CHAPTER 5

Sexual dimorphism and age variation in the social giant mole-rat, *Fukomys mechowii* (Rodentia: Bathyergidae) from Zambia, Central Africa: An analysis based on traditional cranial morphometric data

Belgian Journal of Zoology (under review)

Abstract

Due to difficulties in estimating absolute age in mammals, different methods for its estimation have been proposed, and among these, the degree of molar eruption and wear are considered to be at least one of the reliable indicators of relative age. Consequently, maxillary molar tooth-row eruption and wear were used to assign individuals of the giant mole-rat, *Fukomys mechowii* (Peters, 1881) (Rodentia: Bathyergidae) from two geographically proximal and ecologically similar localities in the Copper-belt Province of Zambia, Central Africa to nine relative age classes. These were in turn used to assess the nature and extent of sexual dimorphism and age variation in this little-studied social mole-rat based on cranial morphometric data with reference to body mass, and a series of both univariate and multivariate statistical analyses. Both univariate and multivariate analyses showed morphological differences between individuals of age classes 1–3 and those of age classes 5–9, while individuals of age class 4 were intermediate between these two age class groupings, suggesting that this age class lies at a point on a hypothetical growth curve where it begins to stabilize. The analysis of the nature and extent of sexual dimorphism revealed its absence in the younger individuals of age classes 1–4 and its presence in older age classes 5–9, and these results are supported by the data on body mass. These results may allow an insight into our understanding of the population and social structures, and reproductive strategies in this little-studied giant mole-rat.

Introduction

Numerous studies have been undertaken to assess the nature and extent of non-geographic variation in rodents, particularly at the level of sexual dimorphism and age variation. These include studies on rats [(*Niviventer cominga)* – Yu & Lin, 1999]; *Dasymys* – Mullin *et al.,* 2004; mole-rats [(*Cryptomys hottentotus*, *F. damarensis*, *F. mechowii*, and *Heterocephalus glaber* Begall & Burda, 1998]; Bennett *et al*., 1990; Davies and Jarvis, 1986; Hagen, 1985; Scharff *et al.,* 1999; mice [(*Peromyscus maniculatus)* – Schulte-Hostedde *et al.,* 2001]; tuco-tucos [(*Ctenomys talarum* – Zenuto *et al.,* 1999]; the highveld mole-rat (common name) [(*Cryptomys hottentotus pretoriae*)– Janse van Rensburg *et al*., 2004] and Cape dune mole-rat [(*Bathyergus suillus*)– Hart *et al*., 2007].

However, due to difficulties in estimating absolute age in mammals, various methods for its estimation have been proposed Hart *et al*., (2007). While body mass has been used in the past for example, in subterranean mole-rats (Bennett, 1988; Bennett *et al.,* 1990; Janse van Rensburg *et al.,* 2004), it is considered to be affected by soil type, the availability and quality of food, and in social species, by the social rank of an individual [Bennett 1988, 1989]; [Jacobs *et al*., 1991; Janse van Rensburg *et al*., 2004; Jarvis, 1979; Morris, 1972; Wallace & Bennett, 1998]. The estimation of relative age based on molar eruption and wear is considered to be at least more reliable, particularly if a sample emanates from a homogenous sample in an attempt to reduce the potential influence of geographic variation (Chaplin & White, 1969; Chimimba & Dippenaar, 1994; Dippenaar & Rautenbach, 1986; Janse van Rensburg *et al.,* 2004; Taylor *et al.,* 1985; Hart *et al.,* 2007).

Consequently, in the present study, the degree of molar eruption and wear is used to assess the nature and extent of sexual dimorphism and age variation in the giant mole-rat, *Fukomys mechowii* Peters, (1881) from geographically proximal and ecologically similar localities in the Copper-belt Province of Zambia, Central Africa based on traditional cranial morphometric data and a range of both univariate and multivariate analyses. Nevertheless, body mass which has previously been used to assess the nature and extent of sexual dimorphism and age variation in other social species such as the highveld mole–rat, [(*Cryptomys hottentotus pretoriae*) Janse van Rensburg *et al*., 2004] was also used in the present study for comparative purposes.

However, of fundamental importance in the assessment of non-geographic variation in general is how the derived data are statistically analyzed during its evaluation. Although previous assessments of non-geographic variation largely involved the use of a range of univariate analyses (reviewed in Chimimba & Dippenaar, 1994), the partitioning of the percent contribution of the sum of squares (%*SSQ*) of each source of variation to the total *SSQ* which can be computed directly from a two-way analysis of variance table ANOVA; Zar, (1996) is considered to be the most appropriate method (Leamy, 1983; Hart *et al.,* 2007). However, the use of this univariate %*SSQ* approach alone in the assessment of non-geographic variation has limitations because of the number of variables that must be statistically significant before unequivocally deciding on the presence of overall statistically significant non-geographic variation Willig *et al.,* (1986). Instead, multivariate analysis of variance (MANOVA; Zar, 1996) which uses rather than ignores correlations among variables has been recommended as the most appropriate method for evaluating overall statistical differences in the analysis of non-geographic Willig *et al.,* (1986).

Consequently, the present study is based on samples from two geographically proximal and ecologically similar localities, and uses ANOVA, %*SSQ*, and a series of multivariate analyses of traditional cranial morphometric data in order to assess the nature and extent of sexual dimorphism and age variation in the giant mole-rat from Zambia. The giant mole-rat is a social subterranean hystricomorph rodent that is restricted to the sub-tropical and tropical Miombo woodlands and grasslands of Central Africa (Bennett & Aguilar, 1995; Sichilima *et al.,* 2008). Given that most studies on mole-rats in Africa have been undertaken in the southern parts of the continent, our study of which part of the results are interpreted with reference to the reproductive biology of the species, forms part of a broader investigation of this little-studied species of mole-rat from the central part of Africa.

