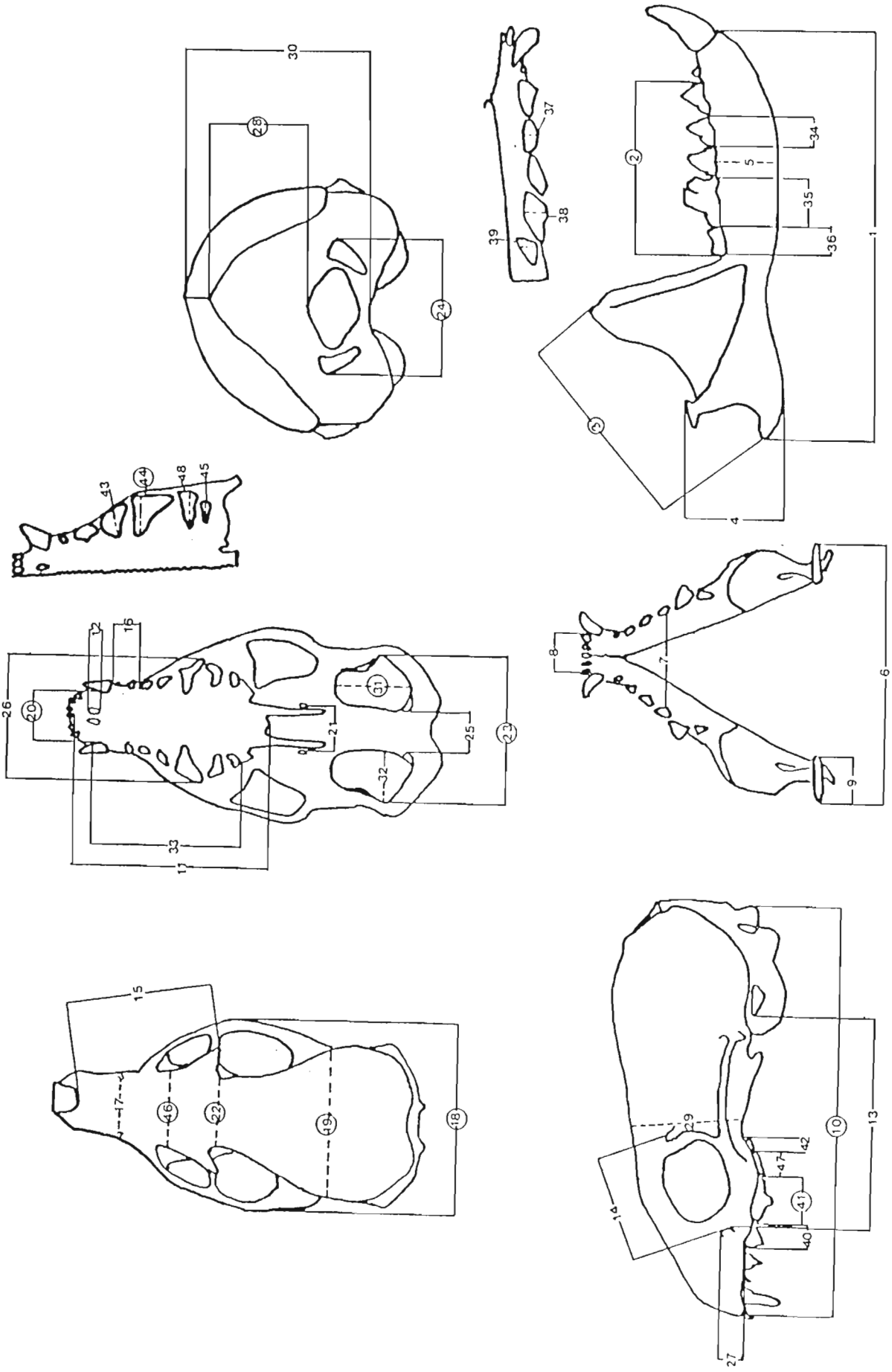

30
28
24
37
39
38
2
34
5
35
36
1
3
4
43
44
48
45
8
7
6
9
26
20
16
2
31
21
25
23
32
33
17
15
17
46
22
19
18
29
42
47
41
40
10
13
14
27

Table 4.17

Table showing correlated subsets of cranial measurements in Cynictis penicillata, as defined by major clusters and subclusters of measurements from a phenogram derived from a correlation matrix of 48 x 48 measurements based on a sample of 27 adult (relative age class 4) male skulls from Wesselsbron in the northern Orange Free State. Roman numerals, numbers, and letters indicate sets of measurements formed at the two, six and 14 - cluster stage of the correlation phenogram respectively. Underlined measurements indicate those that were selected for morphometric analysis from each of the 14 subclusters of measurements. Functional interpretation of clusters and subclusters of measurements was based on the positioning of individual measurements with respect to the major functional units ('F - sets') of the skull as outlined by Cheverud (1982): for example measurements of the brain case (BCW, BCH) relate to the parietal F -set, and measurements which reflect the degree of development of the jaw muscles involved with mastication (MRH, ZYW, MCS) belong to the masticatory F - set (see text for further explanation). Measurements marked with asterisks indicate those that do not belong in their designated F - sets.

Clusters and subclusters	Measurements
I. NEUROPARIETAL FUNCTIONAL UNIT:	
1. ('Mixed' + occipital)	
A. 'Mixed' (skull lengths)	GML, CBL, IOE, PAL, IOP, NPO
B. Occipital	CP^2(*), VCW, WAB
C. Bullae	BUL, BUW
2. (Parietal / occipital)	
A. Parietal	BCW, SHM, BCH
B. Occipital?	SOH
C. Occipital	CNW
3. (Parietal / masticatory)	
A. Masticatory	MRH, MCA
B. Parietal?	POC
4. (Frontal / masticatory)	
A. Masticatory	MCS, ZYW, MCW
B. Frontal	FJW(*), IOW, MWC
II. OROFACIAL FUNCTIONAL UNIT:	
5. (Orofacial)	
A. Facial	MTR, CML, MWP, MAW, HOM
B. Tooth widths	WP^3, WP^4, WM^2
C. Rostrum	LMH(*), ICD, ROW, WM^1(*)
6 (Oral: tooth lengths)	LPF(*), WM_1(*), WM_2(*), LM_2, LM^1, LM^2, LP_3, LP^3, WP_3(*), LM_1, LP^4

the skulls), there appeared to be a close correspondence between correlated subsets of measurements and functional and anatomical units of the skull. The primary functional division of the skull, between (anterior) orofacial and (posterior) neuroparietal 'F - sets' (Cheverud, 1982), is clearly demonstrated at the two - cluster stage of the correlation phenogram (Table 4.17). Mixed, or 'size' measurements fall into the 'neuro - parietal cluster'. P - sets formed at the six - cluster stage can be interpreted as combinations of F - sets, and P - sets formed at the 14 - cluster stage can be interpreted as individual F - sets (frontal, parietal, occipital, oral, facial, masticatory and premaxillary) and anatomical structures (bulla).

Certain F - sets, eg. parietal and occipital, were shared between different P - sets, and certain measurements (indicated by asterisks in Table 4.17) did not belong in their particular designated F - sets. Nevertheless the correspondence between P - sets and functional and anatomical units of the skull (at least in the case of C. penicillata) allows one to determine the functional context of particular measurements prior to morphometric analyses, and this may prove to be useful in understanding the adaptive importance of observed patterns of inter - OTU morphometric variability.

The approach outlined above satisfies two important criteria for selecting measurements for a multivariate study: comprehensiveness (adaquate coverage of the phenotype) and economy (removal of redundant variables). Furthermore, by summarising the patterns of correlations between measurements, this approach is consistent with the concept of morphological integration (Olson and Miller, 1958) which regards the phenotype as a organised, integrated, functional whole comprising different, semi - independent functional parts. Adopting this approach implies that relatively few measurements from different parts of the skull need be taken in order to adequately summarise skull form (see also Kunkel, Cherry and Case, 1980; Cherry, Case, Kunkel, Wyles and Wilson, 1982). Such a philosophy is more realistic than the pheneticist concept that as many characters as possible should be measured in order to approximate 'overall similarity' (Sneath and Sokal, 1973).

The pheneticist approach is not appropriate for selecting measurements for a craniometric study as it leads to unnecessary measurement of redundant variables, increased analysis time and possible analytical problems in processing huge data matrices, inclusion of 'bad' measurements, and distortion of final inter - OTU relationships (Blackith and Reyment, 1971: 35--38). Large numbers of highly correlated variables may result in determinants (calculated from a correlation or covariance / variance matrix) being equal to

zero. A determinant of zero (or very near zero) indicates a singular, or ill - conditioned dispersion matrix. Since only non - singular matrices possess an inverse, and the inverse of the dispersion matrix is necessary for discriminant analysis, discriminant analysis is not possible where the determinant equals zero. In the case of C. penicillata exploratory principal components analyses were performed on both the 48 and the 14 - variable data matrices in order to obtain the determinant from the correlation matrices, using the program MPCA from the computer package BIOΣTAT II (Pimentel and Smith, 1986b). The determinant was zero in the 48 - variable matrix and non - zero in the 14 - variable matrix.

APPENDIX II

GAZETTER

Coordinates and ¼° grid references were obtained from specimen labels, Rautenbach (1978), Lynch (1983), Skead (1973) and from personal field notes belonging to the late Dr R. H. N. Smithers which were stored on microfilm in the library of the Transvaal Museum. Where coordinates were not available, ¼° grid references were given.

SOUTH AFRICA

CAPE. Atherstone, Albany 33° 19'S 26° 23'E. Augrabies, Orange R 2820Cb. Barclay West 2824Da. Bedford 32° 41'S 26° 6'E. Bellsbank Estates, 44km W Warrenton 28° 6'S 24° 25'E. Blaney, N of King Williams Town: see King Williams Town. Blisfontein, Upington 2821Ac. Cnydas (Farm), 12km NW Lutzputs 28° 19'S 20° 34'E. Compagnies Drift, Clanwilliam 32° 7'S 18° 27'E. Cremona (Farm), 26km SSE Vergelee 25° 56'S 24° 25'E. 12km S, 105km W De Aar, De Aar 30° 45'S 23° 54'E. Deelfontein, Richmond 30° 59'S 23° 48'E. Duikerbult (Farm), 16km W Setlagole 26° 17'S 24° 58'E. Duinwal (Farm) 30km W Vorstershoop 25° 57'S 22° 45'E. Eendekuil 3218Dd. Eenriet, Namaqualand 29° 12'S 17° 52'E. Fort Beaufort, Fort Beaufort 32° 46'S 26° 38'E. Fourteen Streams 2824Bb. Franshoek (Farm), 16km NW Olifantshoek 27° 52'S 22° 36'E. Gathlose, 28km ESE Sishen 27° 55'S 23° 14'E. Gonna, 54m E Calvinia (Calvinia = 31° 28'S 19° 47'E). Gosa (Farm), 54km W-WSW Hotazel 27° 18'S 22° 28'E. Graaf - Reinet 32° 16'S 24° 33'E. Graafwater, Clanwilliam 32° 9'S 18° 36'E. Grahamstown 33° 19'S 26° 32'E. Griqualand West 28° 30'S 23° 20'E. Grootfontein (Farm), 19km SW Reivilo 27° 39'S 24° 1'E. Grootdrink, 52km ENE Van Zyl's Rus 26° 26'S 22° 12'E. Hopefield Estates (Farm No. 522), 25km NNE Ginekwastad 28° 38'S 23° 18'E. Junction of Upington and Kuruman, Witdraii 2723Ad. Kaboussie Lake (see King Willians Town). Kangnas (Farm), 48km ENE Springbok 29° 35'S 18° 21'E. Kansvat (Farm), 22km NW Vryburg 26° 50'S 24° 23'E. Kei Road, King Williams Town 32° 42'S 27° 33'E. Keikamspoort (Farm 71), 20km SE Prieska 29° 50'S 22° 47'E. King Williams Town 32° 52'S 27° 23'E. 3km N, 2,1km W King Williams Town, King Williams Town 32° 51'S 27° 22'E. Klaver 31° 47'S 18° 37'E. Kleinpoort, Grahamstown 3326Bc. Klipfontein, Namaqualand 29° 13'S 17° 40'E. Kuruman 27° 27'S 23° 26'E. Lamberts Bay, Clanwilliam 32° 5'S 18° 18'E. Louisvale, near Upington, south bank Orange River, Gordonia 28° 34'S 21° 12'E. 20m SW Mafeking 2525Dc. Marthasdale (Farm No. 190), 23km NNE Danielskuil 27° 58'S 23° 40'E. Marthavale (Farm), 40km NW Kuruman 27° 21'S 23° 8'E. Mata Mata, Kalahari Gemsbok National Park 2520Da. Middelburg 3125Ac. Modder R 33° 29'S 18° 19'E. Mountain Zebra National Park, Cradock 3225Ba. Mydrecht (Farm), Berlin 2327Dc. Naauwte, 23km NNW Prieska

29° 28'S 22° 38'E. Northern Cape Nature Conservation Station, Hartswater 27° 45'S 24° 45'E. Olifants R 3118Cb. Peddie, Peddie 33° 12'S 27° 7'E. Port Elizabeth 3325Dc. Piries (Farm), 29km NW Kuruman 27° 19'S 23° 11'E. Queenstown, Queenstown 31° 54'S 26° 53'E. Riemvasmaak, 47km NW Kakamas 28° 27'S 20° 19'E. Sishen Nature Reserve, Sishen 27° 39'S 23° 0'E. Swartbasrivier, 5km NE Rietfontein 26° 43'S 20° 4'E. Sydney on Vaal, 4km Delportshoop 28° 27'S 24° 19'E. Tarkastad, Tarkastad 32° 00'S 26° 16'E. Uitenhage 33° 46'S 25° 24'E. Uitsigskool, Perseel 8H 11, 6km SW Hartswater 27° 45'S 24° 45'E. 2,9km N, 4,1km E Uniondale, Uniondale 33° 38'S 23° 10'E. Victoria West 31° 30'S 23° 11'E. Vredendal, Van Rhynsdorp 31° 40'S 18° 31'E. Vryburg 2624Dc. Waterford (Farm), 13km NNE Hopetown 29° 36'S 24° 5'E. Welbedacht 3319Ac. Whittelsea, Fort Beaufort 3226Bb.Witput (Farm), 12km NW Campbell.

NATAL. Bellevue (Farm 25) 2730Dd. Bergville, Harrismith 2829Cb. Geluk (Farm), Colenso, Ladysmith 2829Da. Greytown, Umvoti 2830Dc. Kambula, Vryheid 2730Db. Newcastle 27° 45'S 29° 57'E. Spring Grove, Elandslaagte, Harrismith 2829Bd. Uitsicht (Farm 501) 2731Cc.

ORANGE FREE STATE. Abrahamskraal, (Farm 319), Bloemfontein 2825Dc. Allemansdrift (Farm 37), Philippolis 3025Cb. Alyna (Farm), Frankfort 2728Ba. Alpha (Farm), Ladybrand 2927Ba. Angra Pequina (Farm 8), Bothaville 27° 29'S 26° 32'E. Bakenfontein (Farm 33), Winburg 2827Ca. Barbers Pan (Farm 822), Bloemfontein 2825Dd. Beestekraal (Farm 358), Hoopstad 27° 45'S 25° 45'E. Berlin (Farm 394), Parys 2627Dc. 12m Beste Hoop (Farm 192), Theunissen 2826Bc. 15 m W Bethlehem 28° 46'S 28° 2'E.Bishops Glen (Farm 273), Bloemfontein 2826Cd. Bloemhof Dam 2725Da. Brandvallei (Farm 22), Jacobsdal 2925Aa. Bultfontein (Farm 26), Bloemfontein 2825Dd. Buckland Downs (Farm 1803), Harrismith 2829Ac. Carthago (Farm 17), Paris 2627Dc. Dayaartsdam (Farm), Allonridge 2726Da. Donkerhoek (Farm), Hoblause 2927Ca. Dewetsdorp 29° 35'S 26° 40'E. Eendrag (Farm), Bethulie 3025Db. Eindelik (Farm 685), Harrismith 2729Cd. Eldorado District, 2825Bd. Erfdeel (Farm 165), Kroonstad 2727Cb. Fauresmith 29° 45'S 25° 19'E. Gansfontein (Farm 765), Ficksburg 2827Dc. Glasgow (Farm 808), Hoopstad 2725Da. Glen Agricultural College, Bloemfontein 2826Cd. Goeie Hoop (Farm 2604), Bloemfontein 2926Aa. Graspan (Farm 60), Kroonstad 2726Dd. Harala (Farm), Senekal 2827Bb. Harrismith 28° 16'S 29° 8'E. Helena (Farm 162), Vrede 2728Bd. Helena (Farm 780), Vredefort 2627Cd. Heuningspruit 2727Ac. Hex River (Farm 405), Reddersburg 2926Cd. Holmesdale (Farm 95), Bloemfontein 2826Cc. Iedwater (Farm), Bloemfontein 2825Dd. Klipkraal (Farm), Lady Grey 3027Ca. Koppiesdam (Farm 473), Petrusberg 2925Ba. Koppieskraal (Farm 407), Bloemfontein 2926Ac. Kraaifontein (Farm), Rouxville 3026Dd. Kroonstad 27° 40'S 27° 14'E. Krugersdrift Dam, Bloemfontein 2825Dd. Leeukop (Farm 105), Dewetsdorp 2926Ad. Leeukraal (Farm), Hoopstad

2725Dd. Leeupoort (Farm 109), Heilbron 2727Bb. Lemoenboord (Farm 320), Philippolis 3024Bb. Melkspruit (Farm), Aliwal 3026Da. Merino (Farm 14), Bloemfontein 2826Cc. Middeldeel (Farm), Bloemfontein 2926Ac. Mimosa (Farm 1319), Bloemfontein 2826Cc. Nielsview (Farm 393), Dealesville 2825Dd. Nooitgesein (Farm 400), Bloemfontein 2925Bc. Odendaalsrus 2726Dc. Olifantsfontein (Farm), Trompsburg 3025Bb. Paalkraal (Farm 101), Dealesville 2825Dd. Paardenkraal (Farm 349), Bloemfontein 2825Dc. Parma (Farm), Parys 2627Dc. Philip (Farm 318), Wesselsbron 2726Cd. Rooidam (Farm), Jacobsdal 2726Cb. Rouxville 30° 25'S 26° 50'E. Rooikraal (Farm 876), Bloemfontein 2825Dd. Schurwepoort (Farm 448), Koppies 2727Bc. Soutpan (Farm 258), Brandfort 2826Ca. Sunnyside (Farm 337), Bloemfontein 2926Aa. Sussanaskop (Farm), Reitz 2728Da. Toledo (Farm 993), Reitz 2728Cb. Trutersdrift (Farm 783), Bloemfontein 2825Dd. Tussenrivier (Farm), Bloemfontein 2926Aa. Tweerivier (Farm), Jacobsdal 2924Ba. Summerslie (Farm), Harrismith 2829Ac. Veekraal (Farm 164), Hertzogville 2825Ba. Ventersburg (Farm), Bloemfontein 2926Aa. Vereyannelkop (Farm), Ladybrand 2927Ad. Vitulugt (Farm), Vrede 2729Ad. Voorspoed (Farm 1788), Bloemfontein 2926Aa. Vredefort Road (Vredefort = 27° 1'S 27° 22'E). Waaikraal (Farm 534), Bloemfontein 2926Aa. Willem Pretorius Reserve, Winburg 2827Ac. Winburg 2827Ca. Wonderkop (Farm 18), Bloemfontein 2825Dd.

TRANSVAAL. Amsterdam (Farm), Pietersburg 23° 16'S 29° 27'E. Barbers Pan Private Nature Reserve, 24km E Delareyville, Delareyville 26° 35'S 25° 35'E. Blijdschap Private Nature Reserve, 5km N Bandolierskop, Soutpansberg (= Zoutpansberg) 23° 15'S 29° 46'E. Bloemhof 27° 39'S 25° 31'E. Boschop (Farm), Potchefstroom 26° 34'S 27° 7'E. Brandhoek (Farm), 32km ESE Leeudoringstad, Wolmaransstad 27° 17'S 26° 26'E. Carolina, Carolina 26° 4'S 30° 6'E. Delmas 26° 7'S 28° 40'E. Derdepoort Radio Station, Pretoria 25° 43'S 28° 18'E. Ermelo 26° 31'S 30° 0'E. Fort Klipdam (Farm 852), 27km N Pietersburg, Pietersburg 23° 42'S 29° 33'E. Fountain Blue, Johannesburg 26° 6'S 27° 58'E. Goedehoop (Farm 302), 11km S Bethal, Bethal 26° 32'S 29° 27'E. Hartebeesfontein, Randfontein 26° 14'S 27° 37'E. Hatfield, Pretoria 25° 45'S 28° 15'E. Holbank (Farm 265), 15m on road from Ermelo to Amsterdam, Ermelo 26° 33'S 30° 10'E. Jericho (Farm), Brits 25° 17'S 27° 47'E. Joshua Moolman Private Nature Reserve, 9km SW Amsterdam, Ermelo 26° 41'S 30° 36'E. Junction of Limpopo and Matlabis Rivers 23° 41'S 27° 0'E. Kaal Plaas (Farm), 3km N Onderstepoort, Pretoria 25° 39'S 28° 11'E. Klipkuil (Farm 104), Maquassie, Wolmaransstad 27° 19'S 26° 1'E. Leeudoringstad, Wolmaransstad 27° 14'S 26° 14'E. Marico District c. 25° 30'S 26° 0'E. Middelburg, Middelburg 25° 46'S 29° 28'E. Montrose Estates, Soutpansberg (= Zoutpansberg) 22° 55'S 29° 37'E. Mosdene Private Nature Reserve, 1m SE Naboomspruit, Potgietersrus 24° 36'S 28° 46'E. Oorbietjiesfontein (Farm 292), Klerksdorp 26° 47'S 26° 43'E. Panfontein (Farm 270), Bloemhof 27° 35'S 25° 27'E.

Pietersburg 23° 55′S 28° 27′E. Pretoria 25° 43′S 28° 11′E. Pretoria Zoo's Farm, 6km NE Lichtenburg, Lichtenburg 26° 7′S 26° 12′E. Ratzegaaiskraal (Farm 204), 13km W Ventersdorp, Ventersdorp 26° 22′S 26° 32′E. Rhenosterfontein (Farm), 35km E Pretoria 25° 50′S 28° 32′E. Rietondale, Pretoria 25° 43′S 28° 14′E. Rolspruit (Farm 127), 7km E Leslie, Bethal 26° 25′S 29° 0′E. Roodepoort (Farm 383), 5km E Standerton, Standerton. 26° 55′S 29° 23′E. S A Lombard Nature Reserve, Bloemhof 2725Da. Swarthaak (Farm), Soutpansberg 22° 59′S 29° 53′E. Tarlton, Krugersdorp 26° 5′S 27° 38′E. 20m W Ventersdorp, Ventersdorp 26° 20′S 26° 40′E. Wakkerstroom 27° 21′S 30° 9′E. Welgedaan (Farm), 25km NNE Christiana, Christiana 27° 41′S 25° 14′E. Wilgekuil (Farm 181), Rustenburg 25° 14′S 27° 45′E. Witpoort (Farm 419), 24km E Potchefstroom, Potchefstroom 26° 40′S 27° 20′E. Zandspruit (Farm 168), 63km NNW Rustenburg 25° 10′S 26° 57′E.