Exploratory analyses of the derived craniometric measurements revealed the data to be normally distributed. The nature and extent of sexual dimorphism and age variation were first simultaneously univariately assessed by a two-way ANOVA (Zar, 1996) of samples of age classes 1–9 after it was established that tests for normality and homogeneity of variances satisfied the assumptions of ANOVA tests (Zar, 1996). Where statistically significant age differences were detected by the ANOVA, non-significant subsets ($P > 0.05$) were identified by the post hoc Student-Newman-Keuls test SNK; (Gabriel & Sokal, 1969; Sokal & Rohlf, 1981) of ranked means. The derived two-way ANOVA table was in turn used to estimate the %*SSQ* of the four potential sources of variation in the data, namely, sex, age, sex age interaction, and error (= residual) by dividing the *SSQ* associated with each source of variation by the total SSQ.

The nature and extent of sexual dimorphism within *F. mechowii* was also multivariately assessed by an unweighted pair-group method using arithmetic averages (UPGMA) cluster analysis and principal component analysis (PCA) of standardized variables (Sneath & Sokal, 1973). UPGMA cluster analysis was based on Euclidean distances and correlation coefficients among groups, while the PCA was based on correlation coefficients among variables (Sneath & Sokal, 1973). Additional analyses included the computation of standard descriptive statistics. Since exploratory analyses showed that data on body mass were not normally distributed, body mass data within sexes and age classes were evaluated using the non-parametric Mann-Whitney *U* test (Zar, 1996). All statistical analyses in the present study were based on all the 22 cranial measurements recorded, and were undertaken using the statistical programme (STATISTICA, version 8.0 StatSoft Inc. 2008).

Materials and methods

Two hundred and sixty five (265) animals out of the total of three hundred and seventeen (317) that were captured in the field had their skulls undamaged hence 22 measurements of each skull were taken for the assessment of the sexual dimorphism in the giant mole-rat. Further more the right molar row of each of the 265 skulls was thoroughly cleaned and micrographs were taken on them for the assessment of age variation as detailed in Chapter 2.

Results

The ANOVA results showed that all 22 measurements were highly statistically significant ($P < 0.001$) with reference to age, while 19 of the 22 measurements were all highly statistically significant due ($P < 0.001$) to sexual dimorphism and one measurement (AFL), was statistically significant at $P < 0.01$ (Table 5.1). Fourteen out of the 22 measurements showed statistically significant interaction between sexual dimorphism and age at either $P < 0.001$ or $P < 0.01$) (Table 5.1), while one measurement (AFA), was statistically significant at $P < 0.05$. Although there was unequivocal statistically significant sexual dimorphism, the largest *F*-values were mainly associated with age variation rather than either sexual dimorphism or the interaction between these two components of variation (Table 5.1).

The significant contribution of age to the total variation is also evident from the generally high %*SSQ* values for age (%*SSQ*: $\bar{x}$ = 54.62%; range = 28.44–81.25%) than that for sex (%*SSQ*: $\bar{x}$ = 4.40; range = 0.15–3.69%) and the interaction (%*SSQ*: $\bar{x}$ = 2.97; range 1.39–3.83%) between age variation and sexual dimorphism (Table 5.1). Although all the 22 measurements were statistically significant at either $P < 0.001$ or $P < 0.01$ and also with higher %*SSQ* values, the %*SSQ* values for the error component (= residual) for all 22 measurements and their associated means were also relatively high (%SSQ: $\bar{x}$ = 40.01; range = 13.54–64.98%) (Table 5.1) particularly so with reference to the %*SSQ* values for sexual dimorphism and the interaction between sexual dimorphism and age variation. This suggests that apart from the presence of sexual dimorphism and age variation, there are other factors that may be influencing the nature and extent of non-geographic variation within the giant mole-rat.

Table 5.1. *F*-values and percent *SSQ* of each source of variation derived from a two-way analysis of variance (ANOVA) of nine age classes (1–9) based on the degree of tooth eruption and wear in male and female giant mole-rats, *Fukomys mechowii*, from Kakalo and Mushishima farm blocks in Chingola, Copperbelt Province of Zambia. Statistical significance: * = $P < 0.05$; ** = $P<0.01$; *** = $P < 0.001$. Measurements are defined and illustrated in Fig. 2.2.

Measurement	*F*-Value			%*SSQ*			
	Age A)	Sex (S)	A x S	Age (A)	Sex (S)	A x S	Error
GLS	52.74***	24.53***	2.12**	59.39	3.45	2.39	34.77
ITC	62.67***	29.37***	2.34**	62.95	3.69	2.35	31.01
BCW	28.60***	17.96***	1.69	45.11	3.54	2.66	48.69
ZMB	46.47***	21.67***	2.64**	56.19	3.28	3.19	37.34
ZYW	52.48***	18.01***	3.13***	59.14	2.54	3.53	34.79
IOB	13.68***	11.68***	1.51	28.78	3.07	3.17	64.98
WR	44.50***	22.04***	2.92***	54.93	3.40	3.60	38.07
NA	46.81***	15.66***	2.72**	56.83	2.38	3.31	37.48
UTR	185.45***	40.18***	6.90***	81.25	2.20	3.01	13.54
PAC	13.65***	12.72***	1.88	28.44	3.31	3.92	64.33
NPP	64.49***	16.87***	3.04***	64.16	2.09	3.03	30.72
GHS	39.81***	16.76***	1.12	53.31	2.81	2.53	41.35
MLT	103.32***	29.29***	4.91***	72.37	2.56	3.44	21.63
MDL	51.03***	16.08***	2.40**	59.12	2.33	2.78	35.77
MTR	167.87***	30.72***	6.26***	80.38	1.84	3.00	14.78
AFL	23.11***	7.20**	0.77	41.52	1.62	1.39	55.47
MAF	24.33***	12.38***	1.62	41.67	2.65	2.79	52.89
AFA	28.35***	13.39***	1.96*	45.10	2.66	3.12	49.12
MRH	46.64***	9.09***	2.03**	57.81	1.40	2.53	38.26
UJI	33.45***	2.64	2.46**	49.84	0.49	3.68	45.99
LJI	28.13***	0.71	1.29	46.58	0.15	2.15	51.12
WI	45.99***	8.85***	3.10**	56.73	1.36	3.83	38.08
Mean				54.62	4.40	2.97	40.01

The results of the *post hoc* SNK tests that were undertaken in order to identify statistically non-significant subsets ($P > 0.05$) of age class groupings of the 22 measurements revealed three contrasting patterns of ranked means (Table 5.2). The first and major and major pattern which involved 11 of the 22 measurements (BCW, ZMB, IOB, WR, PAC, GHS, MTR, AFA, MRH, UJI and LJI) showed an orderly increase in size with increasing age (Table 5.2). This pattern is also evident in standard descriptive statistics (Table 5.3) where there is a direct relationship between measurement magnitude and age. The second trend in the SNK tests which involved eight of the 22 measurements (ZYW, NA, UTR, NPP, MDL, AFL, MAF and WI) grouped individuals of the younger age classes 1–4, and those of the older age classes 5–9 into two different non-overlapping non-significant subsets (Table 5.2). The third pattern that involved three measurements only (GLS, ITC and MLT) showed statistically significant differences between all the nine age classes of the giant mole-rat examined (Table 5.2).

Table 5.2. *Post hoc* Student-Newman-Keuls (SNK) tests of tooth-wear classes (AC) 1–9 of the giant mole-rat, *Fukomys mechowii* from Kakalo and Mushishima farm blocks, Chingola, Copperbelt Province of Zambia. Non-significant subsets (*P* > 0.05) are indicated by vertical lines, while NS = no significant difference; AS = all means significantly different. Measurements are defined and illustrated in Fig. 2.2.

GLS	AC	*N*	SD	Means	
	I	(18)	3.17	31.60	
	II	(22)	3.00	36.71	
	III	(26)	3.77	39.35	
	IV	(21)	5.25	41.53	
	V	(41)	6.80	44.95	AS
	VII	(15)	5.55	47.00	
	VI	(28)	4.44	47.31	
	VIII	(33)	5.00	49.60	
	IX	(61)	5.43	53.40	

ITC	AC	*N*	SD	Means	
	I	(18)	2.81	30.00	
	II	(22)	3.21	34.92	
	III	(26)	3.91	37.39	
	IV	(21)	5.25	39.57	
	V	(41)	4.25	43.80	AS
	VII	(15)	5.58	44.86	
	VI	(28)	5.09	45.21	
	VIII	(33)	4.77	47.63	
	XI	(61)	5.39	51.41	

BCW	AC	*N*	SD	Means
	I	(18)	1.27	15.08
	II	(22)	0.87	16.33
	III	(26)	1.88	16.51
	IV	(21)	1.11	17.17
	V	(41)	1.21	18.12
	VII	(15)	1.23	18.24
	VI	(28)	1.46	18.30
	VIII	(33)	1.11	18.53
	IX	(61)	1.16	19.37

ZMB	AC	*N*	SD	Means
	I	(18)	1.74	17.52
	II	(22)	1.36	19.01
	III	(26)	1.15	20.07
	IV	(21)	2.00	20.79
	V	(41)	2.07	22.41
	VI	(28)	2.33	22.75
	VII	(15)	2.61	23.44
	VIII	(33)	2.27	23.95
	IX	(61)	2.27	25.70

ZYW	AC	*N*	SD	Means
	I	(18)	3.07	21.88
	II	(22)	3.35	26.28
	III	(26)	2.92	26.48
	IV	(21)	4.22	28.24
	V	(41)	3.91	32.45
	VII	(15)	5.04	33.66
	VI	(28)	4.75	33.68
	VIII	(33)	4.65	36.10
	IX	(61)	5.43	39.66

IOB	AC	*N*	SD	Means
	I	(18)	0.70	9.34
	IX	(61)	0.72	9.45
	III	(26)	0.41	9.75
	II	(22)	0.77	9.81
	IV-	(21)	0.48	9.85
	V	(41)	0.99	10.33
	VII	(15)	0.70	10.47
	VI	(28)	0.97	10.58
	VIII	(33)	0.76	10.59

WR	AC	*N*	SD	Means
	I	(18)	0.66	6.57
	II	(22)	0.96	8.15
	III	(26)	0.87	8.52
	IV	(21)	1.16	8.91
	V	(41)	1.19	8.95
	VI	(15)	1.75	10.66
	VII	(28)	1.96	10.69
	VIII	(33)	1.61	11.36
	IX	(61)	2.63	12.61

NA	AC	*N*	SD	Means
	I	(18)	0.96	4.82
	II	(22)	1.00	6.50
	III	(26)	0.86	6.67
	IV	(21)	1.22	7.16
	V	(41)	1.21	8.31
	VII	(15)	1.53	8.56
	VI	(28)	1.27	8.66
	VIII	(33)	1.43	9.23
	IX	(61)	1.82	10.41

UTR	AC	*N*	SD	Means
	I	(18)	0.72	4.57
	II	(22)	0.39	6.31
	III	(26)	0.62	6.81
	IV	(21)	0.62	7.44
	V	(41)	0.72	8.30
	VII	(15)	0.78	8.54
	VI	(28)	0.66	8.83
	VIII	(33)	0.64	9.24
	IX	(61)	0.72	9.45

PAC	AC	*N*	SD	Means
	I	(18)	0.32	3.00
	III	(26)	0.36	3.49
	II	(22)	0.45	3.50
	IV	(21)	0.65	3.58
	VII	(15)	0.69	3.84
	V	(41)	0.49	3.88
	VI	(28)	0.50	3.96
	IX	(61)	0.56	4.33
	VIII	(33)	1.08	4.36

NPP	AC	*N*	SD	Means
	I	(18)	2.99	28.05
	II	(22)	2.56	33.45
	III	(26)	2.56	34.95
	IV	(21)	3.31	37.37
	V	(41)	4.93	41.70
	VII	(15)	5.11	41.78
	VI	(28)	5.14	43.16
	VIII	(33)	4.36	45.08
	IX	(61)	5.27	48.44

GHS	AC	*N*	SD	Means
	I	(18)	1.05	13.51
	II	(22)	1.26	15.59
	III	(26)	1.30	16.09
	IV	(21)	1.41	16.61
	V	(41)	1.53	18.00
	VI	(28)	1.78	18.39
	VII	(15)	2.04	18.40
	VIII	(33)	1.87	19.06
	IX	(61)	2.65	20.70

MLT	AC	*N*	SD	Means	
	I	(18)	2.59	31.78	
	II	(22)	2.30	33.75	
	III	(26)	2.25	34.56	
	IV	(21)	2.75	35.93	
	V	(41)	3.10	40.34	AS
	VI	(28)	5.66	43.04	
	VII	(15)	5.49	45.01	
	VIII	(33)	5.07	47.77	
	IX	(61)	6.05	52.57	