NAMIBIA

Near Auachab, Namib Desert 2316Bd. Autabib, Windhoek 2317Ba. Bellrode (Farm?), Hoffnung, E Windhoek (Windhoek = 22° 34′S 17° 6′E). Berseba, Great Namaqualand 26° 0′S 17° 46′E. Central Ovamboland 1818Aa. Die Hoek (Farm?), Hereroland East 2120Dd. Elim 1715Cb. Erongo Plateau 21° 35′S 15° 43′E. Gaibis, Keetmanshoop 2619Ba & Bc. Gorrassis (Farm 99), Maltahohe 2515Bd. Gunstelling (Farm 400), Mariental 2319Dd. Hazeldene 1914Bc. Kochena (Farm 306), Karas Mountains 27° 1′S 18° 52′E. Kovares (= Otjokavare), SE Kaokoveld 19° 3′S 14° 22′E. Leutsven Street, Windhoek 2217Cc. Mangetti Quarantine Block 1818Da. Okavakonde, Karabib 2216Ab. 4km Okombake Reserve on road to Vis 2115Ad. Okondera Flats, Etosha National Park 1915Bb. Okorosave, Kaokoveld 18° 11′S 13° 50′E. Ombalantu 1714Dd. Ombombo, Central Kaokoveld 18° 42′S 13° 55′E. Ondangwa (= Ondangua = Ondangua) 17° 54′S 15° 59′E. Oshikanga 1715Bd. Ovamboland 1818Aa. Quickborn (Farm 205), Okahandja 21° 8′S 17° 7′E. Reinfels (Farm), Keetmanshoop 2618Cc. Sandfontein, Damaraland 2219Bd. Southern Kaokoveld 1813Cd. Spitzkoppe (Farm), Keetmanshoop 2618Ad & Bc. Tshandi, Ukualutti 1714Dd. Ukuambi 1715Dc. Ukuanyama 1715Bc. Warmfontein (Farm), Keetmanshoop 2719Ab. Westjolenhof (Farm 23), Karibib 2216Ab. Wolfsnes, Etosha National Park 1915Bb. Wortel, Rebebeth 2317Aa.

BOTSWANA

Bacops 2124Ab. 4m NNW Bokspits 2620Dc. Damara Pan 2222Ab. Damucheche Pan (= Tamuseche) 1926Ac. Debeeti, Karoma area 2326Cb. Lake Dow 2124Ba & Bc. 45m SW Francistown 2126Bd. Gemsbok Pan 2121Da. Kang 232Db. Kaotwe Pan 22° 34′S 23° 14′E. Khuis, Molopo River 2621Dd. Malopo River 1923Db. 77m E Maun 1923Cd. Nakuntsi 2421Bb. Lake Ngami 2022Bd. 7m from Nkomo on Bacops Road 2125Ad. Nkomo Village 2125Ad. 5m N Nokaneng 1922Ca & Cb. 10m W Ramathlabama 25° 38′S 25° 34′E. 14m W Sehitwa 2022Bc. Sekhuma Pan 2423Db. 15m SW Takatokwan

2424Aa. Tamafupi 1926Ac. Toromoja, Botletle River 2124Ba. 5m N Tshabong 2622Ab. Tshane 2421Bb. Xangwa 2022Bd.

CHAPTER 5

GENETIC VARIATION[1]

Introduction

In recent years the technique of allozyme electrophoresis has proved to be an effective tool for resolving systematic problems at both infraspecific and supraspecific levels,[1,2,3,4] as well as for characterising the genetic structure of natural populations of plants and animals.[5] Most mammalian allozyme studies involve smaller mammals, and in particular rodents, with relatively few studies involving species of the order Carnivora.[6] In the Carnivora, most allozyme studies have been concerned with higher level phylogenetic relationships.[7] Data on allozyme variation in species of Carnivora are scarce,[8,9] (and references therein) owing largely to the rarity of many Carnivore species, low population densities in the wild and practical difficulties in collecting large samples of specimens.

---

1. This chapter, together with abstract, is essentially the paper by P. J. Taylor; G. K. Campbell; D. van Dyk; J. P. Watson; J. Pallet and B. H. Erasmus, that is in press in S. A. J. Science under the full title "Genic variation in the yellow mongoose (Cynictis penicillata) in Southern Africa".

This study is the first to examine genetic variability in a member of the family Viverridae (genets, civets and mongooses). While many viverrid species are solitary, nocturnal and difficult to collect in large numbers, the yellow mongoose Cynictis penicillata is a common, diurnal, communal - dwelling species which is widespread throughout (and endemic to) Southern Africa[10] and which is relatively easy to collect in the field. This provided an opportunity to analyse electrophoretically - detectable genetic variability in and among several populations of this species. This investigation will provide baseline data for future studies of genetic variation within and between species of viverrids. A preliminary cladistic analysis of allozyme characters in several viverrid species has recently been conducted (Taylor and Meester, in preparation).

Previous studies of morphometric (Taylor and Meester, in press) and colorimetric (Taylor, Meester and Rautenbach, in press) variation in C. penicillata resulted in the proposal of four parapatric subspecies (the species was previously considered to be monotypic).[11,12] The present study includes specimens from two subspecies, C. p. penicillata and C. p. bradfieldi. The primary purpose of this paper was to determine the genetic basis of morphological differences between these two proposed phena / taxa.

It has been pointed out that tempo and mode of speciation

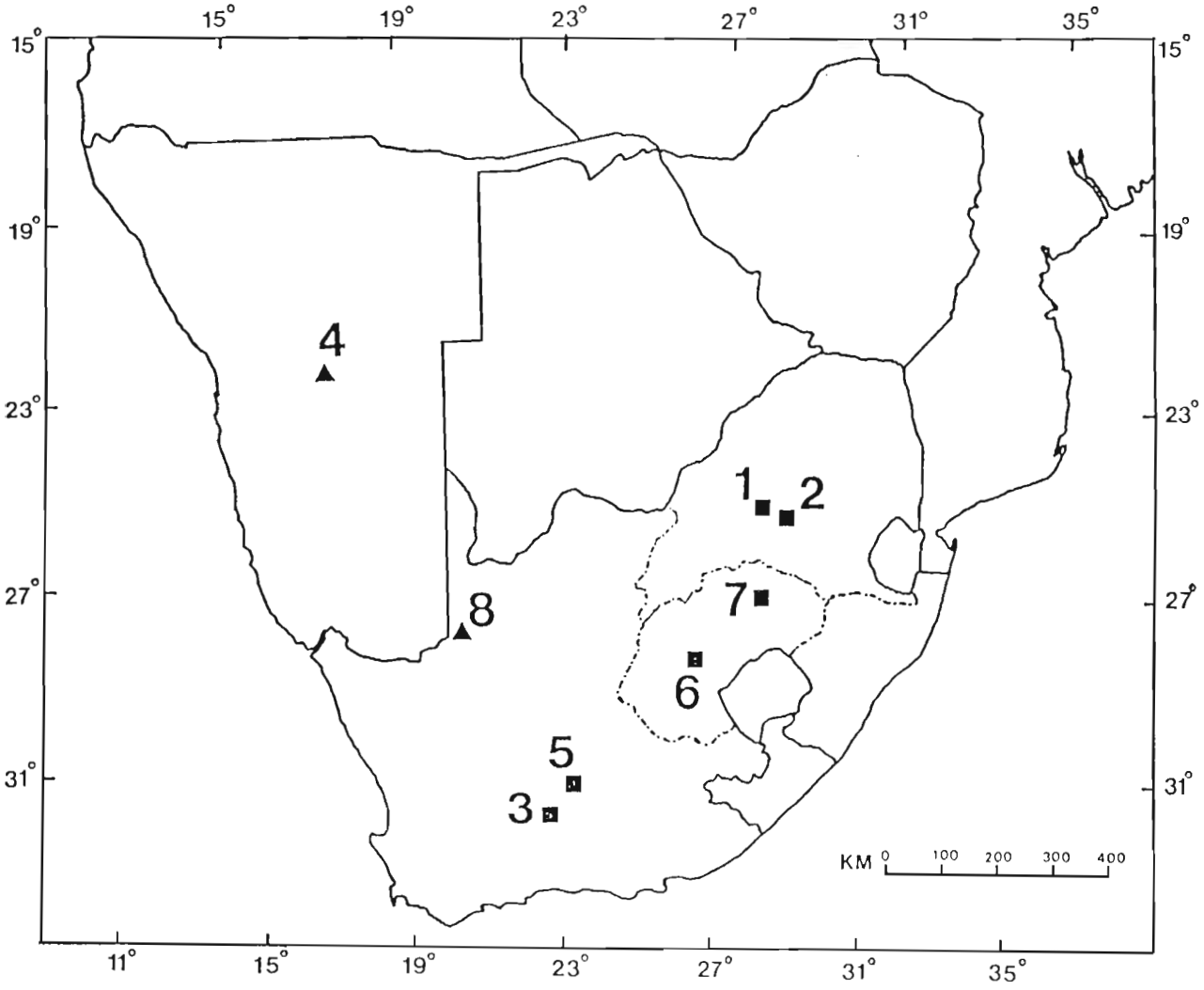
may be largely predicted by the population genetic structure of a species.[13,14,15] A further aim of this paper was therefore to attempt to predict the mode and tempo of (sub)speciation in the yellow mongoose, based on the population genetic structure of the species, and to examine these predictions in the light of morphological and biogeographical evidence.

Material and methods

Thirty five yellow mongooses from eight localities (Fig. 5.1) in South Africa and Namibia were shot or live - trapped between 1985 and 1988. Specimens were terminated using ether or an immobilising drug, 'zolitol'. Liver, kidney (and in some cases heart and serum) samples were collected and stored in liquid nitrogen, prior to later electrophoretic analysis. Voucher specimens were lodged in the Transvaal Museum in Pretoria (TM), the National Museum in Bloemfontein (NM), the Durban Natural Science Museum (DM), and the MacGregor Museum in Kimberley (MM). Locality and specimen details are given in the caption to Fig. 5.1.

Six specimens from Bloemfontein, collected during 1985, were analysed separately from the other specimens. Serum proteins from these specimens were analysed using polyacrylamide gel

Fig. 5.1. Map of Southern Africa showing localities from which C. penicillata specimens were obtained for electrophoretic analyses. Triangles represent C. p. bradfieldi, and squares C. p. penicillata. Localities, sample sizes and specimens examined (abbreviations of institutes explained in text) are as follows: (1) Kaal Plaas (Farm), 3km N Onderstepoort, Pretoria District, Transvaal (N = 3, TM: 39215, 39216, 39265); (2) Rhenosterfontein (Farm), 35km E Pretoria, Cullinan District, Transvaal (N = 4, TM: 39299, 39406, 39436, 39437); (3) Karroo National Park, Beaufort West, Cape Province (N = 1, TM 39448); (4) Windhoek, Namibia (N = 4, TM: 39937, 39947--39949); (5) Victoria West, Cape Province (N = 5, DM: 768--772); (6) Glen Agricultural College, Bloemfontein, Orange Free State (N = 15, TM: 38334, 38335, 38337--38339, NM: 6566--6568, 6576--6580); (7) Erfdeel (Farm), Kroonstad, Orange Free State (N = 2, NM: 6539--6540); (8) Riemvasmaak, 47km NW Kakamas, Cape Province (N = 1, MM: 4784).


15°
19°
23°
27°
31°
35°
11°
4
1
2
8
7
6
5
3
KM 0 100 200 300 400

electrophoresis (PAGE) in the laboratory of the Biology Department, University of Natal (Durban), following procedures in Davis[16]. Other enzymes from liver (and in some cases kidney) homogenates from these six specimens were analysed using starch gel electrophoresis (Connaught starch: 12.5% or 13%), in the laboratory of Dr D. Gordon, Transvaal Museum, following the protocol of Selander et al.[46] All the other specimens (N = 29), which were collected later during 1987 and 1988, were analysed by starch (Sigma: 12.5%) gel electrophoresis in the laboratories of Dr I. L. Rautenbach, Transvaal Museum and the Biology Department, University of Natal (Durban). A standard individual, from the initial study of six specimens, was included in later analyses to facilitate comparison of electrophoretic results between runs.

A total of 37 presumptive structural loci was examined, of which 28 could be accurately scored in some or all specimens (the following enzymes could not be reliably scored, owing to poor staining intensity or resolution, and were therefore excluded from this study: adenylate kinase, acid and alkaline phosphatase, octanol dehydrogenase, glucose-6-phosphate dehydrogenase, hexose-6-phosphate dehydrogenase, leucine aminopeptidase, aldolase, glycerol dehydrogenase). Staining and buffer procedures, which were taken from Davis,[18] Selander et al,[46] Shaw and Prasad,[17] Harris and Hopkinson[18] and Richardson et al,[60] are described in detail

in Table 5.1.

In order to establish that polymorphic alleles were not artifacts of electrophoretic conditions in a particular run, repeat runs were performed in the case of variable loci. In scoring polymorphic loci, different electromorphic alleles were given alphabetical designations, the most anodal being a and successively cathodal electromorphs being designated as b, c, d etc. From the individual genotypes at each locus (including monomorphic loci in which all individuals were scored as AA), allele frequencies were determined and used to calculate measures of expected mean heterozygosity ($\bar{H}$[19]). As esterase, transferrin and prealbumin loci were scored only for the Bloemfontein sample, heterozygosity estimates for this population were calculated with and without these loci. Chi-squared, with Yates' correction for continuity,[20] and Levene's[21] correction for small sample sizes, was utilised to test for departures from Hardy-Weinberg equilibrium. Wright's[22] F statistics, for the partitioning of genetic variances within and between populations, were calculated from allele frequencies, as were Nei's[19] distance (D_N) and identity (I), and Roger's[23] distance (D_R) and similarity (S) coefficients between all pairs of localities. Distance coefficients were summarised by means of UPGMA (unweighted pair group method with averages[24]) phenograms.

All analyses of gene frequency data were performed using

Table 5.1.

Proteins and electrophoretic conditions used in analysis of genetic variation in eight populations of C. penicillata in Southern Africa. With the exception of FUM, GDH, SORD, GPD, LDH, PGD, PGI, PGM and XDH (which were run for about five hours), all gels were run overnight (18 hours). Apart from serum proteins (ALB, TRF, PAL), which were separated on a vertical polyacrylamide system (PAGE), all samples were run on a horizontal starch gel system.

Protein	Enzyme Commission Number	Loci	Tissue[1]	Buffer [2]	Source for stain[3]
Alcohol dehydrogenase	1.1.1.1	ADH	L	5	1
Albumin		ALB	S,L	6, 7	1, 5
Catalase	1.11.1.6	CAT	L	3	2, 4
Creatine kinase	2.7.3.2	CK	L	2	2
Esterase	3.1.1.1	EST-1,2,3	L,K	6,8	1
Fumarase	4.2.1.2	FUM-1,2	L	3	2
Glucose dehydrogenase	1.1.1.47	GDH	L	3	3
Glucosephosphate isomerase	5.3.1.9	PGI	L	4	1
Glutamate-oxaloacetate transaminase	2.6.1.1	GOT-1,2	L	2,3	1
Glycerol-3-phosphate dehydrogenase	1.1.1.8	GPD	L	3	1
Isocitrate dehydrogenase	1.1.1.42	IDH	L	5	1
Lactate dehydrogenase	1.1.1.27	LDH-1,2	L,K	1	1
Malate dehydrogenase	1.1.1.37	MDH-1,2	L	1,3	1
Malic enzyme	1.1.1.40	ME	L	3	4
Phosphoglucomutase	2.7.5.1	PGM	L	4	1
Phosphogluconate dehydrogenase	1.1.1.44	PGD	L	2,4	1
Prealbumins		PAL-1,2	S	7	5
Sorbitol dehydrogenase	1.1.1.14	SORD	L	3	2
Superoxide dismutase	1.15.1.1	SOD	L	1,3	1
Transferrin		TRF	S	7	5
Xanthine dehydrogenase	1.2.1.37	XDH	L	1,3	1

[1] Tissues: L (liver); K (kidney); S (serum)

[2] Buffers (all from ref. 46, except for 7, from ref. 16): 1) discontinuous tris-citrate; 2) tris-citrate I; 3) tris-citrate II; 4) phosphate pH 6.7; 5) phosphate-citrate; 6) lithium hydroxide; 7) tris-glycine; 8) tris-HCl

[3] Sources: 1) ref. 46; 2) ref. 17; 3) recipes used in laboratory of L. Robbins, Southwest Missouri State University; 4) ref. 60; 5) ref. 16; 6) ref. 18

BIOSYS-1[25] on an IBM - compatible PC having an 8087 math coprocessor. Analyses of F statistics and genetic distances and similarities, which require more than one population, were based on 22 loci, as five loci (two esterase loci, transferrin and two prealbumin loci) were scored only in the Bloemfontein sample. F statistics were calculated for all eight localities, and for a subset of five localities having sample sizes of three or greater. This was done to detect possible artifacts due to the presence of very small sample sizes.

Results

Electrophoretic analysis of esterases in C. penicillata revealed the presence of three independent loci, having a pattern of bands which resembled superficially the pattern described by Dew and Kennedy[8] for raccoons (Fig. 5.2). The nomenclature of Dew and Kennedy was adopted: EST-1 for the most anodal system, EST-2 for the most cathodal system, and EST-3 for the intermediate system. Differences existed in the interpretation of esterase patterns between the present study and that of Dew and Kennedy. EST-2 was eserine - sensitive in yellow mongooses, but eserine - insensitive in raccoons. Using NASA (napthyl-as-acetate) as a substrate, EST-2 was discriminated in raccoons, while EST-3 was discriminated in yellow mongooses. The leading band in the

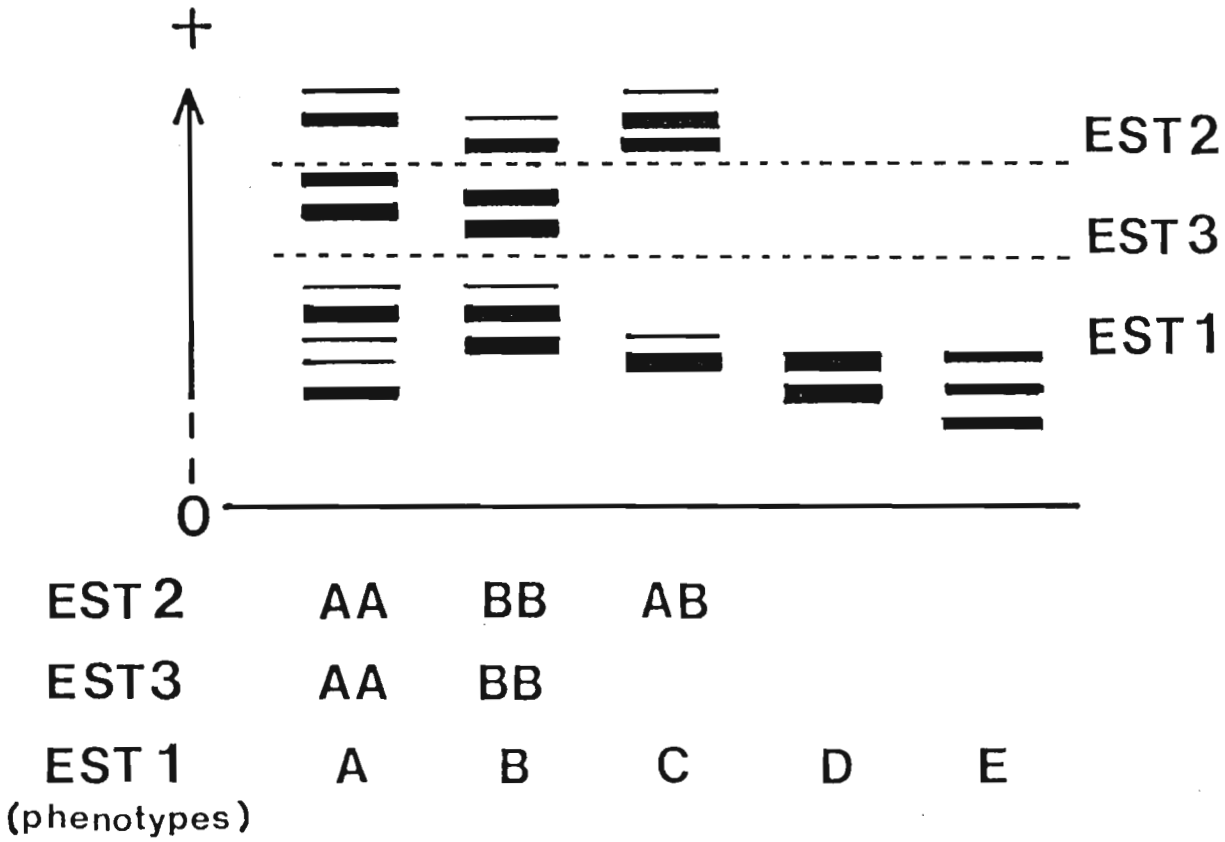


Fig. 5.2. Variation at three esterase loci in C. penicillata. EST-2 and EST-3 could be scored only for six specimens from Glen Agricultural College, Bloemfontein, while EST-1 could be scored for all specimens. The pattern indicated at the left is identical to the esterase pattern described for the raccoon and nomenclature follows these authors[8].

five - banded pattern for EST-1 in yellow mongooses was interpreted as a separate, eserine - sensitive locus (EST-4) by Dew and Kennedy, but did not appear to be eserine - sensitive in the present study. The most anodal esterase band was interpreted as belonging to EST-1 by Dew and Kennedy, but this could not be established in the present study.

While all three esterase loci were monomorphic in raccoons, they were clearly polymorphic in C. penicillata (Fig. 5.2). EST-2 was interpreted as being monomeric as, when only the intense bands within this system were considered, the heterozygote pattern was two - banded. Two distinct, two - banded homozygotes, but no heterozygotes, were detected in EST-3. The genetic basis of variation at EST-1 could not be ascertained because of the complex nature of the different phenotypes observed. The most common phenotype (phenotype A: Fig. 5.2), had a five - banded pattern, and occurred in 17 out of 30 scored individuals. Phenotypes B and C occurred in seven and four individuals respectively, and phenotypes D and E were each observed in single individuals.

While EST-1 was scorable, and gave congruent results, using both Connaught and Sigma starch gels, EST-2 and EST-3 could be scored only on Connaught gels, owing to poor resolution of these loci when esterases were run on Sigma gels (resolution on Sigma gels was not appreciably improved by

varying buffer pH, tissue type, gel strength or run conditions). As most samples were run on Sigma gels (see Methods and Materials), reliable data on EST-2 and EST-3 could be obtained only for six specimens from Bloemfontein (which were run on Connaught starch gels).

Of the 28 loci examined, 15 were monomorphic with all samples fixed for the same allele. Allele frequencies of the 12 genetically interpretable, polymorphic loci are given in Table 5.2. In C. penicillata mean heterozygosity ($\bar{H}$) varied from 0.0% to 6.5% with a mean of 3.4% (Table 5.2). Allozyme variation at all loci, and in all populations, conformed to Hardy - Weinberg expectations (Table 5.3).

The pattern of geographic distribution of electromorphs at variable loci (Tables 5.2, 5.3) indicates a high proportion (82%) of "private" alleles (polymorphic alleles found only in single populations). Only the GOT-1^a and GPD^a electromorphs (as well as the A, B and C EST-1 phenotypes) were detected in more than one population.