MDL	AC	*N*	SD	Means
	I	(18)	3.00	21.57
	II	(22)	4.31	28.10
	III	(26)	4.35	28.75
	IV	(21)	3.10	29.31
	V	(41)	4.91	35.07
	VII	(15)	4.53	35.10
	VI	(28)	4.88	35.97
	VIII	(33)	5.67	40.55
	IX	(61)	5.74	41.27

MTR	AC	*N*	SD	Means
	I	(18)	0.48	4.52
	II	(22)	0.79	6.63
	III	(26)	0.57	6.71
	IV	(21)	0.65	7.36
	V	(41)	0.68	8.21
	VII	(15)	0.79	8.62
	VI	(28)	0.69	8.90
	VIII	(33)	0.61	9.22
	IX	(61)	0.74	9.36

AFL	AC	*N*	SD	Means
	I	(18)	0.60	4.81
	III	(26)	0.95	6.26
	II	(22)	1.13	6.27
	IV	(21)	1.42	6.55
	VII	(15)	1.30	7.47
	V	(41)	1.41	7.85
	VI	(28)	1.55	7.89
	VIII	(33)	1.67	9.00
	IX	(61)	2.55	9.44

MAF	AC	*N*	SD	Means
	I	(18)	1.09	7.26
	II	(22)	1.54	9.89
	IV	(21)	1.82	10.19
	III	(21)	3.15	10.39
	VII	(15)	1.75	11.56
	V	(41)	1.68	11.61
	VI	(28)	1.70	11.65
	VIII	(33)	2.67	13.04
	IX	(61)	1.72	13.71

AFA	AC	*N*	SD	Means
	I	(18)	1.81	9.84
	II	(22)	2.03	11.89
	IV	(21)	2.45	12.53
	III	(26)	2.55	12.54
	V	(41)	1.52	14.10
	VII	(15)	1.95	14.16
	VI	(28)	2.56	14.51
	VIII	(33)	2.50	15.75
	IX	(61)	2.71	17.28

MRH	AC	*N*	SD	Means
	I	(18)	0.88	5.76
	IV	(21)	1.27	7.93
	III	(26)	1.08	8.10
	II	(22)	1.40	8.27
	V	(41)	1.46	8.91
	VII	(15)	1.98	9.52
	VI	(28)	1.76	10.00
	VIII	(33)	2.38	10.88
	IX	(61)	2.03	11.52

UJI	AC	*N*	SD	Means
	I	(18)	0.64	3.87
	III	(26)	0.69	4.65
	II	(22)	0.44	4.66
	IV	(21)	0.60	4.97
	VI	(28)	0.74	5.42
	VII	(15)	O.85	5.56
	V	(41)	O.80	5.58
	VIII	(33)	0.88	6.41
	IX	(61)	1.04	6.54

LJI	AC	*N*	SD	Means
	I	(18)	0.88	5.76
	IV	(21)	1.27	7.93
	III	(26)	1.08	8.10
	II	(22)	1.40	8.27
	V	(41)	1.46	8.91
	VII	(15)	1.98	9.52
	VI	(28)	1.76	10.00
	VIII	(33)	2.38	10.88
	IX	(61)	2.03	11.52

WI	AC	*N*	SD	Means
	I	(18)	0.41	1.51
	II	(22)	0.45	2.29
	III	(26)	0.51	2.55
	IV	(21)	0.55	2.62
	V	(41)	0.61	3.05
	VII	(15)	0.56	3.22
	VI	(28)	0.53	3.28
	VIII	(33)	0.57	3.48
	IX	(61)	0.65	3.83

Table 5.3. Standard descriptive statistics of 22 [craniometric] measurements of male and female giant mole-rat, *Fukomys mechowii* from Kakalo and Mushishima farm blocks in Chingola, Copperbelt Province of Zambia. $\bar{x}$ = arithmetic mean; *SD* = standard deviation; *2SE* = two standard errors; *n* = sample size. Measurements are defined and illustrated in Fig. 2.2.

Sex	Tooth wear class (*n*)	Measurement										
			GLS	ITC	BCW	ZMB	ZYW	IOB	WR	NA	UTR	PAC	NPP
♂	I (7)	$\bar{x}$	42.27	29.69	16.33	17.69	20.57	9.25	6.59	4.89	4.70	3.13	27.58
		SD	6.42	3.19	1.10	1.63	1.81	0.34	0.76	1.10	0.82	0.27	3.12
		2SE	1.85	1.20	0.42	0.61	0.68	0.13	0.29	0.40	0.31	0.10	1.18
	II (5)	$\bar{x}$	47.96	35.80	16.74	19..97	26.11	9.90	8.06	6.41	6.35	3.36	33.60
		SD	5.54	3.73	0.66	1.25	2.66	0.61	0.81	0.87	0.15	0.28	3.13
		2SE	1.75	1.67	0.29	0.56	1.19	0.27	0.36	0.39	0.07	0.12	1.40
	III (7)	$\bar{x}$	48.67	40.54	17.42	20.87	27.35	9.80	8.44	6.59	6.71	3.56	34.73
		SD	4.88	5.53	0.90	1.41	2.11	0.31	0.41	0.51	0.36	0.29	2.67
		2SE	1.30	2.09	0.34	0.53	0.80	0.12	0.15	0.19	0.14	0.11	1.00
	IV (12)	$\bar{x}$	51.58	40.33	17.23	20.78	28.71	9.93	9.17	7.41	7.37	3.53	37.77
		SD	6.04	6.52	1.32	2.40	5.20	0.51	1.45	1.36	0.57	0.73	4.11
		2SE	2.47	1.88	0.38	0.69	1.50	0.15	0.42	0.39	0.16	0.21	1.19
	V (10)	$\bar{x}$	50.41	46.96	18.03	22.64	35.23	10.69	10.62	8.94	8.37	4.06	43.85
		SD	4.98	4.47	1.03	2.12	3.81	0.59	1.37	1.26	0.48	0.59	4.14
		2SE	1.17	1.41	0.33	0.67	1.20	0.19	0.43	0.40	0.15	0.19	1.31
	VI (14)	$\bar{x}$	56.36	46.73	19.09	23.58	35.20	11.08	11.37	9.07	9.39	4.16	45.05
		SD	4.08	5.40	1.50	2.80	5.03	0.99	2.03	1.36	0.30	0.48	5.57
		2SE	0.69	1.44	0.40	0.75	1.34	0.27	0.54	0.36	0.08	0.13	1.49
	VII (6)	$\bar{x}$	31.60	49.31	19.12	25.54	37.74	11.03	11.84	9.66	9.29	4.37	46.19
		SD	3.17	5.94	1.16	2.44	5.42	0.44	2.07	1.81	0.51	0.73	4.69
		2SE	0.75	2.43	0.47	0.99	2.21	0.18	0.85	0.74	0.21	0.30	1.92
	VIII(18	$\bar{x}$	36.71	48.25	18.64	24.18	37.05	10.69	11.84	9.44	9.73	4.66	45.57
		SD	2.99	4.86	1.25	2.31	4.80	0.82	1.68	1.50	0.15	1.34	4.29
		2SE	0.64	1.14	0.29	0.54	1.13	0.19	0.40	0.35	0.03	0.32	1.01
	IX (35)	$\bar{x}$	39.35	54.19	19.83	26.88	42.32	11.63	13.58	11.26	9.87	4.61	50.97
		SD	3.77	4.40	1.05	1.86	4.52	1.20	1.72	1.48	0.52	0.56	4.36
		2SE	0.74	0.74	0.18	0.31	0.76	0.20	0.29	0.25	0.08	0.09	0.74

Sex	Tooth wear class (*n*)		Measurement										
			GHS	MLT	MDL	MTR	AFL	MAF	AFA	MRH	UJI	LJI	WI
♂	I (7)	x̄	13.32	31.38	20.07	4.63	4.69	6.94	9.18	10.50	5.16	3.52	1.29
		SD	1.18	3.30	1.91	0.65	0.77	1.01	0.59	0.87	0.57	0.35	0.33
		2SE	0.45	1.25	0.72	0.25	0.29	0.38	0.22	0.33	0.21	0.13	0.12
	II (5)	x̄	15.51	33.11	28.32	6.56	6.48	10.21	12.60	15.11	8.13	4.81	2.16
		SD	0.92	2.86	1.62	0.49	0.21	1.01	1.23	1.57	1.48	0.28	0.34
		2SE	0.41	1.28	0.72	0.22	0.09	0.45	0.55	0.70	0.66	0.13	0.15
	III (7)	x̄	16.81	35.36	29.98	6.58	6.51	12.46	13.22	15.56	8.32	4.71	2.46
		SD	1.80	2.39	3.70	0.24	0.62	5.41	2.34	2.46	0.97	0.78	0.27
		2SE	0.68	0.90	1.40	0.09	0.24	2.05	0.88	0.93	0.37	0.30	0.10
	IV (12)	x̄	16.80	36.30	30.19	7.31	6.85	10.15	12.72	15.95	7.76	4.71	2.74
		SD	1.78	2.94	3.03	0.59	1.71	2.08	3.14	3.28	1.13	0.50	0.68
		2SE	0.51	0.84	0.87	0.17	0.49	0.60	0.90	0.94	0.32	0.14	0.19
	V (10)	x̄	18.87	41.83	38.04	8.26	8.76	12.57	14.73	19.87	9.02	6.15	3.45
		SD	1.42	2.06	5.17	0.42	1.99	2.36	1.83	2.69	1.07	0.68	0.73
		2SE	0.45	0.65	1.64	0.13	0.63	0.75	0.58	0.85	0.34	0.21	0.23
	VI (14)	x̄	19.21	45.08	36.92	9.45	8.17	11.85	15.20	18.17	10.6	5.44	3.38
		SD	1.99	4.49	5.04	0.29	1.17	1.68	2.07	3.82	1.8	0.78	0.59
		2SE	0.53	1.20	1.35	0.08	0.31	0.45	0.55	1.02	0.5	0.21	0.16
	VII (6)	x̄	20.03	50.14	38.36	9.36	8.48	12.85	15.54	21.07	9.8	6.02	3.63
		SD	2.28	5.18	4.23	0.52	1.59	1.73	2.33	2.90	2.0	1.08	0.57
		2SE	0.93	2.12	1.73	0.21	0.65	0.71	0.95	1.18	0.8	0.44	0.23
	VIII(18	x̄	19.28	49.42	42.25	9.66	8.97	13.33	16.41	21.05	10.8	6.58	3.60
		SD	1.96	5.06	5.99	0.19	1.89	3.34	2.52	3.86	2.6	0.84	0.60
		2SE	0.46	1.19	1.41	0.04	0.45	0.79	0.60	0.91	0.6	0.20	0.14
	IX (35	x̄	21.70	55.80	44.07	9.77	9.84	14.37	18.52	24.70	12.0	6.79	4.13
		SD	2.80	4.96	4.75	0.54	1.57	1.42	2.58	2.82	2.1	1.14	0.53
		2SE	0.47	0.84	0.80	0.09	0.27	0.24	0.44	0.48	0.3	0.19	0.09