Individual polymorphic loci in C. penicillata tended to show both excesses (CAT, GOT-1, GPD) and deficiencies (ADH, GDH, PGD) of heterozygotes, as demonstrated by high positive and high negative F_{IS} values respectively, but the mean, low positive F_{IS} value (Table 5.4: 0.039) indicates an overall balance between the numbers of heterozygotes and homozygotes

Table 5.2.

Allele frequencies, percentage polymorphism, mean heterozygosity ($\bar{H}$) and standard errors (s.e.) of $\bar{H}$ for 12 polymorphic loci in *C. penicillata* from Southern Africa. Locality codes explained in Fig. 5.1.

Locus	Allele	1 N = 3	2 N = 4	3 N = 1	4 N = 4	5 N = 5	6 N = 11	7 N = 2	8 N = 1
ADH	A	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00
	B	1.00	0.50	1.00	1.00	1.00	1.00	1.00	1.00
	C	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00
CAT	A	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00
	B	0.00	0.00	0.00	0.38	0.00	0.00	0.00	0.00
	C	1.00	0.75	1.00	0.62	1.00	1.00	1.00	1.00
EST-2	A	-	-	-	-	-	0.33	-	-
	B	-	-	-	-	-	0.67	-	-
EST-3	A	-	-	-	-	-	0.17	-	-
	B	-	-	-	-	-	0.83	-	-
GDH	A	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	0.50	1.00
GOT-1	A	0.00	0.00	0.50	0.00	0.00	0.00	0.25	0.00
	B	1.00	1.00	0.50	1.00	1.00	1.00	0.75	1.00
GOT-2	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00
GPD	A	0.33	0.00	0.00	0.00	0.00	0.03	0.00	0.00
	B	0.67	1.00	1.00	1.00	1.00	0.97	1.00	1.00
PAL-1	A	-	-	-	-	-	0.50	-	-
	B	-	-	-	-	-	0.20	-	-
	C	-	-	-	-	-	0.30	-	-
PGD	A	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00
	B	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00
	C	1.00	1.00	1.00	0.63	1.00	1.00	1.00	1.00
PGM	A	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
	B	1.00	1.00	0.00	1.00	1.00	1.00	1.00	1.00
TRF	A	-	-	-	-	-	0.90	-	-
	B	-	-	-	-	-	0.10	-	-
Mean %P		4.5	9.1	4.5	9.1	0.0	18.5	9.1	0.0
$\bar{H}$		0.024	0.052	0.030	0.052	0.000	0.065	0.053	0.000
s.e.		0.024	0.037	0.030	0.036	0.000	0.032	0.037	0.000

Table 5.3.

Table showing χ^2 values from tests for conformity of genotypic proportions to Hardy-Weinberg equilibrium in 10 polymorphic loci of C. penicillata from Southern Africa. All χ^2 values were non - significant ($P > 0.05$). Locality codes explained in Fig. 5.1.

	Localities							
Loci	1	2	3	4	5	6	7	8
ADH	-	2.36	-	-	-	-	-	-
CAT	-	0.00	-	0.06	-	-	-	-
EST-3	-	-	-	-	-	0.06	-	-
EST-2	-	-	-	-	-	2.84	-	-
GDH	-	-	-	-	-	-	0.69	-
GOT-1	-	-	0.02	-	-	-	0.00	-
GPD	0.00	-	-	-	-	0.00	-	-
PAL-1	-	-	-	-	-	0.86	-	-
PGD	-	-	-	0.21	-	-	-	-
TRF	-	-	-	-	-	0.00	-	-

Table 5.4.

Results of the analysis of Wright's F statistics for each variable locus for C. penicillata from eight localities in Southern Africa. Double asterisks indicate significance of χ^2 tests of F_{ST} at the 1% level. χ^2 values were determined from the equation: $\chi^2 = 2N\ F_{ST}\ (k - 1)$, with $(k - 1)(s - 1)$ degrees of freedom, where N is the total population size, k is the number of alleles at a locus, and s is the number of populations.

Locus	F_{IS}	F_{IT}	F_{ST}	χ^2
ADH	1.000	1.000	0.344	39.4 **
CAT	-0.481	-0.063	0.282	32.4 **
GDH	1.000	1.000	0.467	27.3 **
GOT-1	-0.714	-0.103	0.356	25.2 **
GOT-2	-	1.000	1.000	70.0 **
GPD	-0.441	-0.048	0.273	18.9 **
PGD	0.529	0.654	0.265	30.2 **
PGM	-	1.000	1.000	58.0 **
Mean	0.039	0.601	0.585	301.5 **

in individual populations. The high positive mean F_{IT} value (Table 5.4: 0.601), however, indicates a greater number of homozygotes than would be expected when data are pooled for all populations. F_{ST} values obtained for both five and eight - population analyses indicate that between 27.1% (five - population analysis: results not shown) and 58.5% (eight - population analysis: Table 5.4) of genetic variability in C. penicillata is accounted for by inter - group differences. The much higher F_{ST} figure obtained for the eight - population analysis results from the "fixation" of private alleles in single - individual populations at the GOT-2 and PGM loci (Tables 5.2, 5.4). There was significant heterogeneity at all variable loci, as indicated by sigificance ($p < 0.01$) of Chi-squared values calculated for F_{ST} statistics (Table 5.4).

Yellow mongoose populations differed very little from one another genetically: I varied from 0.900 to 1.00, and S varied from 0.922 to 0.998 (Table 5.5). No clear genetic groups were distinguished from UPGMA phenograms of D_N and D_R (Fig. 5.3), although the single - individual populations of Karroo National Park and Riemvasmaak were somewhat different from the other populations owing to the apparent "fixation" of polymorphic alleles in these populations as discussed above.

There did not appear to be any correlation between geographic and genetic (D_N) distances, as evidenced by the geographic plot of inter - locality genetic distances in Fig. 5.4. Although the Windhoek population was geographically distant from the South African poulations, D_N values between Windhoek and South African populations (0.008--0.066) were similar in magnitude to D_N values between localities which were very closely spaced geographically (such as Kaal Plaas and Rhenosterfontein in the Transvaal: D_N = 0.012: Fig. 5.4). Since the Windhoek and Riemvasmaak populations represent the subspecies *C. penicillata bradfieldi*, and all the other populations represent *C. p. penicillata*, the present data indicate an absence of electrophoretically - detectable genetic differences between morphologically - defined subspecies of *C. penicillata*.

Discussion

Intrapopulation genetic variability

Previous studies have reported relatively low heterozygosities ($\bar{H}$) for Carnivores,[47,48,8,49,26,50,51,52,9] and for large mammals generally,[27] (and refs. therein), although an absence of empirical correlation between body size and genetic variability in mammals was demonstrated by Wooten and Smith.[27]

Table 5.5.

Value of (A) Nei's standard genetic distance (below the diagonal) and identity (above the diagonal) and (B) Roger's genetic distance (below the diagonal) and similarity (above the diagonal) between eight populations of C. penicillata in Southern Africa, based on 22 loci. Locality codes explained in Fig. 5.1.

A

	1	2	3	4	5	6	7	8
1	-	0.989	0.942	0.989	0.997	0.998	0.989	0.951
2	0.012	-	0.936	0.987	0.992	0.992	0.983	0.945
3	0.059	0.066	-	0.936	0.946	0.946	0.949	0.900
4	0.012	0.013	0.066	-	0.992	0.992	0.983	0.945
5	0.003	0.008	0.055	0.008	-	1.000	0.993	0.955
6	0.002	0.008	0.055	0.008	0.000	-	0.993	0.954
7	0.011	0.017	0.053	0.017	0.007	0.007	-	0.946
8	0.050	0.056	0.105	0.056	0.047	0.047	0.056	-

B

1	-	0.954	0.917	0.953	0.985	0.986	0.951	0.939
2	0.046	-	0.901	0.950	0.969	0.967	0.935	0.923
3	0.083	0.099	-	0.900	0.932	0.930	0.920	0.886
4	0.047	0.050	0.100	-	0.968	0.966	0.934	0.922
5	0.015	0.031	0.068	0.032	-	0.998	0.966	0.955
6	0.014	0.033	0.070	0.034	0.002	-	0.964	0.953
7	0.049	0.065	0.080	0.066	0.034	0.036	-	0.920
8	0.061	0.077	0.114	0.078	0.045	0.047	0.080	-

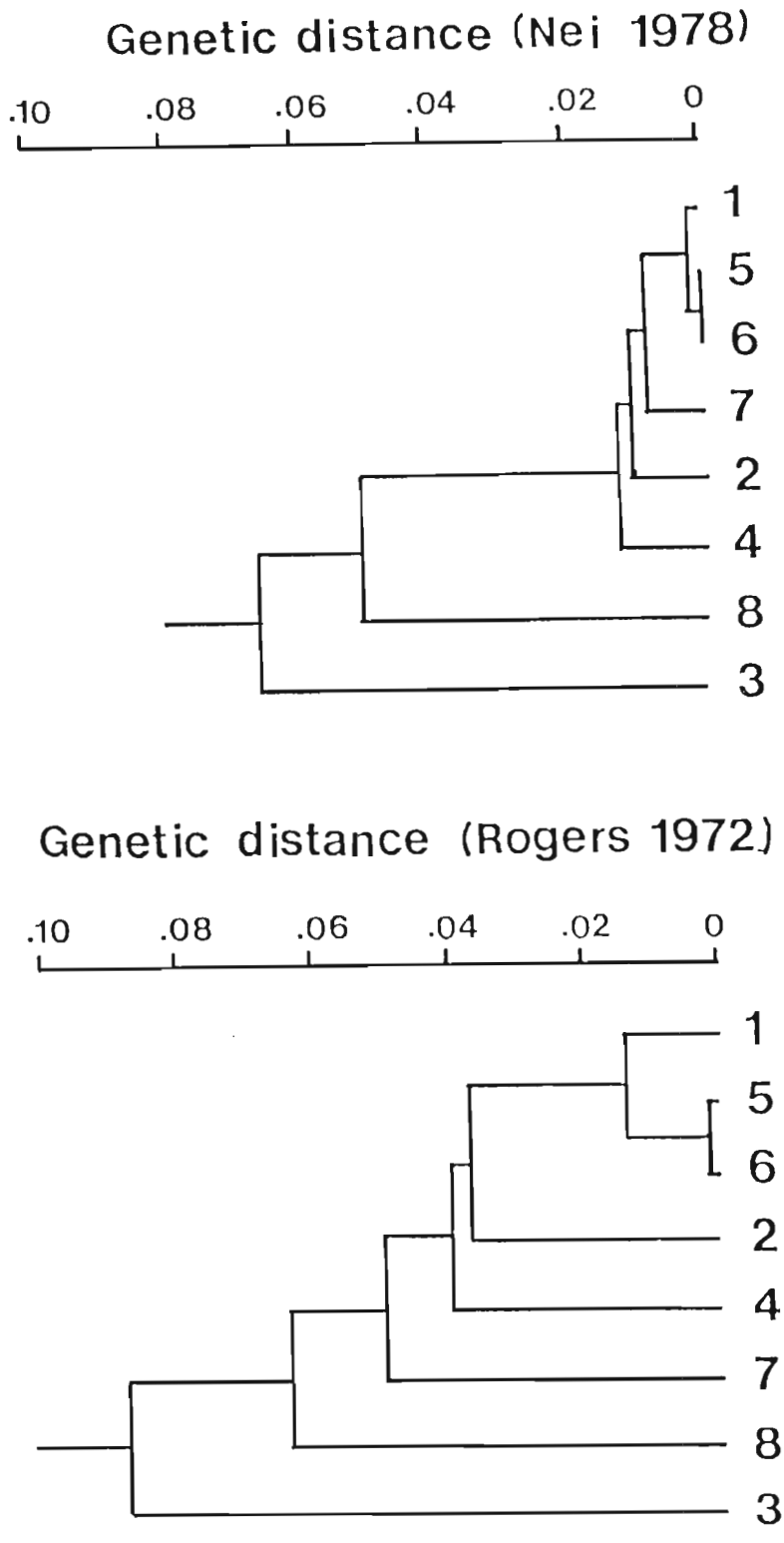


Fig. 5.3. UPGMA phenograms of Nei's[19] (above) and Roger's[23] (below) genetic distances among eight populations of C. penicillata in Southern Africa. Cophenetic correlation coefficients 0.945 and 0.888 respectively.

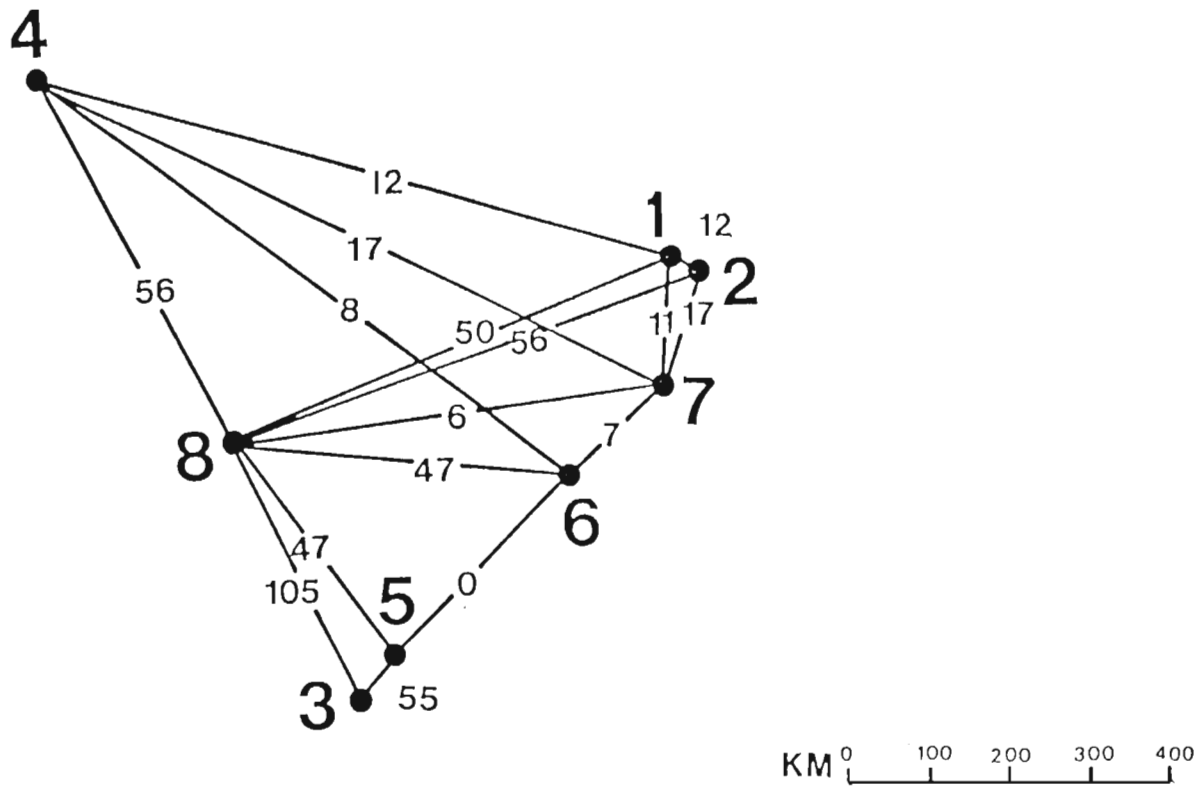


Fig. 5.4. Diagram showing inter - locality genetic distances in C. penicillata in Southern Africa. Locality numbers and geographic positioning of localities shown in Fig. 5.1. Inter - population distances represent Nei's[19] D_N x 1000.

The mean $\bar{H}$ of 0.034 in C. penicillata (Table 5.2) is only slightly lower than the mammalian mean of 0.039 (for 128 species) given by Wooten and Smith,[27] and somewhat higher than mean $\bar{H}$ values obtained for other carnivores such as coyotes (0.009:[9]) and raccoons (0.028:[8]). If the "fast" esterase and serum loci are excluded, the mean $\bar{H}$ for C. penicillata is somewhat lower (Table 5.2: 0.026). On the other hand, if these fast loci had been scored for all specimens (instead of just six specimens: see Materials and Methods), then a somewhat higher mean $\bar{H}$ value would have been obtained for C. penicillata.

Interpopulation variability: F statistics

As a result of the high proportion of loci having "private alleles" (Table 5.1), the mean F_{ST} for Cynictis populations was considerably higher (0.271 and 0.585 for five and eight population analyses respectively: Table 5.4) than recorded for populations of humans (0.148[28]) house mice (0.12[29]), Scandinavian moose (0.096[53]), coyotes (0.080[9]), prairie dogs (0.103 and 0.068 for Cynomys ludovicianus[30] and C. mexicanus[31] respectively), and deer mice (0.075[54]), although not as high as values recorded for pocket gophers (0.412 and 0.752 for Thomomys bottae[32] and T. umbrinus[55] respectively).

This result is unusual as population genetic theory

predicts that, in large, continuously distributed, and potentially mobile animals occupying fairly homogeneous ranges (as applies to C. penicillata in Southern Africa), gene flow would be sufficient to prevent spatial heterogeneity in gene frequencies (i.e. high F_{ST}). The unusual F_{ST} results for Cynictis merit further discussion on the biological reality of these data, given the small mean population sample sizes of 5.0 and 3.6 for the five and eight population analyses respectively.

It might be argued that the high proportion of variable loci having "private alleles" is an artifact of sampling whereby, on average, polymorphic alleles occur at a frequency of only one individual (and therefore a single population) in the entire sample, resulting in an apparent, high mean F_{ST} value for all variable loci. From a probabilistic point of view, though, it seems unlikely that chance effects should result in polymorphic alleles in six out of the eight variable loci occurring only in restricted populations, and that none of these polymorphic alleles should be expressed in the largest population from Bloemfontein (N = 9 or 15 depending on the locus sampled). Furthermore, in a simulation model comparing "true" F_{ST} with estimated values based on different methods and sample sizes, van den Bussche et al[56] demonstrated a general correlation between true and estimated F_{ST} with Nei's[33] method (which was used in this study), at sample sizes varying from five to 50. Finally, in a study of

Mexican prairie dogs,[31] involving a sample size (N = 29) similar to the present study, the mean F_{ST} was relatively low (0.068), and not relatively high as in the present study. Different lines of evidence therefore support the validity of the present gene frequency data for Cynictis, although it is important that preliminary hypotheses based on these data are tested in the light of further data. It is also possible that the predominance of slowly evolving loci in this study has contributed to high F_{ST}, and that the picture may have been somewhat different if data on faster evolving loci such as esterases and transferrin had been obtained for all the populations.

Social organisation and life history attributes may have profound effects on the distribution of genotypes among populations (and therefore on mean F_{ST} values). Spatial heterogeneity of alleles may be promoted by small, inbred breeding units (such as "coteries" of prairie dogs[30]), or by fossorial or sedentary habits and restricted, fragmented distributions (eg. pocket gophers, whose burrows are limited to isolated patches of friable soil[55]). The yellow mongoose is fossorial, colonial and territorial.[34] According to Walker[35] the species seldom moves more than 1km from its warren, and Stuart[36] mentioned that tagged animals were observed feeding up to 1.3km from the burrows. Zumpt[61] found that home ranges of yellow mongooses varied from 600 to 3000 metres in radius from a colony, and that juveniles remain in

a colony until the end of their first year, when the new litters are born. The occurrence of GPD^a polymorphic alleles in two individuals collected from the same colony, one of these a subadult of about one to two years of age, is consistent with the idea that juveniles remain in their natal colony for at least a year.

Further indirect evidence for low vagility in the yellow mongoose comes from the careful documentation of the occurrence and incidence of rabies outbreaks where Cynictis has been shown to be the carrier. Snyman[37] showed that rabies outbreaks caused by Cynictis were always confined to very restricted foci, and successive outbreaks could often be traced back to the same spot on the same farm up to 11 years later. Low vagility in Cynictis - whether this is due to social structure or possibly to the fragmented distribution of suitable soils for burrowing - may therefore be an important factor in explaining the extraordinarily high level of spatial heterogeneity in gene frequencies observed in this species.

Current behavioral studies on the yellow mongoose (Rasa, personal communication) indicate that: (1) the species is spatially and socially stable over periods of years (i.e. vagility is low); (2) the dominant male (whose tenure may encompass several years) conducts the majority of matings; (3) young remain with their parents in the colony and act as

"helpers" over several years; (4) matings occur between neighbouring colonies. These factors promote genetic homogeneity and inbreeding in a restricted area, and consequently genetic heterogeneity over a wider geographic area. In this regard the behavioral results support the genetic data obtained in this study.

The relative strengths of gene flow and gene drift in determining allele frequencies can be estimated by the number of migrating individuals per generation (Nm). Where Nm is greater than one, then gene flow is sufficient to prevent differentiation of populations due to drift.[38,54,39] Nm can be calculated from F_{ST}, using the formula

$$Nm = 1/4(1/F_{ST} - 1)$$

or from the conditional average frequency of "private alleles" (p(1)), by solving for the equation

$$\log_{10}[p(1)] = -0.49 \times \log_{10}(Nm) - 0.95$$

and correcting for the fact that this equation is based on a sample of 10 individuals per population by multiplying by 10 and dividing by the mean sample size for the present study.[39] According to Slatkin and Barton[39] both methods work equally well under ideal conditions but estimates obtained from F_{ST} are more robust under realistic conditions.

Calculated from F_{ST}, Nm in the yellow mongoose was 0.18 and 0.67 for the eight and five population analyses respectively. Nm, calculated from "private alleles", was

0.06. Fewer than one individual per generation is therefore exchanged between local populations, suggesting that gene drift, and not gene flow, is the major factor determining the genetic structure of populations of yellow mongooses. However, these analyses were based, on the whole, on very widespread geographic localities, and these conclusions need to be verified on the basis of samples taken over a more restricted geographic area.

Ryman et al[53] demonstrated significant allele frequency differences among local populations in the moose, a large and potentially highly mobile species, and they conclude that "Even in large mammals local differentiation seems to have been documented in every case for which it has been tested". The data for the yellow mongoose support the idea that spatial heterogeneity in gene frequencies may be more widespread in large mammals than was previously thought.

In species in which gene flow plays a dominant role in moulding the genetic structure of populations, one would expect a correlation between genetic and geographic distances indicative of an "isolation by distance" model. The lack of association of genetic and geographic distances in the yellow mongoose (Fig 5.4) is consistent with the high F_{ST} obtained for the species and indicates a model of drift in which gene flow plays a minor role.

Interpopulation variability: genetic distances

Multivariate craniometric analysis of geographic samples in C. penicillata (Taylor and Meester, in press) resulted in the proposal of four parapatric subspecies, separated by transition zones of variable steepness. The hypothesis was advanced that some measure of genetic divergence had occurred between these craniometrically - defined subspecies. One of the primary aims of the present study was to test this hypothesis, using electrophoretically - detectable genetic characters. The present study includes two subspecies, C. p. bradfieldi (Windhoek and Riemvasmaak localities) and C. p. penicillata (remaining localities).

Genetic identities (I) between populations of C. penicillata varied from 0.900 to 1.000 (Table 5.5) with a mean of 0.968, which is higher than the mean I of 0.96 for 1680 conspecific population pairs, given by Thorpe.[3] Yellow mongoose populations are therefore homogeneous genetically. Phenetic analysis of genetic distances does not indicate any clustering on the basis of morphometrically - defined subspecific affiliation (Fig. 5.3). Disagreement between biochemical and morphological data at the subspecies level appears to be more common[30,40,41,54,57,58] than does agreement.[42,43,55]

Hafner et al[55] have criticised the common assumption among

systematists that taxonomic and genetic distances are generally correlated.[3,44,59] They point out that cladogenetic speciation events (often occurring rapidly, eg. where certain chromosomal changes are implicated) need have no effect on genetic distance per se, and that both temporal as well as spatial aspects of gene flow should be considered, as genic mutations are accumulated in a clockwise fashion over time. Thus, high genetic similarities between populations (as in the present study) may represent either a high degree of gene exchange between present populations, or they may represent recency of divergence of isolated or partially isolated populations. A further possibility, which may apply in the case of C. penicillata, is that extinction of new mutations in relatively large, outcrossed populations (the mean F_{IS} of 0.039 suggests an overall balance in the proportions of heterozygotes and homozygotes) prevents long term genotypic divergence between populations (assuming absence of selection), even though spatial heterogeneity of gene frequencies may be pronounced, as discussed above for Cynictis.

Four hypotheses may be put forward to explain the discordance between morphological and genetic data in Cynictis: 1) morphometric variation may be non - genetic and environmentally induced, as shown by Smith and Patton[43] for pocket gophers (where diet - crops versus natural habitat - determined skull size: this seems unlikely in a carnivorous

species such as Cynictis); 2) allopatric differentiation in skull size may have occurred recently; 3) morphometric transition zones (i.e. clines) separating phena may have arisen parapatrically due to a selection gradient acting on genes affecting skull size but not on neutral enzyme loci; 4) morphometric (craniometric) subspecies can be distinguished genetically, but the level of resolution at the 22 loci employed in the present study was insufficient to detect existing genetic differences (possibly the use of "fast" enzymes such as esterases, or the technique of mitochondrial DNA, may yet uncover genetic markers between subspecies, and consequently help to determine the extent of gene flow in the transition zone between subspecies).

According to Chesser[30], the combination of pronounced spatial heterogeneity of gene frequencies and lack of association of genetic and geographic distances (conditions found in yellow mongoose populations: see above) are in agreement with the expectations of a model of differentiation by founder effect (i.e. allopatric speciation[45] or Type Ib allopatric speciation of Bush[13]). On the other hand, computer simulation studies have shown that high F_{ST} (i.e. reduced gene flow) promotes the formation of stepped clines across selection gradients resulting in parapatric differentiation and speciation.[14] This process is accelerated when partial barriers correspond with existing clines. Such a scenario may help to explain why, in the

yellow mongoose, morphometric clines are steep (i.e. stepped) when associated with potential barriers such as the Orange River, and more gradual when they correspond with an important ecotone marking the limits of Kalahari sands (Taylor and Meester, in press). Furthermore, low vagility, as suggested for the yellow mongoose (see previous discussion), is predictive of parapatric speciation according to Bush.[13]

While the genetic data do not unequivocably support an allopatric rather than a parapatric mode of differentiation, there seems to have been ample opportunity for allopatric origin of subspecies of C. penicillata during the late Pleistocene (Taylor and Meester, in press). Furthermore, a phylogenetic analysis of predicted range expansion in the species suggested that at least the major, north - south transition zone (separating the two phena sampled in the present study) is allopatric in origin. An allopatric mode of morphometric differentiation is therefore taken as being the most parsimonious explanation of the data in C. penicillata.

We are most grateful to Dr C. K. Brain, Director of the Transvaal Museum, and Drs. I. L. Rautenbach and D. Gordon of the Mammal and Evolutionary Biology Departments of the Transvaal Museum, for the use of laboratory and other facilities during 1986 and 1987. Dr D. Gordon is to be

thanked for rendering advice and assistance with laboratory techniques. Mr J. Visser kindly collected additional yellow mongooses. Professor J. van Heerden of the Veterinary Faculty at Medunsa University, Bophutatswana, helped with immobilisation of some of the yellow mongooses. The research was funded by a grant from the Foundation for Research Development to JAJM.

1. Avise J. C. (1974). Systematic value of electrophoretic data. Syst. Zool. **23**(4), 465-481.
2. Ferguson, A. (1980). Biochemical Systematics and Evolution. Blackie, Glasgow and London.
3. Thorpe J. P. (1982). The molecular clock hypothesis: biochemical evolution, genetic differentiation and systematics. Ann. Rev. Ecol. Syst. **13**, 139-168.
4. Buth D. G. (1984). The application of electrophoretic data in systematic studies Ann. Rev. Ecol. **15**, 501-522.5.
5. Nevo E. (1978). Genetic variation in natural populations: pattern and theory. Theoretical Population Biology **13**, 121-177.
6. Smith M. W., Aquadro C. F., Smith M. H., Chesser R. K. and Etges W. J. (1982). Bibliography of electrophoretic studies of biochemical variation in natural vertebrate populations. Texas Tech Press, Lubbock.
7. Wayne R. K., Beneviste R. E., Janczewski D. N. and

O'Brien S. J. (1989). Molecular and biochemical evolution of the Carnivora. In Carnivore behavior, ecology and evolution, edit. J. L. Gittleman, pp. 465-493. Chapman and Hall, London.

8. Dew R. D. and Kennedy M. L. (1980). Genic variation in raccoons, Procyon lotor. J. Mammal. **61**(4), 697-702.
9. Hamilton M. J. and Kennedy M. L. (1986). Genic variation in the coyote, Canis latrans in Tennessee, U.S.A. Genetica **71**, 167-173.
10. Smithers R. H. N. (1983). The Mammals of the Southern African Subregion. University of Pretoria, Pretoria.
11. Lundholm B, G. (1955). A taxonomic study of Cynictis penicillata (G. Cuvier). Annals of the Transvaal Museum **22**, 305-319.
12. Meester J., Rautenbach I. L., Dippenaar N. J. and Baker C. M. (1986). Classification of Southern African Mammals. Transvaal Museum Monograph **5**, 1-359.
13. Bush G. L. (1975). Modes of animal speciation. Ann. Rev. Ecol. Syst. **6**, 339-364.
14. Endler J. A. (1977). Geographic Variation, Speciation and Clines. Princeton University Press, Princeton, New Jersey.
15. Patton J. L. (1985). Population structure and the genetics of speciation in pocket gophers, genus Thomomys. Acta Zoologica Fennica **170**, 109-114.
16. Davis B. J. (1964). Disk electrophoresis - II. Method and application to human serum proteins. Ann. N. Y.

Acad. Sci. **121**, 402-427.

17. Shaw C. R. and Prasad R. (1970). Starch gel electrophoresis of enzymes - a compilation of recipes. Biochem. Genet. **4**, 297-320.
18. Harris H. and Hopkinson D. A. (1976). Handbook of Enzyme Electrophoresis in Human Genetics. North-Holland, Amsterdam.
19. Nei M. (1978). Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics **89**, 583-590.
20. Sokal R. R. and Rohlf F. J. (1981). Biometry. W. H. Freeman, San Francisco, 2nd edition.
21. Levene H. (1949). On a matching problem arising in genetics. Ann. Math. Stat. **20**, 91-94.
22. Wright S. (1965). The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution **19**, 395-420.
23. Rogers J. S. (1972). Measures of genetic similarity and genetic distance. In Studies in Genetics, edit. M. R. Wheeler, chap. VII, pp. 145-153. University of Texas Publication No. 7213.
24. Sneath P. H. A. and Sokal R. R. (1973). Numerical Taxonomy. Freeman, San Francisco.
25. Swofford D. L. and Selander R. B. (1989). BIOSYS-1. A computer program for the Analyis of Allelic Variation in Population Genetics and Biochemical Systematics. David L. Swofford, Illinois Natural History Survey,

Release 1.7.

26. Simonsen V. (1982). Electrophoretic studies on the blood proteins of domestic dogs and other Canidae. Hereditas **82**, 7-18.

27. Wooten M. C. and Smith M. H. (1985). Large mammals are genetically less variable? Evolution **39**, 210-212.

28. Cavalli-Sforza L. L. (1966). Population structure in human evolution. Proc. Roy. Soc., Ser. B **164**, 362-379.

29. Nei M. (1975). Molecular Population Genetics and Evolution. American Elsevier Publ. Co., Inc., New York.

30. Chesser R. K. (1983). Genetic variability within and among populations of the Black-tailed Prairie Dog. Evolution **37**, 320-331.

31. McCullough D. A. and Chesser R. K. (1987). Genetic variation among populations of the Mexican Prairie Dog. J. Mammal. **68**, 555-560.

32. Patton J. L. and Yang S. Y. (1977). Genetic variation in Thomomys bottae pocket gophers: macrogeographic patterns. Evolution **31**, 697-720.

33. Nei M. (1977). F-statistics and analysis of gene diversity in subdivided populations. Ann. Human Genet. **41**, 225-233.

34. Earle R. A. (1981). Aspects of the social and feeding behavior of the Yellow Mongoose Cynictis penicillata (G. Cuvier). Mammalia **45**, 143-152.

35. Walker E. P. (1964). Mammals of the World. Vol. 2. John

Hopkins Press, Baltimore.

36. Stuart C. T. (1981). Notes on the mammalian carnivores of the Cape Province, South Africa. Bontebok **1**, 1-58.

37. Snyman P. S. (1940). The study and control of the vectors of rabies in South Africa. Onderstepoort Journal of Veterinary Science and Animal Industry **15**, 9-139.

38. Wright S. (1931). Evolution of Mendelian populations. Genetics **16**, 97-159.

39. Slatkin M. and Barton N. H. (1989). A comparison of three indirect methods for estimating average levels of gene flow. Evolution **43**, 1349-1368.

40. Kilpatrick C. W. and Zimmerman E. G. (1975). Genetic variation and systematics of four species of mice of the Peromyscus boylii species group. Syst. Zool. **24**, 143-162.

41. Schnell G. D. and Selander R. K. (1981). Environmental and morphological correlates of genetic variation in mammals. In Mammalian Population Genetics, edit. M. H. Smith and J. J. Joule, pp. 60-99. University of Georgia Press, Athens.

42. Werbitsky D. and Kilpatrick C. W. (1987). Genetic variation and genetic differentiation among allopatric populations of Megadontomys. J. Mammal. **68**, 305-312.

43. Smith M. F. and Patton J. L. (1988). Subspecies of pocket gophers: causal bases for geographic differentiation in Thomomys bottae. Syst. Zool. **37**,

163-178.

44. Avise J. C. (1976). Genetic differentiation during speciation. In Molecular Evolution, edit. F. J. Ayala, pp. 106-122. Sinauer and Assoc., Sunderland, Mass.

45. Mayr E. (1963). Animal Species and Evolution. Harvard University Press, Cambridge, Mass.

46. Selander R. K., Smith M. H., Yang S. Y. Johnson W. E. and Gentry J. B. (1971). Biochemical polymorphism and systematics in the genus Peromyscus. I. Variation in the oldfield mouse (Peromyscus polionotus). In Studies in Genetics, edit. M. R. Wheeler, chap. IV, pp. 49-90. Univ. Texas Publication No. 7103.

47. McDermid E. M., Ananthakrishnan R. and Agar N. S. (1972). Electrophoretic investigation of plasma and red cell proteins and enzymes of MacQuarie Island elephant seals. Anim. Blood Groups, Biochem. Genet. **3**, 85-94.

48. Allendorf F. W., Christiansen F. B., Dobson T., Eanes W. F. and Frydenberg O. (1979). Electrophoretic variation in large mammals. I. The polar bear, Thalarctos maritimus. Hereditas **91**, 19-22.

49. Manlove M. N., Baccus R., Pelton M. R., Smith M. H. and Graber D. (1980). Biochemical variation in the black bear. In Bears - Their Biology and Management, edit. C. J. Martinka and K. L. McArthur, pp. 37-41. U.S. Government Printing Office, Washington, D. C.

50. Simonsen V., Allendorf F. W., Eaves W. F., and Kapel F.

O. (1982a). Electrophoretic variation in large mammals. III. The ringed seal, Pusa hispida, the harp seal, Pagophilus groenlandlica, and the hooded seal, Cystophora cristata. Hereditas **97**, 87-90.

51. Simonsen V., Born E. W. and Kristensen T. (1982b). Electrophoretic variation in large mammals. IV. The Atlantic walrus, Odobenus rosmarus rosmarus (L.) Hereditas **97**, 91-94.

52. O'Brien S. J., Wildt D. E., Goldman D., Merril C. R., and Bush M. (1983). The cheetah is depauperate in genetic variation. Science **221**, 459-462.

53. Ryman N., Reuterwall C., Nygren K., and Nygren T. (1980). Genetic variation and differentiation in Scandinavian moose (Alces alces): Are large mammals monomorphic? Evolution **34**, 1037-1049.

54. Calhoun S. W., Greenbaum I. F., Fuxa K. P. (1988). Biochemical and karyotypic variation in Peromyscus maniculatus from western North America. J. Mammal. **69**, 34-45.

55. Hafner M. S., Hafner J. C., Patton J. L. and Smith M. F. (1987). Macrogeographic patterns of genetic differentiation in the pocket gopher Thomomys umbrinus. Syst. Zool. **36**, 18-34.

56. Van den Bussche R. A., Hamilton M. J., and Chesser R. K. (1986). Problems of estimating gene diversity among populations. The Texas Journal of Science **38**, 281-287.

57. Robbins L. W., Smith M. H., Wooten M. C. and Selander R.

K. (1985). Biochemical polymorphism and its relationship to chromosomal and morphological variation in Peromyscus leucopus and Peromyscus gossypinus. J. Mammal. **66**, 498-510.

58. Van der Bank F. H. and Ferreira J. T. (1987). Electrophoretic analysis of serum transferrins and esterases of three morphometrical different populations of Oreochromis mossambicus (Peters). S. Afr. J. Wildl. Res. **17**, 13-16.

59. Zimmerman E. G., Kilpatrick C. W., and Hart B. J. (1978). The genetics of speciation in the rodent genus Peromyscus. Evolution **32**, 565-579.

60. Richardson V. J., Baverstock P. R., Adams M. (1986). Allozyme Electrophoresis: a Handbook for Animal Systematics and Population Studies. Academic Press, Sydney.

61. Zumpt I. F. (1976). The yellow mongoose (Cynictis penicillata) as as a latent focus of rabies in South Africa. Jl. S. Afr. vet. Ass. **47**, 211-213.

CHAPTER 6

CHROMOSOMAL VARIATION[1]

Introduction

Giemsa-stained karyotypes of some 15 species of mongooses have been documented (WURSTER and BENIRSCHKE 1968; FREDGA 1972). More recently, G-banded karyotypes of a number of carnivore species have shown extensive homology in G-banded sequences between different families of Carnivora (WURSTER HILL and GRAY 1975; WURSTER HILL and CENTERWELL 1982). However, G-banded karyotypes have been obtained for only three species of mongooses: Mungos mungos, Bdeogale nigripes and Atilax paludinosus (WURSTER HILL and GRAY 1975; DUTRILLAUX and COUTURIER 1983).

As a part of a wider study on the infraspecific systematics of the yellow mongoose C. penicillata, this report investigates the possibility of chromosomal variability in the species, and also presents, for the first time, G- and

---

1. This chapter, together with abstract, is essentially the paper, by P. J. Taylor, and J. Meester, that is to be submitted to Z. Saugetierkunde under the title "Karyotypic analysis of the yellow mongoose Cynictis penicillata".

C-banded karyotypes for the species. The yellow mongoose is a diurnal, colonial, burrow-dwelling carnivore, endemic to and widespread throughout Southern Africa (SMITHERS 1983). The species varies geographically in colour and size, and a morphologically - based taxonomic revision of the species resulted in the proposal of four subspecies (TAYLOR et al. in press; TAYLOR AND MEESTER submitted). A recent population genetical study provided preliminary, indirect evidence (high spatial heterogeneity in gene frequencies) for restricted vagility in the species (TAYLOR et al. submitted). This finding is supported by behavioral studies in progress which show that the species is highly sedentary, colonies remaining spatially and socially stable over a period of several years (RASA, personal communication). As noted by BUSH (1975), and as found in the raccoon dog (MAKINEN; KUOKKANEN and VALTONEN 1986) and the silver fox (KUOKKANEN; LOHI and MAKINEN 1985), such ecological and behavioral factors are often associated with rapid chromosome evolution.

Material and methods

Details of the 12 animals analysed karyotypically are given in Table 6.1. Voucher specimens were deposited in the Transvaal Museum, Pretoria (TM) and the Durban Natural

Table 6.1.

Specimen details and methods of karyotypic analysis of 12 yellow mongooses Cynictis penicillata collected from five localities throughout Southern Africa.

Museum No.	Sex	Locality	N[1]	Method[2]	Bands
TM38334	Male	Glen Agricultural Coll., Bloemfontein, OFS	1	1	-
TM38338	Female	" " " " "	1	1	-
TM38339	Male	" " " " "	1	1	-
TM39215	Female	Kaal Plaas Farm, N. of Pretoria, Transvaal	1	2	-
TM39216	Male	" " " " " " "	2	2	-
TM39265	Female	" " " " " " "	2	2, 4	-
TM39437	Female	Rhenosterfontein Farm, Cullinan Dist., Tvl.	3	5	-
TM39947	Female	Windhoek, Namibia	1	3	-
TM39948	Female	" "	3	3	-
TM39949	Female	" "	3	3	G
DM768	Female	Victoria West, Cape Province	5	3	G, C
DM769	Female	" " " "	2	3	G, C

[1] N refers to the number of karyotypes examined for each specimen

[2] Methods of karyotypic analysis: 1 (in vivo bone marrow); 2 (in vitro bone marrow); 3 (improved in vitro bone marrow); 4 (lymphocyte culture: method A); 5 (lymphocyte culture: method B). See Methods for explanation of methods.

Science Museum (DM). Chromosome preparations were obtained from either bone marrow or lymphocyte sources, using one of five standard methods as follows:

Method 1. In vivo bone marrow. The method of ROBBINS and BAKER (1978) was followed, with the addition of a preliminary yeast treatment administered 24 hours before harvesting (LEE and ELDER 1980).

Method 2. In vitro bone marrow. A standard procedure contained in the laboratory manual of the South African Institute for Medical Research (S.A.I.M.R.) was followed. This technique differed from the previous technique, in the in vitro rather than in vivo application of the inhibitor (colchicine), and in the use of potassium chloride rather than sodium citrate as a hypotonic treatment.

Method 3. Improved in vitro bone marrow. The procedure outlined in SHILOH and COHEN (1978) was followed, with the exception that the medium used was Dulbecco's Modifed Eagle Medium, and not Hams F10 as specified by SHILOH and COHEN (1978). The supplementation of the incubation medium with 20% foetal calf serum distinguished this method from the previous one. Method 3 produced significantly better results than Methods 1 and 2: mitotic index was noticeably increased, and chromosome quality was equivalent to that

obtained from lymphocyte cultures. Slides obtained using Method 3 generally produced good quality G- and C-banded metaphases.

Method 4. Lymphocyte culture (Method A). The procedure contained in the S.A.I.M.R. laboratory manual was followed. The incubation medium used was RPMI, and the mitogen was phytohaemogluttinin (PHA). Very low mitotic indices were obtained using this method, although chromosome quality was generally superior to preparations obtained from bone marrow.

Method 5. Lymphocyte culture (Method B). Peripheral blood samples were incubated with a range of mitogens (PHA and Concanalavin) and media (M150, F12 and RPMI), and at different temperatures (37°C and 40°C) for a duration of 72 hours. Poor or no results were obtained using PHA, and exceptionally good results (high mitotic indices, good chromosome quality) were obtained using Concanalavin, irrespective of the medium used, and particularly at an incubation temperature of 40°C (body temperature of one male yellow mongoose, TM39437, was measured and found to be 39°C).

A total of 25 good quality (unbanded) metaphases, representing between one and five per individual (Table 6.1), was photographed and karyotypes were constructed from

the photographs. Karyotypes were arranged by relative size (rl) and centromeric index (ci) according to the method of FREDGA (1972). Thus, chromosomes 1 to 9 represent metacentric chromosomes (ci between 37.5% and 50%), in order of decreasing size, chromosomes 10 to 16 represent submetacentric chromosomes (ci between 25% and 37.5%), in order of decreasing size, and chromosome 17 represents the only subtelocentric chromosome (ci less than 25%). Measurements of relative length (length of individual chromosomes as a percentage of the total female haploid length) and centromeric index (length of short arm as a percentage of total length) were measured for each chromosome pair from 21 unbanded karyotypes, and ANOVA was used to test for significant differences between the five localities. Although this method of ordering chromosomes is inherently inaccurate where chromsomes differ in minor gradations in rl and ci (as is the case in C. penicillata), the absence of G-bands for most preparations necessitated application of this method.

G-banding of chromosomes was carried out using the trypsin method of SEABRIGHT (1971). C-banding followed the procedure outlined by MODI (1987).

Results

The karyotype of the yellow mongoose obtained from the

present study (2n = 36, FN = 72) is identical to that presented by FREDGA (1972), consisting of nine pairs of metacentric autosomes (ci > 37.5%), seven pairs of submetacentric autosomes (ci between 25% and 37.5%), one pair of subtelocentric autosomes (ci < 25%), a medium - sized, metacentric X chromosome and a very small, metacentric Y chromosome (Fig. 6.1). Relative length (rl) of individual chromosomes did not differ significantly ($p < 0.01$) between the five different populations sampled (Table 6.2). Similarly, centromeric index (ci) of all chromosomes except chromosome 3 showed no significant geographic variation (Table 6.2). In chromosome 3, centromeric index was consistently low in three metaphases analysed from one individual from Farm Rhenosterfontein (mean = 37.4), as well as in three individuals sampled from the nearby Farm Kaal Plaas (mean = 39.0), while it was much higher (mean = 46.7) in the Bloemfontein sample (Table 6.2).

FREDGA (1972) reports the occasional presence of satellites in the shorts arms of chromosomes 6, 8, 12 and 17 of C. penicillata. In the present study, satellites were detected on chromosomes 6, 12, 14 and 17 (Fig. 6.2), although these were evident in only two of the 21 unbanded karyotypes examined. In chromosome 6, the satellite is much clearer on one member of the pair, as also noted by FREDGA (1972).

Fig. 6.1. Karyotype of the yellow mongoose Cynictis penicillata: (a) female, DM768, from Victoria West, Cape Province; (b) male, TM39437, from Farm Cullinan, Transvaal.

a

b

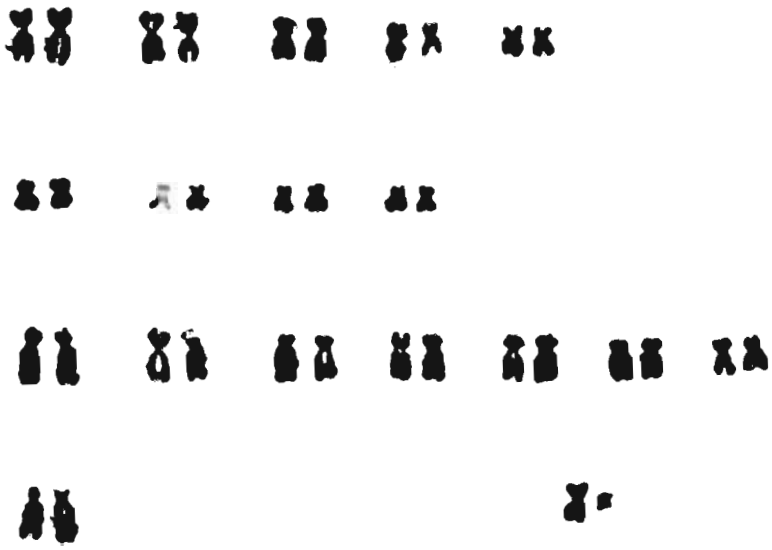


Table 6.2

Chromosome measurements of *C. penicillata* from five localities in Southern Africa. Figures represent means (and standard deviation in parentheses) of relative lengths and centromeric indices of individual chromosomes. F values are from ANOVA of population means. Significance of F values indicated by: NS (non-significant); * (significant at the 5% level); ** (significant at the 1% level).