Sex	Tooth wear class (n		Measurement										
			GLS	ITC	BCW	ZMB	ZYW	IOB	WR	NA	UTR	PAC	NPP
♀	I (11)	$\bar{x}$	40.53	30.13	14.93	17.40	27.71	9.39	6.55	4.78	4.49	2.99	28.35
		SD	3.22	2.69	1.40	1.87	3.48	0.88	0.62	0.92	0.68	0.34	3.02
		2SE	1.07	0.81	0.42	0.57	1.05	0.26	0.19	0.27	0.20	0.10	0.91
	II (17)	$\bar{x}$	43.98	34.66	16.20	18.73	26.33	9.78	8.17	6.53	6.30	3.54	33.40
		SD	6.96	3.13	0.90	1.28	3.60	0.83	1.02	1.06	0.44	0.49	2.06
		2SE	1.25	0.76	0.22	0.31	0.88	0.20	0.25	0.26	0.10	0.12	0.50
	III (19)	$\bar{x}$	45.96	36.24	16.18	19.77	26.15	9.73	8.56	6.71	6.84	3.46	35.03
		SD	3.61	2.40	2.05	0.91	3.16	0.46	0.99	0.96	0.69	0.38	2.16
		2SE	0.97	0.55	0.47	0.21	0.72	0.11	0.23	0.22	0.16	0.08	0.50
	IV (9)	$\bar{x}$	43.93	38.54	17.11	20.82	27.61	9.74	8.58	6.83	7.53	3.65	36.84
		SD	2.17	2.89	0.83	1.44	2.57	0.43	0..52	0.98	0.72	0.57	1.91
		2SE	0.72	0.96	0.28	0.48	0.85	0.14	0.17	0.32	0.24	0.19	0.64
	V (31)	$\bar{x}$	48.63	42.78	18.15	22.33	31.55	10.21	9.73	8.11	8.28	3.82	40.99
		SD	4.99	3.70	1.29	2.09	3.55	1.06	1.06	1.14	0.79	0.45	5.02
		2SE	1.29	0.66	0.23	0.38	0.64	0.19	0.19	0.21	0.14	0.08	0.90
	VI (14)	$\bar{x}$	49.41	43.68	17.51	21.93	32.15	10.09	9.94	8.25	8.27	3.76	41.27
		SD	4.39	4.43	0.92	1.40	4.06	0.67	1.05	1.07	0.38	0.46	4.04
		2SE	0.86	1.16	0.24	0.37	1.08	0.18	0.28	0.29	0.10	0.12	1.08
	VII (9)	$\bar{x}$	31.09	41.90	17.65	22.04	30.93	10.10	9.31	7.83	8.04	3.49	38.84
		SD.	3.37	2.78	0.91	1.65	2.33	0.60	0.61	0.74	0.45	0.40	2.76
		2SE	1.27	0.93	0.30	0.45	0.78	0.20	0.21	0.25	0.15	0.13	0.92
	VIII(15	$\bar{x}$	38.09	46.88	18.40	23.68	34.97	10.47	10.78	0.98	8.65	4.00	44.38
		SD	2.88	4.71	0.93	2.27	4.34	0.68	1.36	1.35	0.49	0.47	4.50
		2SE	1.89	1.22	0.24	0.59	1.12	0.18	0.35	0.35	0.13	0.12	1.16
	IX (26	$\bar{x}$	42.11	47.66	18.76	24.11	36.07	10.76	11.31	9.26	8.88	4.07	45.03
		SD	5.94	4.25	1.02	1.76	4.45	0.96	2.19	1.60	0.55	0.42	4.45
		2SE	2.24	0.83	0.20	0.34	0.87	0.19	0.43	0.31	0.11	0.08	0.87

Sex	Tooth wear class (*n*)	Measurement											
			GHS	MLT	MDL	MTR	AFL	MAF	AFA	MRH	UJI	LJI	WI
♀	I (11)	x̄	13.62	32.03	22.53	4.45	4.88	7.46	10.26	11.19	4.10	6.14	1.65
		SD	1.00	2.20	3.23	0.36	0.48	1.13	2.20	1.44	0.70	0.84	0.42
		2SE	0.30	0.65	0.97	0.10	0.15	0.34	0.66	0.43	0.21	0.25	0.13
	II (17)	x̄	15.61	33.94	28.04	6.66	6.21	9.80	11.69	14.75	4.61	8.31	2.33
		SD	1.37	2.17	4.75	0.87	1.29	1.68	2.20	2.91	0.47	1.42	0.47
		2SE	0.33	0.53	1.15	0.21	0.31	0.41	0.53	0.71	0.11	0.35	0.12
	III (19)	x̄	15.82	34.27	28.30	6.76	6.16	9.62	12.29	14.17	4.63	8.02	2.58
		SD	0.99	2.18	4.57	0.65	1.05	1.32	2.63	2.99	0.52	1.13	0.58
		2SE	0.23	0.50	1.04	0.15	0.24	0.31	0.60	0.69	0.12	0.26	0.13
	IV (9)	x̄	16.37	35.44	28.16	7.44	6.16	10.26	12.29	15.78	5.33	8.16	2.45
		SD	0.69	2.56	3.46	0.75	0.86	1.53	1.13	2.25	0.57	1.47	0.25
		2SE	0.23	0.85	1.15	0.25	0.29	0.51	0.38	0.75	0.19	0.49	0.08
	V (31)	x̄	17.66	39.86	34.12	8.19	7.55	11.30	13.89	17.71	5.39	8.88	2.91
		SD	1.46	3.35	4.51	0.76	1.04	1.30	1.38	2.82	0.75	1.58	0.51
		2SE	0.26	0.60	0.80	0.14	0.19	0.23	0.24	0.51	0.13	0.28	0.09
	VI (14)	x̄	17.56	40.99	35.01	8.36	7.60	11.45	13.82	18.02	5.40	9.40	3.18
		SD	1.08	3.35	4.71	0.51	1.86	1.76	2.31	2.54	0.71	1.45	0.45
		2SE	0.29	0.89	1.26	0.13	0.50	0.47	0.62	0.68	0.19	0.38	0.12
	VII (9)	x̄	17.31	41.79	32.94	8.13	6.80	10.70	13.24	17.77	5.26	9.33	2.95
		SD	0.83	2.80	3.38	0.49	0.70	1.15	0.96	1.78	0.50	2.05	0.36
		2SE	0.28	0.94	1.13	0.16	0.23	0.38	0.32	0.59	0.17	0.68	0.12
	VIII(15	x̄	18.81	45.80	38.50	8.69	9.04	12.70	14.95	20.57	6.20	10.86	3.35
		SD	1.79	4.48	4.66	0.51	1.42	1.61	2.31	2.52	0.91	2.10	0.52
		2SE	0.46	1.15	1.20	0.13	0.37	0.41	0.60	0.65	0.23	0.54	0.13
	IX (26)	x̄	19.55	48.23	37.50	8.81	8.91	12.82	15.60	21.20	6.20	10.79	3.44
		SD	1.86	4.49	4.75	0.60	2.89	1.70	1.85	2.75	0.77	1.65	0.58
		2SE	0.36	0.88	0.93	0.12	0.57	0.33	0.36	0.54	0.15	0.32	0.11

The first principal components axis from the PCA which represents size-related variation explains 77.57% of the total variance and had high negative loadings in all the 22 measurements used in the analysis (Table 5.4). Only two measurements (UTR and MTR) had relatively high positive loadings on the second principle components axis which represents shape-related variation and explains 4.05% of the total variance (Table 5.4).