Chromosome	Glen (N=3)	Kaal Plaas (N=5)	Cullinan (N=3)	Windhoek (N=6)	Victoria West (N=4)	F	p
			Relative length (%)				
1	7.6 (0.26)	7.2 (0.11)	7.2 (0.36)	6.9 (0.45)	7.1 (0.43)	2.01	NS
2	7.0 (0.55)	6.7 (0.19)	6.5 (0.29)	6.5 (0.27)	6.7 (0.24)	1.63	NS
3	5.7 (0.25)	6.1 (0.15)	6.0 (0.40)	6.0 (0.23)	6.2 (0.40)	1.48	NS
4	4.5 (0.46)	4.5 (0.30)	4.6 (0.25)	4.2 (0.33)	4.4 (0.21)	1.10	NS
5	4.1 (0.46)	4.0 (0.35)	4.2 (0.20)	3.9 (0.28)	4.3 (0.15)	1.27	NS
6	4.0 (0.12)	3.6 (0.27)	4.0 (0.06)	3.8 (0.13)	4.0 (0.38)	2.61	NS
7	3.4 (0.36)	3.6 (0.19)	3.6 (0.06)	3.7 (0.16)	3.9 (0.16)	3.06	*
8	3.7 (0.40)	3.2 (0.15)	3.4 (0.17)	3.5 (0.26)	3.4 (0.31)	1.89	NS
9	3.4 (0.49)	3.1 (0.27)	3.3 (0.25)	3.0 (0.42)	3.1 (0.32)	1.64	NS
10	8.0 (0.61)	8.0 (0.23)	8.0 (0.32)	8.4 (0.23)	8.5 (0.39)	2.21	NS
11	7.2 (0.32)	7.7 (0.28)	7.1 (0.12)	7.6 (0.42)	7.2 (0.44)	2.45	NS
12	6.8 (0.32)	7.0 (0.34)	6.6 (0.21)	6.7 (0.49)	6.5 (0.32)	1.14	NS
13	6.2 (0.25)	6.6 (0.25)	6.4 (0.10)	6.6 (0.40)	6.2 (0.13)	2.21	NS
14	5.8 (0.45)	6.2 (0.38)	6.0 (0.32)	6.2 (0.18)	6.2 (0.19)	1.22	NS
15	5.4 (0.32)	5.6 (0.36)	5.6 (0.26)	5.8 (0.30)	5.9 (0.38)	1.30	NS
16	5.1 (0.50)	5.1 (0.16)	5.1 (0.06)	5.2 (0.55)	5.2 (0.44)	0.08	NS
17	6.5 (0.46)	6.8 (0.24)	7.2 (0.17)	7.1 (0.36)	7.0 (0.53)	1.91	NS
X	5.4 (0.75)	4.9 (0.25)	5.1 (0.29)	4.9 (0.36)	5.2 (0.36)	1.10	NS
Y	2.2, 3.1 (N=2)	2.3, 1.9 (N=2)	1.9 (0.12)	-	-	-	-
			Centromeric index (%)				
1	39.8 (2.57)	42.8 (3.61)	39.4 (1.77)	40.2 (3.82)	41.8 (2.53)	0.84	NS
2	45.1 (2.76)	48.1 (1.78)	47.1 (1.12)	46.1 (2.42)	46.2 (2.97)	0.97	NS
3	46.7 (1.17)	39.0 (2.28)	37.4 (1.82)	43.5 (1.50)	40.8 (1.90)	14.45	**
4	45.8 (2.25)	45.0 (1.52)	45.7 (2.00)	42.7 (2.92)	46.6 (2.76)	1.94	NS
5	44.4 (2.45)	46.9 (0.69)	45.0 (3.07)	42.4 (4.45)	45.9 (2.76)	1.60	NS
6	41.6 (3.08)	44.8 (2.49)	44.5 (0.62)	45.6 (3.34)	42.4 (2.21)	1.62	NS
7	36.2 (7.36)	40.5 (4.07)	41.3 (1.40)	40.3 (3.30)	38.8 (0.82)	0.90	NS
8	44.7 (2.46)	45.8 (2.86)	44.9 (1.80)	42.8 (2.05)	43.7 (4.11)	0.90	NS
9	45.8 (3.23)	45.4 (2.33)	42.6 (0.45)	47.0 (2.67)	46.2 (2.57)	1.64	NS
10	29.7 (2.14)	26.3 (0.50)	28.5 (2.64)	26.5 (2.54)	26.7 (3.14)	1.48	NS
11	36.0 (2.53)	35.3 (1.67)	37.2 (4.11)	35.0 (3.65)	37.4 (2.60)	0.73	NS
12	23.5 (1.10)	27.0 (3.76)	28.3 (1.25)	25.6 (1.13)	25.8 (1.37)	2.20	NS
13	33.0 (3.18)	31.2 (2.23)	35.1 (4.88)	32.9 (4.01)	30.9 (1.00)	1.02	NS
14	32.5 (4.52)	32.1 (2.09)	31.9 (2.93)	30.8 (3.29)	35.1 (2.01)	1.29	NS
15	30.2 (4.16)	30.2 (2.93)	32.6 (5.43)	26.8 (4.59)	29.5 (5.03)	0.99	NS
16	36.7 (2.59)	31.3 (2.02)	33.2 (2.28)	33.2 (3.05)	32.4 (3.56)	1.83	NS
17	18.3 (2.12)	19.5 (1.75)	21.9 (1.26)	18.6 (2.25)	17.5 (1.17)	2.82	NS
X	43.5 (7.23)	43.2 (0.63)	43.5 (1.86)	43.3 (3.89)	44.3 (2.77)	0.06	NS
Y	44.4, 47.4 (N=2)		43.1 (N=1)	45.4, 47.6 (N=2)	-	-	-

Fig. 6.2. Chromosomes 6, 12, 14, and 17 of C. penicillata, showing the presence of satellites in one metaphase from TM39215.

6 12 14 17

The presence of a single supernumerary microchromosome (Fig. 6.3) was detected in five individuals: TM38334 (detected in the only karyotype analysed from this animal), TM39215 (detected in one of two karyotypes analysed), TM39265 (detected in one of three karyotypes analysed),TM39437 (detected in one of five karyotypes analysed), and TM39948 (detected in all of three karyotypes analysed).

Figure 6.4 presents G-banded karyotypes of yellow mongooses from Windhoek and Victoria West. Differences of banding resolution and quality between these two karyotypes makes it impossible to establish whether complete homology exists between them, although this would be expected from the identical diploid numbers, fundamental numbers, and the degree of conservatism that generally exists in carnivoran chromosomes. The C-banded karyotype in Fig. 6.5 indicates the presence of heterochromatin in chromosomes 4, 8, 9, 10, 13, 15 and 17. While the entire short arm of chromosome 13 is heterochromatic (although this is not clear in one of two individuals analysed: Fig. 6.5b), and heterochromatin appears to be located interstitially in chromosome 10 (also not clear in Fig. 6.5b), the majority of chromosomes contain heterochromatin in the terminal portion of the short arms.

Fig. 6.3. Somatic metaphases of C. penicillata showing the presence of a single microchromosome: (a) female, TM 39265; (b) male, TM39437. Arrows indicate the presence of microchromosomes. The Y chromosome, the smallest of the species' basic complement, is indicated in (b), to illustrate the relative size of the microchromosome.

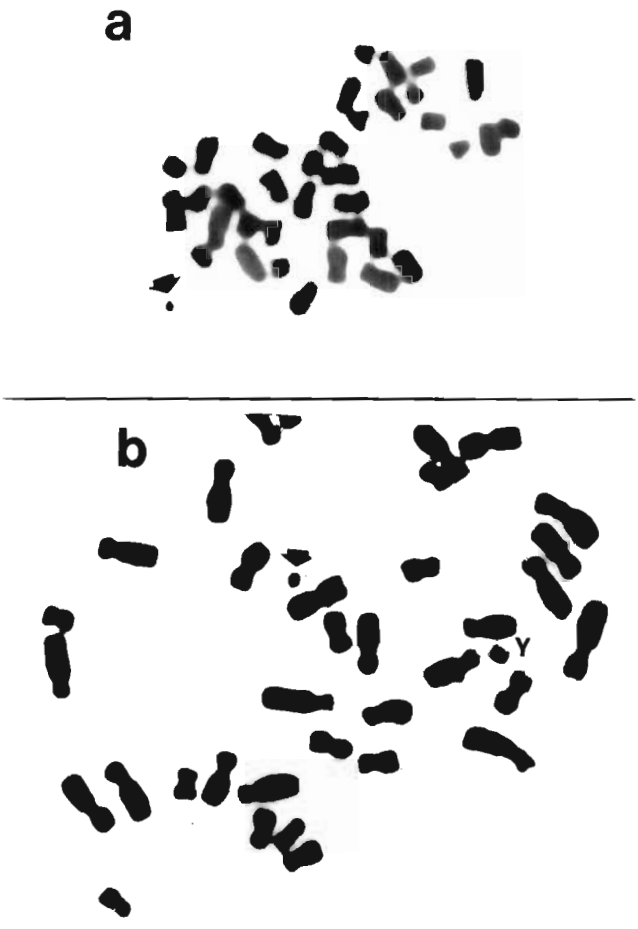
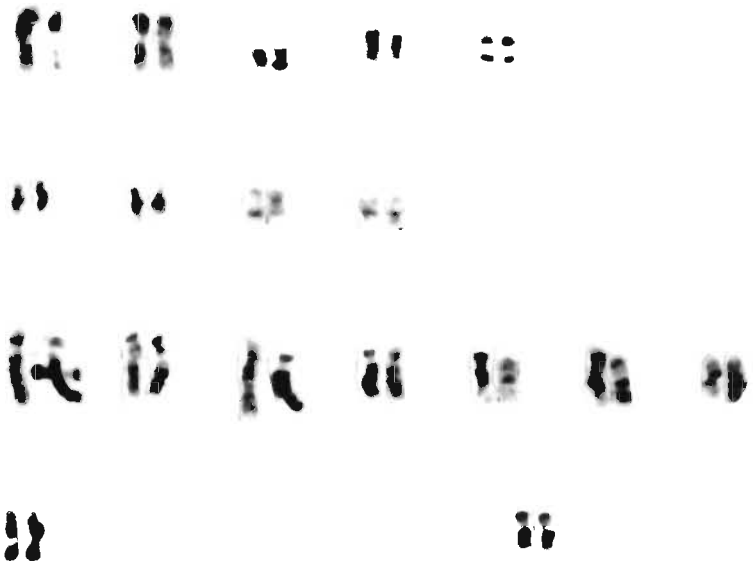

a
b
Y

Fig. 6.4. G-banded karyotypes of C. penicillata from: (a) Victoria West; (b) Windhoek, Namibia. Individual members of pairs 10, 15 and 17 were absent from the metaphase from which (b) was prepared.

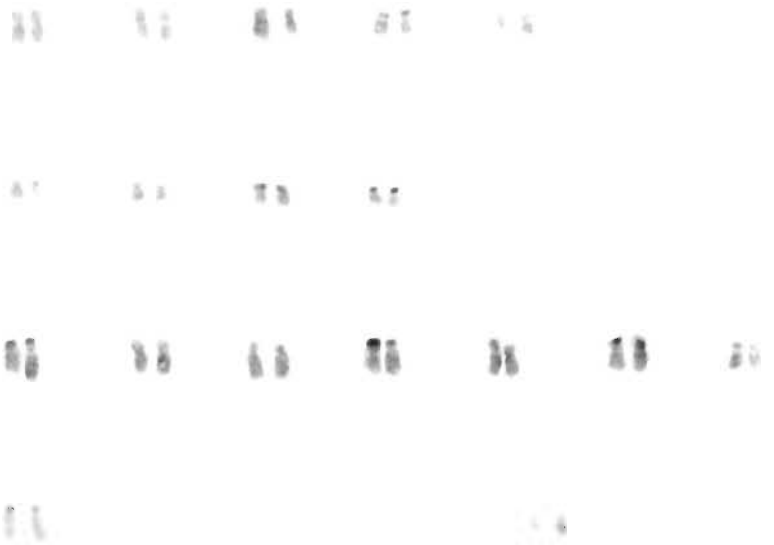
a



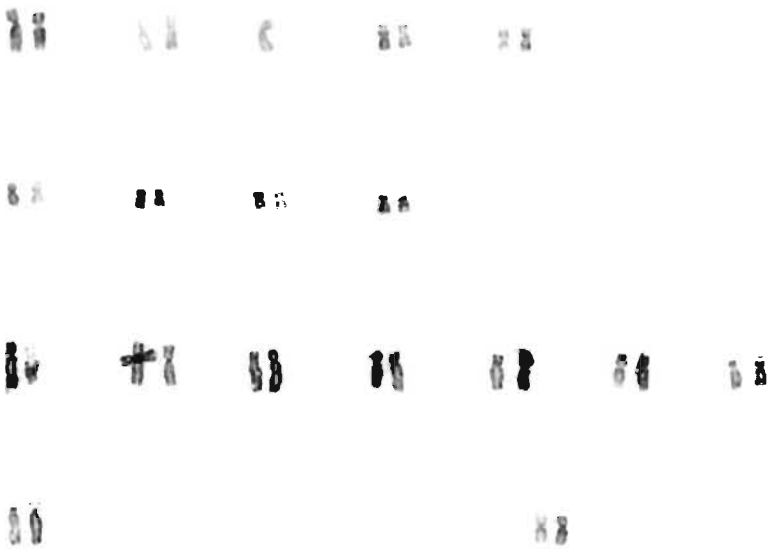
b

Fig. 6.5. C-banded karyotypes of *C. penicillata* from Victoria West: (a) DM768; (b) DM769.

a



b



Discussion

Based on a previous craniometric study (TAYLOR and MEESTER submitted), four subspecies of yellow mongooses are recognised. The material examined in this study represents two subspecies of C. penicillata, C. p. penicillata (Victoria West, Bloemfontein, Kaal Plaas and Cullinan) and C. p. bradfieldi (Windhoek). The two yellow mongooses examined by FREDGA (1972) were obtained from Botswana and therefore were almost certainly representative of a third subspecies, C. p. coombsii. The basic karyotypes from thedifferent populations were identical to one another (Figs 6.1, 6.4, Table 6.2) and to the published karyotype of FREDGA (1972). The infraspecific stability of the species' karyotype indicates that morphometric differentiation in the yellow mongoose has been unaccompanied by chromosomal changes. The reverse situation is typical of many rodent species where, "observed cytological rearrangements have had no discernible phenotypic effects" (PATTON and SHERWOOD 1983). As a recent example, marked chromosomal variation (2n: 23 - 30) unaccompanied by phenotypic change has been reported for the vlei rat Otomys irroratus (MEESTER 1988, CONTRAFATTO et al. submitted).

While the basic karyotype of the yellow mongoose showed no infraspecific differences, individuals varied from one

another in the presence or absence of a single microchromosome (Fig. 6.3). Variation in microchromosome number has been reported in other carnivore species such as the silver fox (KUOKKANEN et al. 1985) and the raccoon dog (MAKINEN et al. 1986). Mosaicism (the presence of microchromosomes in some but not all cells of the same animal) was found in four out of the five yellow mongooses in which microchromosomes were detected. Mosaic karyotypes were reported in 85% of silver foxes, 21% of Finnish raccoon dogs and 100% of Japanese raccoon dogs (KUOKKANEN et al. 1985, MAKINEN et al. 1986).

The presence of microchromosomes in the yellow mongoose karyotype (Fig. 6.3) may provide a useful subspecific or populational marker. Microchromosomes were detected in all of the populations sampled except Victoria West. Presumably, they were absent from the individuals from Botswana analysed by FREDGA (1972). Further work based on larger samples is necessary before the distribution and frequency of microchromosomes can be accurately determined for the four subspecies of C. penicillata.

Among the mongooses, species of Herpestes and Atilax are characterised by having an unusual sex - determining mechanism involving an Y-autosome translocation (males have one fewer chromosome than females). Diploid number varies from 35/36 to 43/44 among the species of these two genera

(FREDGA 1972). Apart from three species, the fundamental number (FN) throughout is 72. Among the other mongoose genera (Mungos, Helogale, Bdeogale, Crossarchus, Cynictis, Suricata, Ichneumia), diploid number (2n = 36) and fundamental number (FN = 72) are constant throughout, differences between the species being due to the numbers of metacentric, submetacentric and subtelocentric autosomes present and the size and shape of the Y chromosome (WURSTER and BENIRSCHKE 1968; FREDGA 1972). Cynictis has the highest number of metacentric chromosomes, and the smallest Y chromosome.

Further studies involving the simultaneous analysis of several species using standard experimental techniques are necessary to allow a comparison of G-bands, and to provide an explanation for the shifts in centromeric position that differentiate the karyotypes of the different mongoose species. Possible explanations for these differences may be pericentric inversions, or the addition or deletion of heterochromatin on the short arms of certain chromosomes. The latter mechanism was largely responsible for the pattern of chromosomal variation reported in the vlei rat Otomys irroratus (CONTRAFATTO et al. in press). In view of the presence of C-positive heterochromatin on the distal region of the short arms of many of the chromosomes of C. penicillata (Fig. 6.5), heterochromatin additions or deletions may well be responsible for observed patterns of

chromosomal variability among the mongooses.

Further chromosome banding studies involving different mongoose species should provide characters for cladistic analysis which may prove useful in reconstructing the phylogeny of the group. At present many discrepancies exist in interpreting the evolutionary relationships among the mongooses (WOZENCRAFT 1989; TAYLOR et al. submitted).

Acknowledgements

Dr C. K. BRAIN, Director of the Transvaal Museum, and Dr I. L. RAUTENBACH, mammal curator of the Transvaal Museum, are gratefully thanked for allowing us full access to laboratory, library and field collecting facilities. Mr G. CONTRAFATTO provided friendly advice and assistance in the laboratory, and with photographic aspects. Mr J. WATSON, Mr J. ECKSTEIN, Mr J. VISSER, Mr J. PALLET and Mr C. JOUBERT assisted with collection of specimens for karyotyping. The financial assistance of the Foundation for Research Development (F.R.D.) to JM is gratefully acknowledged.

References

BUSH, G. L. (1975): Modes of animal speciation. Ann. Rev. Ecol. Syst. **6**, 339-364.

CONTRAFATTO, G.; MEESTER, J.; WILLAN, K.; TAYLOR, P. J.;

ROBERTS, M. A.; BAKER, C.: Genetic variation in the African rodent subfamily Otomyinae (Muridae). II. Chromosomal changes in some populations of Otomys irroratus. S. Afr. J. Sci. (submitted).

DUTRILLAUX, B.; COUTURIER, J. (1983): The ancestral karyotype of Carnivora: comparison with that of platyrrhine monkeys. Cytogenet. Cell Genet. **35**, 200-208.

FREDGA, K. (1972): Comparitive chromosome studies in mongooses (Carnivora, Viverridae). I. Idiograms of 12 species and karyotypic evolution in Herpestinae. Hereditas **71**, 1-74.

KUOKKANEN, M.; LOHI, O.; MAKINEN, A. (1985): Variation in microchromosome number in the silver fox (Vulpes vulpes L.) Acta Agric. Scand. **35**, 432-437.

LEE, M. R.; ELDER, F. F. B. (1980): Yeast stimulation of bone marrow mitosis for cytogenetic investigations. Cytogenet. Cell Genet. **26**, 36-40.

MAKINEN, A.; KUOKKANEN, M.; VALTONEN, M. (1986): A chromosome-banding study in the Finnish and the Japanese raccoon dog. Hereditas **105**, 97-105.

MEESTER, J. (1988): Chromosomal speciation in Southern African small mammals. S. Afr. J. Sci. **84**, 721-724.

MODI, W. S. (1987): C-banding analyses and the evolution of heterochromatin among Arvicolid rodents. J. Mamm. **68**, 704-714.

PATTON, J. L.; SHERWOOD, S. W. (1983): Chromosomal evolution

and speciation in rodents. Ann. Rev. Ecol. Syst. **14**, 139-158.

RASA, O. A. E. (Personal communication). Department of Zoology, University of Pretoria, Pretoria 0002.

ROBBINS, L. W.; BAKER, R. J. (1978): Karyotypic data for African mammals, with a description of an _in vivo_ bone marrow technique. Bull. Carnegie Mus. Nat. Hist. **6**, 188-210.

SEABRIGHT, M. (1971): A rapid banding technique for human chromosomes. Lancet **2**, 971-972.

SHILOH, Y.; COHEN, M. M. (1978): An improved technique of preparing bone marrow specimens for cytogenetic analysis. In vitro **4**, 510-515.

SMITHERS, R. H. N. (1983): The mammals of the Southern African subregion. Pretoria: University of Pretoria.

TAYLOR, P. J.; CAMPBELL, G. K.; VAN DYK, D.; WATSON, J.; PALLET, J.; ERASMUS, H.: Genic variation in the yellow mongoose (_Cynictis penicillata_) in Southern Africa. S. Afr. J. Sci. (submitted).

TAYLOR, P. J.; MEESTER, J.; RAUTENBACH, I. L.: A quantitative analysis of geographical colour variation in the yellow mongoose _Cynictis penicillata_ Cuvier, 1829, in Southern Africa. Ann. Transv. Mus. (in press).

TAYLOR, P. J.; MEESTER, J: Morphometric variation in the yellow mongoose _Cynictis penicillata_ Cuvier, 1829, in Southern Africa. Ann. Transv. Mus. (submitted).

WURSTER, D. H.; BENIRSCHKE, K. (1968): Comparitive cytogenetic studies in the order Carnivora. Chromosoma **24**, 336-382.

WURSTER-HILL, D. H.; CENTERWALL, W. R. (1982): The interrelationships of chromosome banding patterns in canids, mustelids, hyena and felids. Cytogenet. Cell Genet. **34**, 178-192.

WURSTER-HILL, D. H.; GRAY, C. W. (1975): The interrelationships of chromosome banding patterns in procyonids, viverrids, and felids. Cytogenet. Cell Genet. **15**,306-331.

CHAPTER 7

ALLOZYME EVOLUTION IN THE AFRICAN MONGOOSES[1]

Introduction

Relationships among the mongooses (Viverridae: Herpestinae) are poorly understood (WOZENCRAFT 1989a). Several, largely conflicting, phylogenetic schemes have been proposed for the mongooses, based on independent studies involving morphological (GREGORY and HELLMAN 1939; PETTER 1969; BAKER 1987), palaeontological (HENDEY 1974), karyological (FREDGA 1972) and behavioral (BAKER 1987) evidence. Furthermore, a lack of consensus is evident in certain aspects of mongoose classification, such as the status of Galerella (subgenus of Herpestes (WOZENCRAFT 1989b) or a full genus (MEESTER et al. 1986)), and the recognition of the mongooses as a separate family (WOZENCRAFT 1989b) or as a subfamily of Viverridae (ROSEVEAR 1974; MEESTER et al. 1986). Taxonomic instability also exists concerning the numbers of species that should be

---

1. This chapter is essentially the paper, by P. J. Taylor, G. K. Campbell, J. A. J. Meester, and D. van Dyk, that has been submitted to Z. Säugetierkunde under the full title "A preliminary study of allozyme evolution in the African mongooses (Viverridae: Herpestidae)".

recognised in certain genera such as Galerella (sensu MEESTER et al. 1986), Helogale, Bdeogale, and Crossarchus (see ROSEVEAR 1974; HONACKI et al. 1982; GOLDMAN 1984; MEESTER et al. 1986; WATSON and DIPPENAAR 1987; WOZENCRAFT 1989b).

Molecular techniques, including allozyme electrophoresis, have proved to be useful in resolving evolutionary and taxonomic relationships in the carnivoran families Felidae, Canidae and Ursidae (for a review see WAYNE et al. 1989). The aim of the present study was to analyse allozyme variation in seven species of Southern African mongooses and one species of genet Genetta tigrina, in an attempt to resolve evolutionary and taxonomic relationships in the carnivoran family Viverridae (Herpestinae). Allozyme data were analysed as genetic distances and as qualitative characters, using both phenetic and cladistic (parsimony) approaches.

Material and methods

Tissues (liver, kidney, heart and/or muscle) were collected from 48 specimens representing seven species of Southern African mongooses and one species of genet Genetta tigrina, and these were stored in liquid nitrogen prior to electrophoretic analysis. Viverrid specimens were collected by live-trapping, shooting and by retrieving tissues from

previously frozen carcasses obtained from fresh road kills. In the latter case most carcasses were donated by the Natal Parks Board. In three specimens, carcasses had been de-gutted and only muscle (or muscle and kidney) tissue could be obtained. Of the total sample of specimens collected, 35 specimens, representing eight populations of the yellow mongoose Cynictis penicillata, have been previously analysed for within-species allozyme variation at 28 loci (TAYLOR et al. submitted).

Details of specimens, methods of collection and sample sizes are given in Table 7.1. Voucher specimens were deposited in the Durban Natural Science Museum, the MacGregor Museum, Kimberley, the National Museum, Bloemfontein, and the Transvaal Museum, Pretoria.

The present study is based on starch (SIGMA: 12.5%) gel electrophoretic results from 18 genetic loci encoding the following 15 proteins and enzymes (electrophoretic procedures, which are taken mainly from SELANDER et al. 1971; SHAW and PRASAD, 1969; HARRIS and HOPKINSON 1976; and RICHARDSON et al. 1986, are described in detail in TAYLOR et al. submitted): albumin (ALB), catalase (CAT), glucose dehydrogenase (GDH), glutamate-oxaloacetate transaminase (GOT), glycerol dehydrogenase (GCDH), glycerol-3-phosphate dehydrogenase (GPD), haemoglobin (HB), isocitrate dehydrogenase (IDH), lactate dehydrogenase (LDH), malate

Table 7.1.
Species and locality data of specimens of eight African viverrid species analysed for allozyme electrophoresis.

Species and locality	n	Method[1]	Tissue[2]
Cynictis penicillata:			
Kaal Plaas Farm, Pretoria, Transvaal	3	T	L,K,H,M
Rhenosterfontein Farm, Cullinan, Transvaal	4	T,S	L,K,H,M
Karroo National Park, Cape Province	1	T	L,K,H,M
Windhoek, Namibia	4	T,R	L,K,H
Victoria West, Cape Province	5	T	L,K,H
Glen Agricultural Coll., Bloemfontein, OFS	15	T,S	L,K,B
Erfdeel Farm, Kroonstad, OFS	2	T	L,K
Riemvasmaak, northern Cape Province	1	T	L,K
Galerella sanguinea:			
Weenen Nature Reserve, Natal	1	T	L,K,M
Blydschap Private Nature Reserve, N. Trvl.	1	T	L,K,H,M
Galerella pulverulenta:			
Karroo National Park, Cape Province	1	T	L,K,H,M
Riemvasmaak, northern Cape Province	1	T	K,H
Atilax paludinosus:			
Hilton, Pietermaritzburg, Natal	1	R	L,K,H,M
Howick, Pietermaritzburg, Natal	1	R	M
Wagondrift Farm, western Cape	1	T	L,K,H,M
Herpestes ichneumon:			
Colchester Farm, Natal	1	R	M
Suricata suricatta:			
On N1, near Kimberley, Cape Province	1	R	L,K,H,M
Helogale parvula:			
Blydschap Private Nature Reserve, N. Trvl.	1	T	L,K,H,M
Genetta tigrina:			
Skewbridge, Pietermaritzburg, Natal	1	R	K,M
Blydschap Private Nature Reserve, N. Trvl.	2	T	L,K,H,M

[1] Methods of collection of specimens: T (live trapped); R (road kill); S (shot)

[2] Tissues collected: L (liver); K (kidney); H (heart); M (muscle); B (blood)

dehydrogenase (MDH), malic enzyme (ME), phoshogluconate dehydrogenase (PGD), glucosephosphate isomerase (PGI), phosphoglucomutase (PGM), superoxide dismutase (SOD). Haemoglobin was present in sufficient quantities in blood associated with the tissue homogenates to permit its resolution in the present study. Optimum resolution of haemoglobin was obtained using a discontinuous buffer system (in this case, the lithium hydroxide-tris citrate buffer of SELANDER et al. 1971). Intensity of haemoglobin bands was enhanced by staining with napthyl blue black.

Since muscle tissue only was available from three specimens, both muscle and liver tissues of one individual of C. penicillata was examined, to establish the homology of observed staining patterns between the different tissue types.

Electromorphic alleles were described according to their relative mobilities on the gel, with the fastest (most anodal) being designated as A, and successively cathodal alleles being designated as B, C, D etc. Two approaches were taken in the analysis of the allozyme data: (1) analysis of allele frequencies, using the computer program BIOSYS-1 (SWOFFORD and SELANDER 1989); and (2) cladistic (parsimony) analysis of qualitative allozyme characters, using the computer program PAUP (SWOFFORD 1985). Computer programs were run on an IBM-compatible, XT personal computer.

Analysis of allele frequencies

From the individual genotypes at each locus (including monomorphic loci in which all individuals were scored as AA), allele frequencies were determined and used to calculate genetic distances and similarities (NEI's (1978) D_N and I, and ROGERS' (1972) D_R and S) and mean heterozygosities ($\bar{H}$). In calculating $\bar{H}$, owing to the fact that localities were generally represented by single individuals (with the exception of the yellow mongoose, for which $\bar{H}$ was obtained from TAYLOR et al. submitted), data were pooled for each species. Genetic distances were summarised using both phenetic (unweighted pair group method with averages (UPGMA) phenogram: SNEATH and SOKAL 1973) and cladistic (distance Wagner tree: FARRIS 1972) methods, for NEI's D_N and ROGERS' D_R values respectively. Analysis of allele frequency data was based on 17 loci, as missing data for GDH for three species prevented analysis of this locus.

Cladistic analysis of qualitative locus characters

Qualitative allozyme characters may be coded for cladistic analysis by: (1) treating alleles as characters and presence or absence of alleles as character states ("independent alleles model"); and (2) treating the locus as a character and alleles as character states. Although the first approach

has the advantage of producing binary characters which are easily ordered using the outgroup method (WATROUS and WHEELER 1981), this method can hypothetically give rise to loci having no alleles, and BUTH (1984) recommends that the latter approach (treating the locus as character) should be used for cladistic analysis of allozyme data. Several models have been described for ordering multistate locus characters (MICKEVICH and MITTER 1983), and BUTH (1984) recommends that researchers should explicitly state their ordering procedure. However, SWOFFORD (1985) suggests that there is no need to order multistate characters when there is no obvious evolutionary sequence (see also BEZY and SITES 1987; STASZ et al. 1989).

In the present study, the locus was recognised as character, and PAUP was performed on both ordered (using the "relative mobilities model": MICKEVICH and MITTLER 1983) and unordered data, representing allelic variants at ten loci showing inter-specific differences. All PAUP analyses were run with the options: MULPARS, SWAP=GLOBAL and ROOT=OUTGROUP, and the genet Genetta tigrina was taken as the outgroup. Analyses involving unordered data resulted in 97 equal length trees. A consensus tree, obtained from these trees using the CONTREE program of PAUP, was uninformative in producing an unresolved polychotomy involving six mongoose species. The analysis of ordered data produced six equal length trees, and a more completely resolved consensus tree. For this

reason, only the results of the ordered character data are presented in this paper.

Results

Genetic heterozygosities and genetic distances

Of the 18 loci scored, 14 were polymorphic, either between or within species. Of these, ten loci showed consistent allelic differences between species or groups of species (Table 7.2). From Tables 7.2 and 7.3, no allelic variation was found in Galerella pulverulenta (Cape grey mongoose), Atilax paludinosus (water mongoose), Herpestes ichneumon (large grey mongoose), Suricata suricatta (suricate) and Helogale parvula (dwarf mongoose). Mean heterozygosity ($\bar{H}$) was 0.026 in Cynictis penicillata (yellow mongoose); 0.039 in Galerella sanguinea (slender mongoose); and 0.051 in Genetta tigrina (genet; Table 7.3).

NEI's D_N varies from 0.06 (between G. pulverulenta and H. ichneumon) to 0.63 (between G. tigrina and S. suricatta), with a mean of 0.30. ROGERS' D_R varies from 0.06 (between G. pulverulenta and H. ichneumon) to 0.47 (between G. tigrina and S. suricatta), with a mean of 0.26 (Table 7.4). The UPGMA phenogram, based on D_N (Fig. 1A), indicates the genetic separatedness of the genets (Viverrinae) from the mongooses (Herpestinae), at a distance of 0.53. Beyond this,

Table 7.2.

Allelic designations of 14 polymorphic genetic loci for eight species of African Viverridae. Abbreviations for species explained in Fig. 7.1. Abbreviations for loci explained in text.

Locus	Species							
	Cp	Gs	Gp	Ap	Hi	Ss	Hp	Gt
ALB	A	A	A	A	A	A	B	C
CAT	E,G,H	D,F	F	B	C	C	C	A
GDH	E	C	-	-	-	F	D	A,B
GOT-1	A,B	B	B	B	B	B	B	B
GOT-2	A,B	B	B	B	B	B	B	B
GPD	A,B	B	B	B	B	B	B	C
HB	E	C	C	C	C	B	A	D
IDH	A	B	A	A	A	A	A	A
MDH-1	B	B	B	B	B	B	B	A,B
MDH-2	A	A	A	B	A	A	A	B
ME	B	C	B	B	B	A	C	D,E
PGD	A,B,C	C	C	C	C	C	C	C
PGM	A,C	C	C	C	C	C	C	B
SOD	B	B	B	B	B	B	A	B

Table 7.3.

Estimates of percentage polymorphic loci (%P), mean heterozygosity ($\bar{H}$), and standard error (s.e.) of $\bar{H}$ in eight species of Viverridae (data for Cynictis penicillata represent the mean for eight populations and were taken from a separate study: TAYLOR et al. submitted).

Species	N[1]	%P	$\bar{H}$	s.e.
Cynictis penicillata	29.3	6.8	0.026	0.020
Galerella sanguinea	2.0	5.9	0.039	0.039
Galerella pulverulenta	2.0	0	0	0
Atilax paludinosus	2.8	0	0	0
Herpestes ichneumon	1.0	0	0	0
Suricata suricatta	1.0	0	0	0
Helogale parvula	1.0	0	0	0
Genetta tigrina	2.8	11.8	0.051	0.036

[1] Mean sample size per locus

no clear groupings are evident, and most splitting events appear to occur over a rather narrow range of genetic distances. The solitary species (Herpestes, Galerella and Atilax) and the semi-social Cynictis are loosely grouped together genetically, and the social species (Helogale, Suricata) appear somewhat distinct.

The topology of the outgroup-rooted, distance Wagner trees (Figs 7.1B, 7.1C) is different from the UPGMA phenogram (Fig. 7.1A). Figure 7.1B was based on the same data as the UPGMA phenogram. Figure 7.1C was "optimised" by recoding the allelic character states at the ME locus so as to eliminate an obvious convergence (the shared possession of allele C in G. sanguineus and H. parvula): allele C in H. parvula was recoded as D and alleles D and E were recoded as E and F respectively. The "optimised" tree had a "f" value (FARRIS 1972) of 0.654 and a cophenetic correlation coefficient of 0.965, compared to a "f" value of 1.121 and a cophenetic correlation coefficient of 0.930 in the "unoptimised" tree.

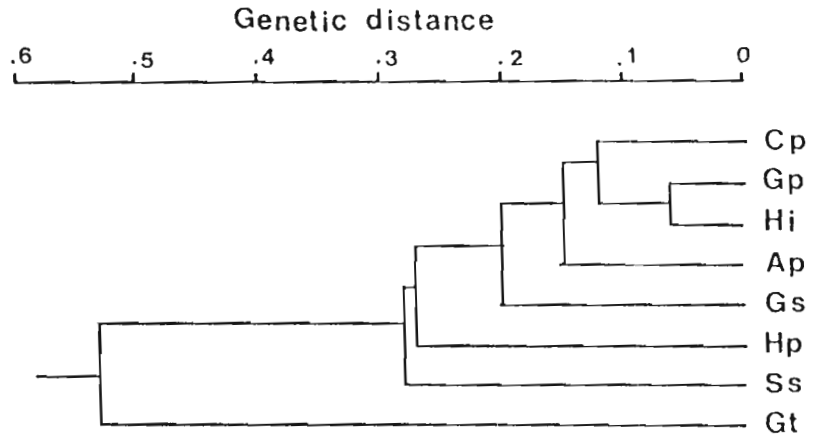
Both distance Wagner trees resulted in the early splitting off of Atilax, and the subsequent trichotomous split. In the "unoptimised" tree these three lineages comprise: (1) Cynictis; (2) Galerella, and the two social genera, Helogale and Suricata; (3) Herpestes. In the "optimised" tree the three lineages comprise: (1) all the social species (Cynictis, Helogale, Suricata); (2) Galerella; (3)

Table 7.4.
Values of (A) NEI'S (1978) genetic distance (below diagonal) and identity (above the diagonal), and (B) ROGERS' (1972) genetic distance (below the diagonal) and similarity (above the diagonal), between eight species of Southern African Viverridae. Abbreviations for species given in Fig. 7.1

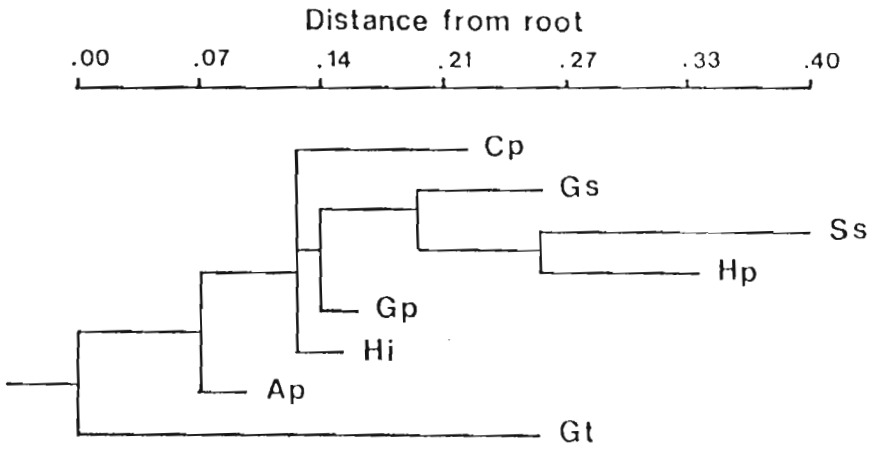
	Species							
	Cp	Gs	Gp	At	Hi	Ss	Hp	Gt
A								
Cp	-	0.78	0.88	0.83	0.88	0.77	0.77	0.60
Gs	0.25	-	0.87	0.78	0.84	0.72	0.78	0.54
Gp	0.12	0.14	-	0.88	0.94	0.76	0.76	0.59
At	0.19	0.25	0.12	-	0.88	0.71	0.71	0.65
Hi	0.12	0.17	0.06	0.12	-	0.82	0.82	0.59
Ss	0.27	0.33	0.27	0.35	0.19	-	0.76	0.53
Hp	0.27	0.25	0.27	0.35	0.19	0.27	-	0.59
Gt	0.52	0.61	0.52	0.42	0.52	0.63	0.52	-
B								
Cp	-	0.77	0.88	0.82	0.88	0.76	0.76	0.58
Gs	0.23	-	0.85	0.77	0.83	0.71	0.77	0.53
Gp	0.12	0.15	-	0.88	0.94	0.76	0.76	0.58
At	0.18	0.23	0.12	-	0.88	0.71	0.71	0.64
Hi	0.12	0.17	0.06	0.12	-	0.82	0.82	0.58
Ss	0.24	0.29	0.24	0.29	0.18	-	0.76	0.53
Hp	0.24	0.23	0.24	0.29	0.18	0.24	-	0.58
Gt	0.42	0.47	0.42	0.36	0.42	0.47	0.42	-

Fig. 7.1. UPGMA tree (A) and "unoptimised" (B) and "optimised": (C) distance Wagner trees, based on allele frequencies from 17 genetic loci in eight species of Southern African Viverridae. Distance Wagner trees were outgroup-rooted taking the genet Genetta tigrina as the outgroup. The procedure for "optimising" the distance Wagner tree in (C) is explained in the text. Abbreviations for species as follows: Ap = Atilax paludinosus (water mongoose); Cp = Cynictis penicillata (yellow mongoose); Gp = Galerella pulverulenta (Cape grey mongoose); Gs = Galerella sanguinea (slender mongoose); Gt = Genetta tigrina (large-spotted genet); Hi = Herpestes ichneumon (large grey mongoose); Hp = Helogale parvula (dwarf mongoose); Ss = Suricata suricatta (suricate).

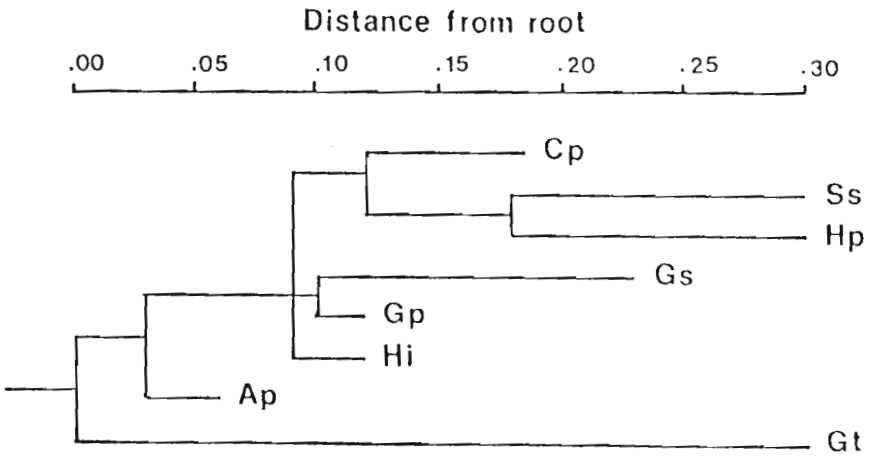
A


Genetic distance
.6
.5
.4
.3
.2
.1
0
Cp
Gp
Hi
Ap
Gs
Hp
Ss
Gt

B


Distance from root
.00
.07
.14
.21
.27
.33
.40
Cp
Gs
Ss
Hp
Gp
Hi
Ap
Gt

C


Distance from root
.00
.05
.10
.15
.20
.25
.30
Cp
Ss
Hp
Gs
Gp
Hi
Ap
Gt

Herpestes.

Phylogenetic analysis of discrete allozyme characters

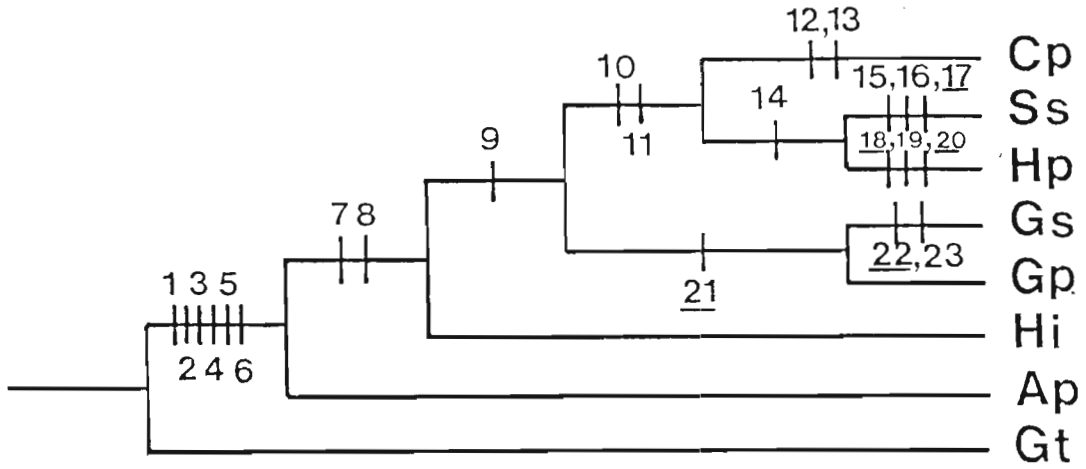
Figure 7.2A shows one of six trees produced by parsimony, cladistic analysis (PAUP) of ordered, multistate locus characters (the data on which this analysis was based are shown in Table 7.5). All six trees had a length of 27 and a consistency index of 0.815. Character state changes (i.e. apomorphies) have been superimposed on the tree in Fig. 7.2A, and homoplasies are indicated by underlining. Figure 7.2B shows the strict consensus tree obtained from these six trees. Areas of instability, as indicated by unresolved trichotomies on the consensus tree, concern the resolution of the three social species (three of the six trees supported a Suricata-Helogale clade, while the other three supported a Cynictis-Suricata clade), and the recognition of a Galerella-Cynictis-Helogale-Suricata clade (supported by two trees).

The consensus tree in Fig. 7.2B is similar in overall topology to the "optimised" distance Wagner tree (Fig. 7.1C), in recognising the early separation of Atilax, and the subsequent trichotomy involving the same three lineages (social species, Galerella and Herpestes).

Discussion

Fig. 7.2. Cladograms of seven Southern African mongoose species, resulting from phylogenetic analysis using parsimony (PAUP package) of allozyme data, using loci as characters and alleles as character states. Abbreviations for species given in Fig. 1. (A) One of six, equal length, most parsimonious cladograms (length = 27; consistency index = 0.815). (B). Consensus tree resulting from the six most parsimonious cladograms. Numbers on cladogram (A) represent character state changes as follows (abbreviations of loci explained in text): 1=GPD(0-->1); 2=PGM(0-->1); 3=ME(0-->2); 4=HB(0-->1); 5=CAT(0-->1); 6=ALB(0-->2); 7=MDH-2(0-->1); 8=CAT(1-->2); 9=GDH(0-->1); 10=HB(1-->2); 11=GDH(1-->2); 12=GDH(2-->3); 13=CAT(2-->3); 14=HB(2-->3); 15=SOD(0-->1); 16=ME(2-->3); 17=GDH(2-->4); 18=ME(2-->1); 19=HB(3-->4); 20=ALB(2-->1); 21=CAT(2-->4); 22=ME(2-->1); 23=IDH(0-->1). Underlined numbers represent homoplasies (convergences and reversals).