Table 5.4. Relative loadings of measurements from the first two principal components of a principal components analysis of the giant mole-rat, *Fukomys mechowii* of tooth-wear classes 1–9 from Kakalo and Mushishima farm blocks in Chingola, Copperbelt Province of Zambia. Measurements are defined and illustrated in Fig. 2.2.

	Principal components axes	
Measurement	I	II
GLS	-0.95	-0.00
ITC	-0.97	-0.02
BCW	-0.83	-0.02
ZMB	-0.93	-0.04
ZYW	-0.97	-0.10
IOB	-0.77	-0.32
WR	-0.96	-0.15
NA	-0.96	-0.10
UTR	-0.83	0.46
PAC	-0.72	-0.22
NPP	-0.97	-0.03
GHS	-0.95	-0.13
MLT	-0.95	-0.00
MDL	-0.86	0.12
MTR	-0.83	0.46
AFL	-0.85	-0.22
MAF	-0.83	-0.06
AFA	-0.89	-0.14
MRH	-0.89	0.02
UJI	-0.74	0.33
LJI	-0.75	0.21
WI	-0.91	0.02
% variance explained	Axis 1 = 77.57%	Axis 2 = 4.05%

A plot of the first two principal components axis (Fig. 5.1), which for clarity does not show individuals, reveal that although individuals of tooth-wear classes 2 and 3 overlap extensively, there is a clear separation between individuals of tooth-wear classes 1–3 and those of extensively overlapping tooth-wear classes 5–9 on the first principal components axis. Individuals of tooth-wear class 4 lie intermediate between individuals of tooth-wear classes 1–3 and those of tooth-wear classes 5–9 (Fig. 5.1).

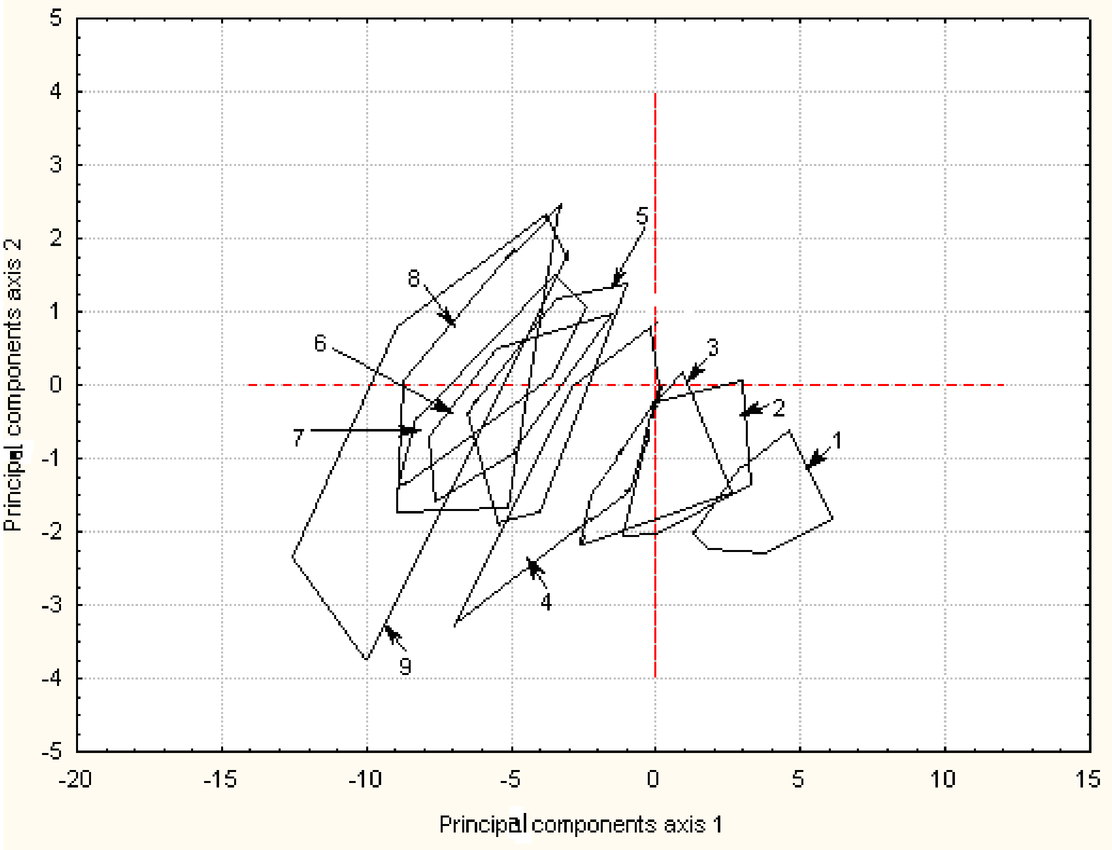

Figure 5.1. A plot of the first two principal components from a principal components Analysis of the giant the mole-rat, *Fukomys mechowii* of tooth-wear classes 1–9 from Kakalo and Mushishima farm blocks, Chingola, Copperbelt Province of Zambia. Minimum convex polygons enclose individuals of each tooth-wear class, which together with their associated sexes have been omitted.

A distant phenogram from the UPGMA cluster analysis (Fig. 5.2) showed three biologically meaningful clusters of individuals in multivariate space. The first cluster (1) mainly comprised a combination of male and female individuals of the younger age classes 1–4 with two females of age class 6. This strongly suggests the absence of sexual dimorphism within these younger age classes. While the second cluster (2), predominantly comprised individuals of the older age classes 5–9 with some females of age class 3 and males of age class 4, and some minor sub-clusters of individuals of the same sex. Apart from three females of age class 6, the third cluster (3) mainly comprised males of the older age classes 5–9. These males, which are larger than females, strongly suggest the presence of sexual dimorphism in the older age classes of the giant mole-rat.