A


12,13
10
15,16,17
14
9
11
18,19,20
7 8
22,23
1 3 5
21
2 4 6
Cp
Ss
Hp
Gs
Gp
Hi
Ap
Gt

B

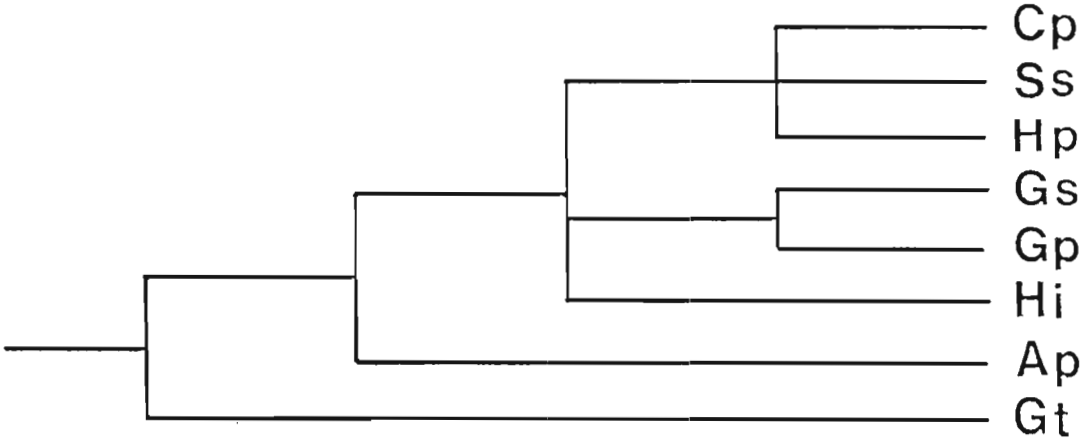

Cp
Ss
Hp
Gs
Gp
Hi
Ap
Gt

Table 7.5.

Ordered allozyme locus characters used in parsimony cladistic analysis (PAUP) of seven Southern African mongoose species. Trees were outgroup-rooted, taking the genet Genetta tigrina as the outgroup. Character states (alleles) were ordered using the "relative mobility model", which assumes that alleles closer in mobility on a gel to the allelic state possessed by the outgroup are more primitive than alleles which are further away from the outgroup allele state. Abbreviations of loci explained in text.

Species	ALB	CAT	GDH	HB	IDH	MDH-2	ME	PGM	SOD	GPD
Cp	2	3	3	2	0	1	2	1	0	1
Gs	2	4	1	1	1	1	1	1	0	1
Gp	2	4	-	1	0	1	2	1	0	1
Ap	2	1	-	1	0	0	2	1	0	1
Hi	2	2	-	1	0	1	2	1	0	1
Ss	2	2	4	3	0	1	3	1	1	1
Hp	1	2	2	4	0	1	1	1	0	1
Gt	0	0	0	0	0	0	0	0	0	0

Genetic distance analyses

Allelic variation within species was minimal ($\bar{H}$ = 0-0.051: Table 7.3). For the ten loci that showed between-species polymorphism, the pattern of distribution of alleles was species and group specific (Table 7.2). Species differed from one another therefore, in the presence or absence of alleles rather than in allele frequency. These factors promote the stability of dendrograms based on genetic distances (particularly when sample sizes are very small), as shown by ARCHIE et al. (1989), and they also provide suitable qualitative characters for cladistic analysis.

NEI's (1978) genetic identity values (I) between pairs of viverrid species (including the genet G. tigrina: Table 7.4) invariably exceed the mean value for congeneric species given by THORPE (1982: I=0.54, s.d.=0.17, n=824). I values between species of mongooses (Table 7.4) generally exceed the mean value for incipient species of mammals, given by AYALA (1975: I=0.77). These results suggest a recent radiation of the Viverridae, and are rather surprising, given the fact that mongooses and genets are separated at the subfamily level (or the family level: WOZENCRAFT 1989b), and that most of the species of mongooses included in this study represent separate genera.

However, palaeontological and morphological data provide

support for a recent, and somewhat "explosive", radiation of African herpestines. Three lineages of mongooses were present in the Pliocene Langebaanweg deposits, a Galerella-type form, a Herpestes-type form and a Mungos-type form (HENDEY 1974, and unpublished data). The close resemblance of the Mungos form to Herpestes suggested that these two lineages had only recently split (HENDEY 1974; furthermore, earlier fossil herpestines are represented only by unspecialised Herpestes - type forms: SAVAGE 1978). By the early Pleistocene, fossil representatives of all the extant genera had appeared (HENDEY 1974; SAVAGE 1978). On the basis of dental characters and fossil evidence, PETTER (1969) suggested a recent origin of the extant African Viverridae. Further allozyme analyses, based on larger numbers of loci, species and specimens, are needed to verify the apparently high genetic similarity between viverrid species.

Comparison of phenetic and cladistic allozyme approaches

Although the two species of Galerella are not clustered together on the UPGMA phenogram, they are cladistically similar as shown by the "optimised" distance Wagner (Fig. 7.1C) and PAUP (Fig. 7.2) trees. The UPGMA phenogram in Fig. 7.1A shows a close genetic relationship between Galerella pulverulenta and Herpestes ichneumon (the two species are separated by a D_N of only 0.06), which would appear to support the argument for including Galerella in Herpestes

(WOZENCRAFT 1989). However, the "optimised" distance Wagner tree (Fig. 7.1C) and the PAUP consensus tree (Fig. 7.2B) show Herpestes and Galerella to be distinct lineages which separated at the same time as the origin of the "social" lineage. The trichotomous split on the cladistic trees in Fig. 7.1C and Fig. 7.2 is supported by palaeontological evidence, which shows the existence of three lineages of mongooses in Langebaanweg deposits (3-5 MYA): a Galerella-type form, a Herpestes-type form and a Mungos-type (i.e. social) form (HENDEY 1974, and unpublished data).

BUTH (1984) has pointed out that UPGMA trees based on electrophoretic data represent the true phylogeny only when the assumption of equal rates of evolution in different lineages is met. The marked difference in topology between the UPGMA phenogram and the cladistic (i.e. distance Wagner and PAUP) trees in this study results from unequal rates of evolution in different lineages of mongooses, as is evident from the distance Wagner trees (Figs 7.1B, 7.1C) and the PAUP tree in Fig. 7.2A. A similar explanation was given for conflicting phenetic and cladistic analyses of electrophoretic data by BAVERSTOCK et al. (1979) and HILLIS (1985). Anagenic change (as measured by branch length in the distance Wagner trees in Fig. 7.1, or by the number of character state changes in Fig. 7.2A) appears to occur at a faster rate in the "advanced", social mongooses (Suricata, Helogale, Cynictis) than in the "primitive", solitary

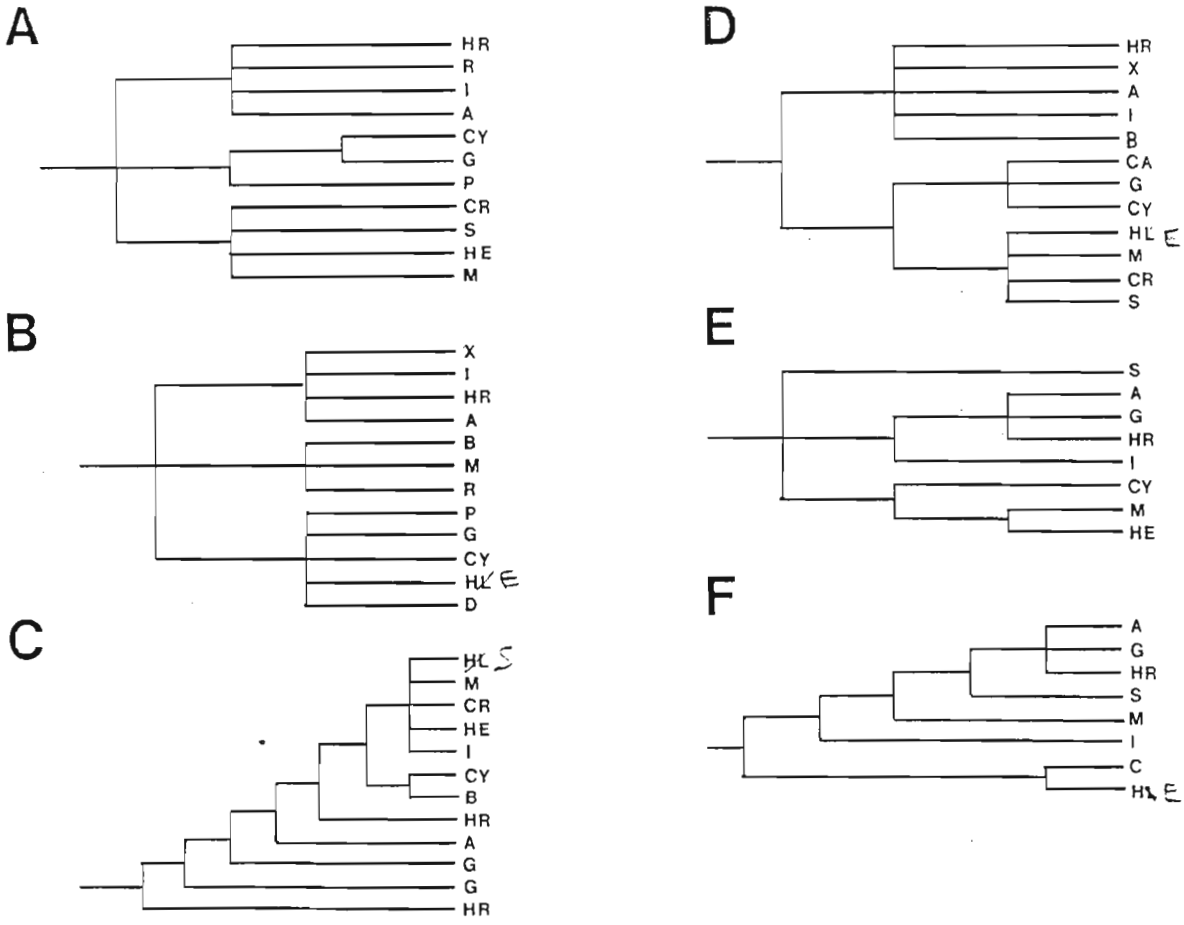
species (Galerella, Herpestes, Atilax), giving rise to an UPGMA tree in which the social species appear to split off before the origin of the extant solitary species. The genetic similarity between Herpestes, Galerella, Atilax and Cynictis on the UPGMA phenogram is clearly a result of symplesiomorphic (i.e. shared primitive) characters (see Fig. 7.2A).

Comparison of allozyme and other data sets

Figure 7.3 illustrates six previous phylogenetic schemes for the Herpestinae, based on morphological, palaeontological, karyological and behavioral evidence. From Fig. 7.3, there is clearly little consensus regarding phylogenetic relationships among the mongooses. However certain comparisons can be made between the various published phylogenetic schemes and the allozyme trees presented in the present study.

The "optimised" distance Wagner tree (Fig. 7.1C) and PAUP trees (Fig. 7.2) support a phylogenetic split between the social and the solitary mongooses. This conclusion is supported by karyological (FREDGA 1972), palaeontological (HENDEY 1974), and morphological (GREGORY and HELLMAN 1939) evidence (Fig. 7.3), although HENDEY (1974) and GREGORY and HELLMAN (1939) place the "semi-social" genus Cynictis closer to Galerella than to the social species (Fig. 7.3A, D). In

Fig. 7.3. Dendrograms summarising relationships among genera of mongooses (Herpestinae), based on independent, published studies involving different suites of characters: (A) based on palaeontological data, in HENDEY (1974, and unpublished phylogenetic tree); (B) based on groups identified by PETTER (1969) on the basis of size and dental characters; (C) modified from FREDGA (1972), on the basis of karyological data; (D) modified from GREGORY and HELLMAN (1939), based on characters of the skull and teeth; (E) based on phenogram from behavior data (BAKER 1987); (F) based on phenogram from morphological data (BAKER 1987). Abbreviations of genera are as follows: A = Atilax; B = Bdeogale; CA = Calogale; CR = Crossarchus; CY = Cynictis; D = Dologale; G = Galerella; HR = Herpestes; HE = Helogale; I = Ichneumia; M = Mungos; P = Paracynictis; R = Rhynchogale; S = Suricata; X = Xenogale.


A
HR
R
I
A
CY
G
P
CR
S
HE
M
B
X
I
HR
A
B
M
R
P
G
CY
HL E
D
C
HL S
M
CR
HE
I
CY
B
HR
A
G
G
HR
D
HR
X
A
I
B
CA
G
CY
HL E
M
CR
S
E
S
A
G
HR
I
CY
M
HE
F
A
G
HR
S
M
I
C
HL E

this respect, from the cladistic analyses of the allozyme data, Cynictis separates first from the "social" lineage, and therefore shares greater symplesiomorphic similarity with Galerella than do Helogale and Suricata (this is reflected in the position of Cynictis on the UPGMA phenogram in Fig. 7.1A). BAKER (1987) groups Helogale, Mungos and Cynictis on behavioral grounds, while maintaining that Suricata is behaviorally unique (Fig. 7.3E). However, these behavioral differences in Suricata are clearly autapomorphies, and, cladistically speaking, Suricata would probably be grouped with Helogale and Mungos on behavioral grounds.

The close genetic similarity between Atilax, Herpestes and Galerella (Fig. 7.1A) is supported by phenetic analyses of behavioral and morphological data (BAKER 1987: Fig. 7.3E, F). However, as shown in the cladistic allozyme trees, and as discussed above, this similarity is symplesiomorphic in nature. The phylogenetic separation of the Galerella and Herpestes lineages, as suggested by the cladistic, allozyme trees (Figs 7.1B, 7.1C, 7.2), is supported by palaeontological (HENDEY 1974), morphological (GREGORY and HELLMAN 1939; PETTER 1969) and karyological (FREDGA 1972) data (see Fig. 7.3). As mentioned above, these results argue against the inclusion of Galerella in Herpestes, as suggested by WOZENCRAFT (1989b).

BAKER (1987) has suggested the possibility of an Atilax-like ancestor of the Herpestinae, an idea that is supported by cladistic analysis of allozymes in the present study (Figs 7.1B, 7.1C, 7.2). Although the earliest mongoose fossils, from the Miocene in Africa and Europe, are generally recognised as unspecialised Herpestes-type forms (SAVAGE 1978), a diverse array of these primitive viverrid genera existed during the Miocene, of which many lineages became extinct (e.g. Kichechia, Leptoplesictis, Herpestides, Legetetia: SCHMID-KITTLER 1987). There need not therefore have been a direct line of descent from the earliest unspecialised viverrids to all of the extant species (HENDEY, personal communication), and it is quite plausible that a more recent Atilax-like ancestoral species gave rise to the apparently recent (Pliocene and early Pleistocene) extant mongoose radiation.

Acknowledgements

Dr O. BOURQUIN of the Natal Parks Board, Dr I. L. RAUTENBACH, G. BRONNER and SANDRA WEBER of the Transvaal Museum, and H. ERASMUS of the Cape Nature Conservation Department, Kimberley, are thanked for providing additional viverrid specimens. Dr Q. B. HENDEY, director of the Durban Natural Science Museum, provided advice and fruitful discussions on palaeontological aspects of this project. E. HERHOLDT kindly provided the English translation of the

French paper by G. PETTER. The financial assistance of the Foundation for Research Development (F.R.D.) to JAJM, is gratefully acknowledged.

References

ARCHIE, J. W.; SIMON, C.; MARTIN, A. (1989): Small sample size does decrease the stability of dendrograms calculated from allozyme-fequency data. Evolution **43**, 678-683.

BAKER, C. M. (1987): Biology of the water mongoose (Atilax paludinosus). PhD thesis, University of Natal.

BAVERSTOCK, P. R.; COLE, S. R.; RICHARDSON, B. J.; WATTS, C. H. S. (1979): Electrophoresis and cladistics. Syst. Zool. **28**, 214-219.

BEZY, R. L.; SITES, J. W. (1987): A preliminary study of allozyme evolution in the lizard family Xanthusiidae. Herpetologica **43**, 280-292.

BUTH, D. G. (1984): The application of electrophoretic data in systematic studies. Ann. Rev. Ecol. Syst. **15**, 501-522.

FARRIS, J. S. (1972): Estimating phylogenetic trees from distance matrices. Am. Nat. **106**, 645-668.

FREDGA, K. (1972): Comparitive chromosome studies in mongooses (Carnivora, Viverridae). I. Idiograms of 12 species and karyotypic evolution in Herpestinae. Hereditas **71**, 1-74.

GOLDMAN, C.. A. (1984): Systematic revision of the African mongoose genus Crossarchus (Mammalia: Viverridae). Canadian J. Zool. **62**, 1618-1636.

GREGORY, W. K.; HELLMAN, M. (1939): On the evolution and major classification of the civets (Viverridae) and allied fossil and recent Carnivora: a phylogenetic study of the skull and dentition. Proc. Amer. Philos. Soc. **81**, 309-392.

HARRIS, H.; HOPKINSON, D. A. (1976): Handbook of enzyme electrophoresis in human genetics. Amsterdam: North Holland.

HENDEY, Q. B. (Personal communication). Director, Durban Natural Science Museum, P. O. Box 4085, Durban 4000.

HENDEY, Q. B. (1974): Faunal dating of the late Cenozoic of Southern Africa, with special reference to the Carnivora. Quatern. Res. (N.Y.) **4**, 149-161.

HILLIS, D. M. (1985): Evolutionary genetics of the Andean lizard genus Pholidobolus (Sauria: Gymnophthalmidae). Phylogeny, biogeography, and a comparison of tree construction techniques. Syst. Zool. **34**, 109-126.

HONACKI, J. H.; KINMAN, K. E.; KOEPPL. J. W. (1982): Mammal species of the world: a taxonomic and geographic review. Lawrence, Kansas: Association of Systematics Collections.

MEESTER, J. A. J.; RAUTENBACH, I. L.; DIPPENAAR, N. J.; BAKER, C. M. (1986): Classification of Southern African mammals. Transv. Mus. Monograph No. **5**, 1-359.

MICKEVICH, M. F.; MITTER, C. (1983): Evolutionary patterns in allozyme data: a systematic approach. In: Advances in Cladistics, Vol. 2, Proc. 2nd Meet. Willi Hennig Soc. Ed. by N. I. PLATNICK; V. A. FUNK, pp. 169-176. New York: Columbia Univ. Press.

NEI, M. (1978): Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics **89**, 583-590.

PETTER, G. (1969): Interpretation evolutive des characters de la denture des viverrides Africains. Mammalia **33**, 607-625.

RICHARDSON, V. J.; BAVERSTOCK, P. R.; ADAMS, M. (1986): Allozyme Electrophoresis: a Handbook for Animal Systematics and Population Studies. Sydney: Academic Press.

ROGERS, J. S. (1972): Measures of genetic similarity and genetic distance. In: Studies in Genetics, pp. 145-153. Ed. by M. R. Wheeler. Univ. Texas Publication No. 7213.

ROSEVEAR, D. R. (1974): The Carnivores of West Africa. Publication No. 723. London: Trustees of the British Museum (Natural History).

SAVAGE, R. J. G. (1978): Carnivora. In: Evolution of African Mammals, pp. 249-267. Ed. by V. J. MAGLIO; H. B. S. COOKE. Cambridge (Mass.), London: Harvard University Press.

SCHMIDT-KITTLER, N. (1987): The Carnivora (Fissipedia) from

the lower Miocene of East Africa. Palaeontographica **197**, 85-126.

SELANDER, R. K.; SMITH, M. H.; YANG, S. Y.; JOHNSON, W. E.; GENTRY, J. B. (1971): Biochemical polymorphism and systematics in the genus Peromyscus. I. Variation in the oldfield mouse (Peromyscus polionotus). In: Studies in Genetics, pp. 49-90. Ed. by M. R. WHEELER. Univ. Texas Publication No. 7103.

SHAW, C. R.; PRASAD, R. (1970). Starch gel electrophoresis of enzymes - a compilation of recipes. Biochem. Genet. **4**, 297-320.

SNEATH, P. H. A.; SOKAL, R. R. (1973). Numerical Taxonomy. San Francisco: Freeman.

STASZ, T. E.; NIXON, K.; HARMAN, G. E.; WEEDEN, N. F.; KUTER, G. A. (1989): Evaluation of phenetic species and phylogenetic relationships in the genus Trichoderma by cladistic analysis of isozyme polymorphism. Mycologia **81**, 391-403.

SWOFFORD, D. L. (1985): P.A.U.P. Phylogenetic Analysis Using Parsimony. Version 2.4. Illinois Natural History Survey.

SWOFFORD, D. L.; SELANDER, R. B. (1989): BIOSYS-1. A Computer Program for the Analysis of Allelic Variation in Population Genetics and Biochemical Systematics. Release 1.7. Illinois Natural History Survey.

TAYLOR, P. J.; CAMPBELL, G. K.; VAN DYK, D; WATSON, J. P.; PALLET, J.; ERASMUS, H.: Genic variation in the yellow

mongoose (Cynictis penicillata) in Southern Africa. S. Afr. J. Sci. (submitted).

THORPE, J. P. (1982): The molecular clock hypothesis: biochemical evolution, genetic differentiation and systematics. Ann. Rev. Ecol. Syst. **13**, 139-168.

WATROUS, L. E.; WHEELER, Q. D. (1981). The outgroup comparison method of character analysis. Syst. Zool. **30**, 1-11.

WATSON, J. P.; DIPPENAAR, N. J. (1987). The species limits of Galerella sanguinea (Ruppell, 1836), G. pulverulenta (Wagner, 1839) and G. nigrata (Thomas, 1928) in Southern Africa (Carnivora: Viverridae). Navors. nas. Mus. Bloemfontein **5**(14), 356-413.

WAYNE, R. K.; BENVENISTE, R. E.; JANCZEWSKI, D. N.; O'BRIEN, S. J. (1989): Molecular and biochemical evolution of the Carnivora. In: Carnivore Behavior, Ecology and Evolution. Ed. by J. L. GITTLEMAN. London: Chapman and Hall.

WOZENCRAFT, W. C. (1989a): The phylogeny of the recent Carnivora. In: Carnivore Behavior, Ecology and Evolution, pp. 495-535. Ed. by J. L. GITTLEMAN. London: Chapman and Hall.

WOZENCRAFT, W. C. (1989b). Classification of the recent Carnivora. In: Carnivore Behavior, Ecology and Evolution, pp. 569-593. Ed. by J. L. GITTLEMAN. London: Chapman and Hall.

CHAPTER 8

SYNTHESIS

Patterns of geographic variation

Geographically ordered patterns of variation occurred in morphological (colour and size), but not in genetic (allelic and chromosomal) characters, in the yellow mongoose. Allelic polymorphisms were distributed geographically in a random manner, and in six out of the eight polymorphic loci, were detected only in single populations. There was no relationship between geographic and genetic distances between pairs of localities. The basic karyotype of the species was invariant geographically (2N=36; NF=72), although a single, supernumerary microchromosome was detected in four out of the five populations sampled.

Colour varied predominantly in a north-south direction, with northern specimens being yellower and more faded (lower 'dominant wavelength' (DOM) and 'excitatory purity' (PUR)) than southern specimens. The pattern of contours in trend surface maps of DOM and PUR indicate a stepped clinal rather than a smooth clinal pattern of geographic variation. However a more gradual pattern of variation was observed in trend surface maps of a third colorimetric variable, 'brightness' (BRT), with colour becoming darker (lower BRT)

towards the east, north and south.

Morphometric variation also followed a predominantly north-south geographic pattern. On the basis of principal components analysis (PCA) and cluster analysis (CA) of 14 cranial characters in 39 pooled localities (OTUs), parapatric, small-sized northern and large-sized southern phena could be distinguished. The northern phenon could be separated into parapatric, larger-sized western (Namibia) and smaller-sized eastern (Botswana, northern Transvaal) sub-phena. The different phena and sub-phena were relatively homogeneous, although a gradual northwards cline of decreasing cranial and body size was apparent in the southern phenon. Parapatric phena and sub-phena were separated by continuous transition zones (stepped clines) of variable steepness.

Concordance in geographic trends between different character sets

Although the pattern of colour variation was essentially continuous and the pattern of size variation essentially discontinuous, a high degree of concordance in geographical trends existed between the two sets of characters. Specimens representing extremes in size and colour occurred in Botswana and northern Transvaal (lowest cranial size, DOM and PUR values), and in the southern and eastern Cape

(highest values of cranial size, DOM and PUR). Specimens of intermediate size and colour occurred in Namibia. The zone of rapid change of DOM and PUR corresponds approximately (although it is wider) with craniometric transition zones separating the northern (Botswana, northern Transvaal) phenon from adjacent phena to the west (Namibia) and south (South Africa). However, populations in South Africa and in Namibia are not sharply differentiated in colour, as they are in size.

The association between zones of morphometric differentiation and zones of partial or complete isolation (i.e. potential barriers such as the lower Orange River and the Soutpansberg Mountains) between neighbouring populations of C. penicillata suggests that phenotypic divergence has a genetic basis. A similar correspondence between zones of morphometric differentiation, subspecies boundaries and zones of partial or complete isolation was described in the kangaroo rat Dipodomys merriami by Lidicker (1962). The absence of genetic (electrophoretic) correlates of phenotypic variation in C. penicillata, as determined from the present study, does not necessarily imply that morphological variation does not have a genetic basis, although such a correlation would have provided strong evidence for this.

Three hypotheses can be put forward to explain the

discordance between morphological (colour and size) and genetic (electrophoretic, karyotypic) patterns of geographic variation in Cynictis: 1) morphological variation is largely non-genetic, i.e. environmentally induced; 2) natural selection has resulted in genetic changes in adaptive phenotypic characters, but not in the neutral enzyme loci or karyotypic characters analysed in the present study; 3) the level of resolution in the genetic characters examined in the present study was insufficient to detect existing trends in neutral genetic characters.

The first hypothesis appears highly unlikely in Cynictis. It is well known that light, temperature and other environmental factors may cause colour changes in mammal study skins. However, the pattern and (uneven) rate of geographic variation in trend surface maps of colour variables cannot easily be explained by geographic patterns of variation in climatic variables such as temperature and total daily radiation (Chapter 3). Moreover, colour changes similar to those desribed in the yellow mongoose have been demonstrated to have a genetic basis by Hershkovitz (1968) and Sumner (1931).

The direct influence of diet on skull size (but not on skull shape) has been demonstrated in herbivorous pocket gophers occurring in crop fields and in natural habitat (Smith and Patton, 1988). However, in the carnivorous yellow mongoose,

the diet is varied and does not show any geographic trends that would explain size variation in the species.

According to the second hypothesis mentioned above, natural selection may have acted on adaptive (colour, size) but not on neutral (allozymes, karyotypic) characters. The third hypothesis assumes that genetic changes have occurred in both adaptive and selectively neutral characters, but that the latter have not been measured by the present sample of enzyme loci. The second hypothesis is more consistent with a parapatric than an allopatric model of differentiation, since the parapatric model explains differentiation in positively selected, but not in neutral characters (Endler, 1977). The third hypothesis is consistent with an allopatric model since, according to the molecular clock hypothesis (Thorpe, 1982), neutral alleles tend to accumulate mutations with time in separately evolving, isolated lineages, and should therefore mirror genetic differences in adaptive characters resulting from natural selection acting in isolated populations.

In order to distinguish between the second and third hypotheses mentioned above, it would be necessary to conduct further allozyme studies involving a greater number of fast evolving enzyme loci, or alternatively to analyse variable mitochondrial DNA haplotypes. The discovery of neutral alleles which mimic the morphometric pattern of geographic

variation would provide strong circumstantial evidence for allopatric subspeciation (i.e. third hypothesis above)

Causal basis of geographic variation

Traditionally, observed geographical patterns of colour and size variation in animals have been explained in terms of ecological generalisations. Gloger's rule refers to the common trend towards increased melanism in regions of relatively high humidity. Bergmann's rule refers to a decrease in body size at lower altitudes and latitudes (i.e. higher temperatures). Allen's rule specifies that animals from colder climates have relatively shorter appendages than animals from warmer climates. In addition to these ecological factors, phylogenetic and biogeographical causes such as past patterns of range expansion and fragmentation in a species, and the existence of barriers to gene flow, may contribute towards observed geographic patterns of morphological variation.

Colour variation in Cynictis follows the predictions of Gloger's rule in that specimens from Namaqualand, much of which receives less than 100 mm rainfall, are conspicuously paler (i.e. higher BRT) than more easterly specimens from higher rainfall areas. Although the relationship between BRT and the climatic variables, relative humidity (RH) and average annual rainfall (AAR), was not statistically

significant, the trend surface maps for BRT reflected a longitudinal pattern of variation which resembled the climatic map for AAR over Southern Africa. Variation in DOM and PUR could not easily be explained. Although both variables were significantly correlated with mean annual temperature (MAT), the causal basis of this correlation is obscure. Since the zone of rapid change in DOM and PUR is correlated with the limits of Kalahari sands, it is likely that changes in DOM and PUR may be explained by vegetational or soil factors. One possible explanation is that the need for cryptic coloration may explain the occurrence of brighter, tawny-coloured specimens in open habitats. Specimens from more closed Kalahari thornveld habitats may rely more on vegetation cover for protection from avian predators, hence their duller, greyer coloration.

Hershkovitz (1968) provided a phylogenetic explanation for patterns of colour variation in marmosets and tamarins in South American rain forests. Colour races were found to be delimited by rivers, and colour changes were found to occur in a progressive, geographic and phylogenetic sequence involving a transition from a primitive agouti coloration (alternating orange and black pigment bands in guard hairs) to a saturated (either orange or black) coloration, followed by a gradual bleaching sequence (principle of metachromism). While an agouti coloration persisted throughout in the yellow mongoose, metachromic changes, such as the relative

amounts of black and orange pigments, and the degree of bleaching of orange pigments, explained the observed geographic pattern of colour variation. The grizzled-greyish coloration of northern specimens results from wider black bands in guard hairs, alternating with bleached yellow bands. This coloration is closely associated with the extent of Kalahari sands, and since the limits of Kalahari sands have contracted and expanded considerably during the Pleistocene, it is feasible that past climatic events may have resulted in the isolation of Kalahari populations of yellow mongooses, and the allopatric origin of genetic differences in pelage colour.

While both ecological and phylogenetic factors may be important in explaining colour variation in the yellow mongoose, the latter appear to be particularly important in explaining patterns of craniometric variation. However, Bergmann's rule applies generally in that the northern group (lower latitude; higher temperature) is smaller than the southern. Moreover, since there is a westerly trend of decreasing mean annual temperature in Namibia, the increase in size from Botswana to Namibia can also be explained by Bergmann's rule.

Thorpe (1984a,b) used a cladistic (distance Wagner) approach to reconstruct the historical pattern of range expansion in the grass snake in Europe. This approach discriminates

between ecological and phylogenetic causes of observed patterns of geographic variation. Where the pattern of geographic variation is determined by phylogeny, populations occupying that part of the range where the ancestoral population was postulated to occur can be predicted to reflect a greater degree of anagenic change than populations from more recently occupied areas. The approach of Thorpe was used to analyse cranial characters in 15 regional populations of Cynictis. Trees constructed using the ancestor-rooting method were consistent with a phylogenetic interpretation, in that the greatest degree of anagenic change occurred in the proposed ancestral (largest-sized) population from the eastern Cape. Little or no anagenic change, but a much higher degree of cladogenesis (splitting), occurred in more recent northern populations.

Independent causes relate to patterns of interpopulation and intrapopulation genetic variability. Interpopulation variation is summarised by means of genetic distances (Nei, 1978), as well as by Wright's (1965) F_{ST} statistic. Genetic distance between two populations is assumed to be a measure of the level of spatial gene flow and/or time since divergence (Thorpe, 1982). Wright's (1965) F_{ST} statistic measures the importance of gene flow in preventing populational differentiation due to genetic drift. It is usually determined by the breeding or population structure of a species. In the yellow mongoose genetic distances are

very low (0.000--0.105 for Nei's D_N). While these data suggest a high degree of gene flow between populations, the high value obtained for Wright's F_{ST} (0.585) results from high spatial heterogeneity in allele frequencies of polymorphic loci, and is indicative of low levels of gene flow. This apparent contradiction is explained by the high proportion of monomorphic loci surveyed in the present study (which leads to high genetic distances), which may be a sampling artifact (i.e. a bias in favour of conservative loci), or it may result from the possibility that the species is recently evolved, leaving insufficient time for accumulation of genetic mutations in more than a few loci.

In species in which gene flow plays a dominant role in moulding population genetical structure, one would expect a correlation between genetic and geographic distances indicative of an 'isolation by distance' model. The discordance between genetic and geographic distances is further evidence for restricted gene flow in the yellow mongoose. A possible explanation of restricted gene flow in the yellow mongoose is low vagility, a possibility that is supported by a current behavioral study of the species (Rasa, pers. comm.).

Intrapopulation genetic variability is measured by Nei's (1978) expected heterozygosity ($\bar{H}$). With the advent of electrophoresis in the last three decades, it was possible

to obtain estimates of heterozygosity in natural populations. Measured levels of heterozygosity turned out to be much higher than predicted by classical population genetical theory which held that neutral polymorphisms were generally unstable and therefore rapidly removed from the population by drift (Nei, 1988). Attempts to explain the maintenance of high levels of, and interspecies variation in, genetic heterozygosity in nature led to the neutralist-selectionist controversy. The neutral theory maintained that genetic variability could be explained as a function of effective population size and the mutation rate (Kimura, 1968; Nei, 1988). Selectionists, on the other hand, argued that environmental factors could adequately explain variation in genetic variability in nature (Nevo, 1978).

Most selectionists adhere to the niche-width variation hypothesis, which suggests that the amount of genetic variation may be regarded as an adaptive strategy for increasing population fitness in a spatio-temporally heterogeneous and uncertain environment. On the basis of this hypothesis, Selander and Kaufman (1973) suggested that larger animals such as vertebrates should be genetically less variable than smaller animals such as invertebrates. However, Wooten and Smith (1985) demonstrated an absence of empirical correlation between body size and heterozygosity in 138 mammal species. The mean heterozygosity obtained for the yellow mongoose, a relatively large mammal (compared to

rodents which are represented in the majority of electrophoretic studies), is very similar to the mean obtained by Wooten and Smith (0.034 compared to 0.039), and not somewhat lower as would have been expected from Selander and Kaufman's (1973) hypothesis. Size per se does not therefore explain the level of heterozygosity in the yellow mongoose. The heterozygosity data presented in this dissertation provides a baseline for comparison with data from other viverrid species. Once such a data set is available, it will be possible to test the neutralist hypothesis by searching for environmental or demographic correlates of interspecies variation in heterozygosity. Viverrids vary considerably in demographic (from highly social to completely solitary) and environmental (from arid-adapted to semi-aquatic) characteristics. Tests of the niche-width variation hypothesis, involving comparisons of narrow-niche, specialist species (eg. the water mongoose) and wide-niche, generalist species (eg. the slender mongoose), are also possible. Nevo (1978) has pointed out the necessity of conducting such tests in taxonomically homogeneous groups, rather than in broad groups such as vertebrates versus invertebrates. However, due to the statistical properties of genetic heterozygosity, great caution should be exercised in interpreting small differences in heterozygosity (Archie, 1985).

Pattern and mode of subspeciation

Four parapatric subspecies of C. penicillata were described on the basis of craniometrically-defined geographic groups, and the existence of continuous transition zones between these. According to Endler (1977), the prevalence of parapatric subspecies in nature is evidence for widespread occurrence of parapatric speciation. However, fragmentation and compression of a species' range due to past climatic and vegetational changes (allopatric speciation) may also account for the present parapatric distribution of subspecies and species (Mayr, 1982; Vrba, 1985a,b).

To the extent that craniometric transition zones represent a localised reduction in gene flow between neighbouring demes, the mode of subspeciation in Cynictis depends on the probable causes (i.e. extrinsic barriers to gene flow (allopatric) or selection gradients (parapatric)) of restrictions in gene flow. The Orange River, below its confluence with the Vaal, and the Soutpansberg Mountains in the northern Transvaal, both constitute effective physical barriers to gene flow, as evidenced from the non-overlap in discriminant scores of individuals occurring to the north and south of these barriers (Chapter 4). The upper reaches of the Vaal and Orange Rivers are not associated with craniometric transition zones, and probably do not constitute important barriers to gene flow.

Where transition zones between subspecies are not associated with potential barriers, they correspond closely with the ecotone marked by the limits of Kalahari sands. While this association might suggest a parapatric mode of differentiation along a selection gradient, an alternative allopatric explanation is possible. There is substantial evidence (Broadley, 1968; 1978; Cooke, 1962; Deacon and Lancaster, 1988) that Kalahari sands have expanded and contracted considerably during pluvial and interpluvial episodes during the Pleistocene. Additional evidence is provided by the occurrence of an isolated population of Cynictis on Kalahari sandveld in the northern Transvaal. Past climatic and vegetational changes during the Pleistocene may have resulted in fragmentation of the species range and isolation of Kalahari populations, which became differentiated in size and pelage coloration.

Overlap in discriminant scores between parapatric subspecies occûrs across transition zones associated with the limits of Kalahari sands, but not across transition zones associated with physical barriers. As a result the former are noticeably less sharp than the latter. The more gradual clines corresponding with Kalahari limits may be explained by intergradation following secondary contact of previously isolated populations (secondary transition zone), or they may be explained by parapatric differentiation along a selection gradient (primary transition zone).

The narrowness of the transition zone separating C. p. penicillata, C. p. bradfieldi and C. p. coombsii in the northern Cape (see Chapter 4) suggests either that some degree of reproductive isolation has occurred between previously isolated subspecies (speciation by reinforcement: Dobzhansky, 1937), or that strong selection gradients are acting to maintain stepped clines in cranial size. The theory of reinforcement supposes that, provided that sufficient genetic differences have accumulated in allopatry, secondary contact will result in the fixation of genetic differences due to the production of hybrids of reduced fitness (i.e. postzygotic isolation). In time, natural selection will favour the development of ethological and ecological (prezygotic) isolating mechanisms. If sufficient genetic divergence has not occurred during allopatry, secondary contact will result in the swamping by gene flow of phenotypic and genetic differences. According to Moore (1977), the existence of numerous, stable stepped clines in natures is evidence against the 'ephemeral zone hypothesis' (i.e. speciation by reinforcement). However, without knowing the stability of observed transition zones in the yellow mongoose, and without direct measurements of the degree of reproductive isolation within transition zones (eg. by analysing the frequency of genetic markers, such as a polymorphic allele specific to a certain subspecies, in transition zone populations in the northern Cape), it is not

possible to predict the mode of subspeciation, nor the fate (dedifferentation or speciation) of present yellow mongoose subspecies.

In conclusion, present and past (vegetational barriers associated with movements of Kalahari sands during Pleistocene pluvials and interpluvials) barriers can account for an allopatric mode of subspeciation in Cynictis. However, parapatric subspeciation cannot be discounted. A correlation between stepped clines and ecotones and / or (partial?) barriers, as found in Cynictis, is predicted by parapatric models (Endler, 1977). As mentioned earlier, the absence of neutral genetic (electrophoretic) differences between morphologically-based subspecies is more consistent with a parapatric than an allopatric model of subspeciation.

Validity of the subspecies category

The recognition of yellow mongooses subspecies satisfies the four criteria suggested by Lidicker (1962): 1) the presence of sharp, continuous zones of differentiation; 2) diversity of the two postulated adaptive peaks; 3) differences in the environments to which the adjacent populations are adapted; 4) geologic or paleontologic evidence of separate evolution (see above discussion on pattern and mode of subspeciation). A further criterion of subspecies, which distinguishes them from species, is the ability to interbreed. This can be

estimated indirectly from the degree of overlap in discriminant scores of individuals from different subspecies.

The subspecific criteria outlined above amount to what may be termed an 'evolutionary subspecies concept'. Adoption of an evolutionary subspecies concept leads to a phylogenetic subspecies classification, as opposed to the phenetic subspecies classification which resulted in the proliferation of subspecies throughout the early half of this century. A phylogenetic subspecies classification is more stable and conservative than a phenetic classification, as evidenced by the description of four subspecies in the present study, compared with 12 subspecies described by Roberts (1951). According to the evolutionary subspecies concept, the presence of character clines is not, in itself, antithetical to the recognition of subspecies, as was assumed by Lundholm (1955). In fact, in the yellow mongoose, stepped clines (transition zones) in colour and size provided strong evidence of reduced gene flow and separate evolution of different lineages.

Critics of the subspecies category have argued that the recognition of subspecies is a subjective exercise. The 90% joint non-overlap rule of Mayr (1969) is somewhat arbitrary, and may apply to some characters and not others. However, the application of modern multivariate methods, coupled with

the delimitation and analysis of transition zones, results in a much more objective recognition of subspecies, as was evidenced in the present study.

Multivariate analysis of cranial measurements, involving cluster analysis, principal components analysis and discriminant functions analysis, resulted in the definition of reasonably distinct, meaningful geographic groups of yellow mongooses. Univariate methods of analysis failed to produce the same meaningful geographic groups (see Chapter 4). Preliminary geographic groups decribed by multivariate analysis ('putative subspecies') were further tested by the delimitation and analysis of transition zones between groups, and by biogeographic, ecological and palaeoclimatic evidence for separate evolution in the different groups. The delimitation of transition zones is an objective process since it depends on relative, not absolute, amounts of differentiation between neighbouring populations. Such zones can easily be defined by a geographic plot of taxonomic distances between pairs of adjacent localities or pooled localities, as was found in the present study. Thus, multivariate analysis can be used to distinguish potential subspecies. The hypothesis that these groups are separately evolving evolutionary lineages which have not yet achieved reporoductive isolation can be tested by providing further evidence for reduced gene flow, intergradation and separate evolution of groups.

This study has attempted to demonstrate the evolutionary reality of the subspecies category in a continuously distributed species. Further, it is maintained that evolutionary subspecies can be objectively defined in nature, given sufficient data, by the following steps: 1) description of geographic groups by means of multivariate analysis of a representative sample of localities or homogeneous pooled localities (OTUs); 2) definition of transition zones between groups (subspecies boundaries) by means of geographic plots of phenotypic distances between adjacent pairs of localities or OTUs; 3) consideration of possible ecological, palaeoecoogical and biogeographical correlates of transition zones; 4) indirect analysis of intergradation across transition zones, by means of measuring overlap in discriminant scores of individuals; 5) analysis of the probable pattern of range expansion in the species, as inferred from distance Wagner analysis of regional groups (method of Thorpe, 1984a, b); 6) where possible, analysis of genetic (electrophoretic, karyotypic, mitochondrial DNA) correlates of morphometric variation; 7) where possible, use of genetic markers to measure the degree of reporoductive isolation in transition zone populations.

References

Archie, J. W. (1985). Statistical analysis of heterozygosity

data: independent sample comparisons. Evolution 39: 623--637.

Bohme, W. (1978). Das Kuhnelt'sche Prinzip der regionalen Stenozie und seine Bedeutung fur das Subspezies-Problem: ein theoretischer Ansatz. Zeitschrift fur zoologische Systematik und Evolutionsforschung 16: 256--266.

Broadley, D. G. (1968). A revision of the African genus Typhlosaurus Wiegmann (Sauria: Scincidae). Arnoldia (Rhodesia) 3: 1--20.

Broadley, D. G. (1978). A revision of the genus Platysaurus A. Smith (Sauria: Cordylidae). Occasional papers of the National Museums and Monuments of Rhodesia, Series B, 6: 129--185.

Cooke, H. B. S. (1962). The Pleistocene environment in Southern Africa. Hypothetical vegetation in Southern Africa during the Pleistocene. Annals of the Cape Provincial Museums 2: 11--15.

Deacon, J. & Lancaster, N. (1988). Late Quaternary palaeoenvironments of Southern Africa. Oxford: Clarendon Press.

Dobzhansky, T. (1937). Genetics and the origin of species. New York: Columbia University Press.

Endler, J. A. (1977). Geographic variation, speciation and clines. Princeton: Princeton University Press.

Hershkovitz, P. (1968). Metachromism or the principle of evolutionary change in mammalian tegumentary colours.

Evolution 22: 556--575.

Kimura, M. (1968). Evolutionary rate at the molecular level. Nature, London 217: 624--626.

Lidicker, W. Z. (1962). The nature of subspecies boundaries in a desert rodent and its implications for subspecies taxonomy. Systematic Zoology 11: 160--171.

Lundholm, B. G. (1955). A taxonomic study of Cynictis penicillata (G. Cuvier). Annals of the Transvaal Museum 22: 305--319.

Mayr, E. (1969). Principles of systematic zoology. New York: McGraw-Hill.

Mayr, E. (1982). Speciation and macroevolution. Evolution 36: 1119--1132.

Moore, W. S. (1977). An evaluation of narrow hybrid zones in vertebrates. The Quarterly Review of Biology 52: 263--277.

Nei, M. (1978). Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583--590.

Nei, M. (1988). Relative roles of mutation and selection in the maintenance of genetic variability. Phil. Trans. R. Soc. Lond. (B) 319:615--629.

Nevo, E. (1978). Genetic variation in natural populations: patterns and theory. Theoretical Population Biology 13: 121--177.

Roberts, A. (1951). The mammals of South Africa. Johannesburg: 'The mammals of South Africa' Book Fund.

Selander, R. K., & Kaufman, D. W. (1973). Genic variability and strategies of adaptation in animals. Proc. Nat. Acad. Sci. USA 70: 1875--1877.

Smith, M. F. & Patton, J. L. (1988). Subspecies of pocket gophers: causal bases for geographic differentiation in Thomomys bottae. Systematic Zoology 37: 163--178.

Sumner, F. B. (1930). Genetic and distributional studies of three subspecies of Peromyscus. Journal of Genetics 23: 275--376.

Thorpe, J. P. (1982). The molecular clock hypothesis: biochemical evolution, genetic differentiation and systematics. Annual Review of Ecology and Systematics 13: 139--168.

Thorpe, R. S. (1984a). Primary and secondary transition zones in speciation and population differentiation: a phylogenetic analysis of range expansion. Evolution 38: 233--243.

Thorpe, R. S. (1984b). Coding morphometric characters for constructing distance Wagner networks. Evolution 38: 244--255.

Vrba, E. S. (1985a). Environment and evolution: alternative causes of the temporal distribution of evolutionary events. South African Journal of Science 81: 229--236.

Vrba, E. S. (1985b).Introductory comments on species and speciation. In Species and speciation, ed. Vrba, E. S., pp. ix--xvii. Pretoria: Transvaal Museum Monograph No. 4.

Wooten, M. C. & Smith, M. H. (1985). Large mammals are genetically less variable. Evolution 39: 210--212.

Wright, S. (1965). The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution 19: 395--420.