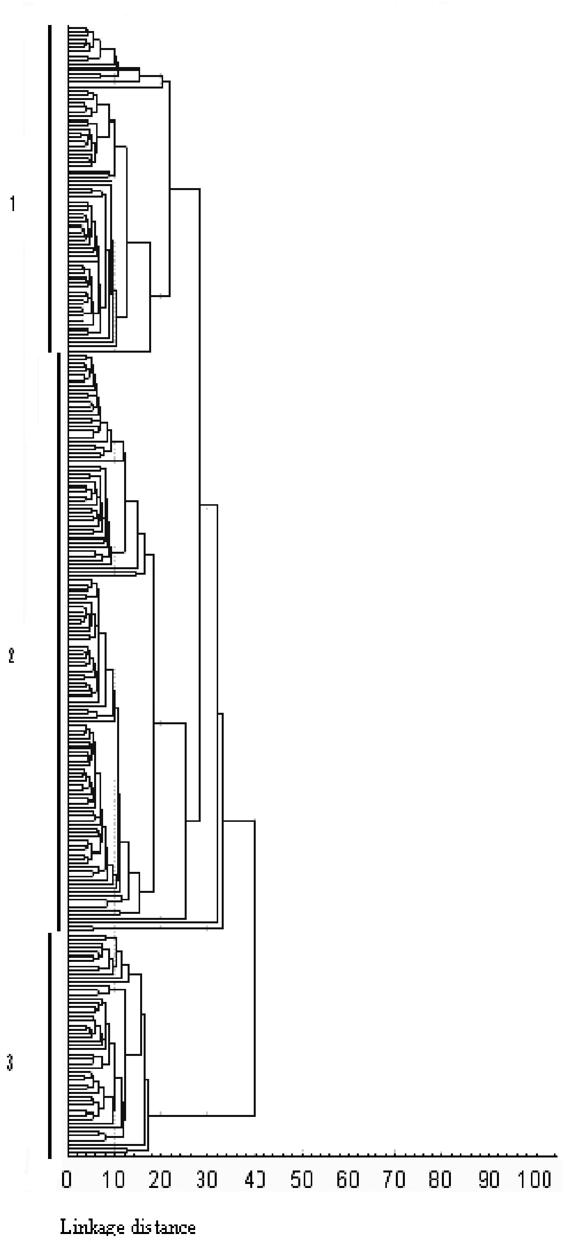

Figure 5.2. A distance phenogram from an unweighted pair-group method using arithmetic averages (UPGMA) cluster analysis male and female giant mole-rat, *Fukomys mechowii* of age tooth-wear classes 1–9 from Kakalo and Mushishima farm blocks, Chingola, Zambia, showing 3

distinct clusters of individuals comprising the following sample sizes, tooth-wear classes and sexes (M = male; F = female), respectively: 1) Cluster 1 – 4:1F, 2:1M, 8:2F, 6:2M, 6:3F, 4:3M, 8:4F, 5:4M and 2:6F; 2) Cluster 2 – 13:5F, 6:5M, 7:6F, 3:6M, 5:7F, 3:7M, 11:8F, 7:8M, 18:9F, 8:9M, 2:3F and 3:4M; and 3) Cluster 3 – 2:5M, 3:6F, 8:8M, 5.7M, 9:9M.

A confirmation on the absence of sexual dimorphism in the younger age classes and its presence in the older age classes was assessed by two independent ANOVAs and %*SSQ* of individuals of age classes 1–4 and age classes 5–9. All the 22 measurements differed statistically significantly for age (20 measurements at $P < 0.001$, one at $P < 0.01$, and one at $P < 0.05$) (Table 5.5). None of the measurements differed significantly for sex while one measurement only (UJI) differed significantly for the interaction between sexual dimorphism and age at $P < 0.05$ (Table 5.5). The importance of age variation rather than sexual dimorphism in the younger age classes 1–4 was also shown by the higher %*SSQ* values for age (%*SSQ*: $\bar{x}$ = 37.38; range = 9.75–77.58%) than for sex (%*SSQ*: $\bar{x}$ = 0.80; range = 0.00–2.99%) or the interaction between age and sex (%*SSQ*: $\bar{x}$ = 2.07; range = 0.30–6.26%) (Table 5.5). The analysis of %*SSQ* of age classes 1-4 also showed higher mean %*SSQ* values for the error component than for age (%*SSQ*: $\bar{x}$ = 59.75), sex or the interaction between age and sex (Table 5.5) suggesting that other factors may be responsible for non-geographic variation in the giant mole-rat rather sexual dimorphism and age variation alone.

Table 5.5. *F*-values and percent *SSQ* of each source of variation derived from a two-way analysis of variance (ANOVA) of four age classes (1–4) based on the degree of tooth eruption and wear in male and female giant mole-rats, *Fukomys mechowii*, from Kakalo and Mushishima farm blocks, Chingola, Copperbelt Province of Zambia. Statistical significance: * = $P < 0.05$; ** = $P<0.01$; *** = $P < 0.001$. Measurements are defined and illustrated in Fig. 2.2.

Measurement		*F*-Value				%*SSQ*			
		Age A)	Sex (S)	A x S		Age (A)	Sex (S)	A x S	Error
GLS		24.23***	3.22	1.13		45.92	2.04	2.13	49.91
ITC		22.65***	3.55	1.25		44.05	2.30	2.43	51.22
BCW		7.73***	3.22	0.62		21.61	2.99	1.74	73.66
ZMB		15.66***	3.14	0.75		35.76	2.40	1.70	60.14
ZYW		12.10***	0.00	0.94		30.89	0.00	2.37	66.74
IOB		2.88*	0.16	0.24		9.75	0.18	0.82	89.25
WR		20.62***	0.20	0.62		43.29	0.15	1.30	55.26
NA		16.96***	0.24	0.49		38.66	0.18	1.12	60.04
UTR		74.35***	0.00	0.36		73.58	0.00	0.36	26.06
PAC		4.41**	0.02	0.48		14.10	0.02	1.55	84.33
NPP		37.83***	0.00	0.33		58.65	0.00	0.51	40.84
GHS		22.32***	0.73	0.98		44.76	0.49	1.96	52.79
MLT		9.61***	0.04	0.73		26.19	0.04	1.99	71.78
MDL		17.52***	0.18	1.30		38.75	0.13	2.88	58.24
MTR		63.51***	0.14	0.27		70.44	0.05	0.30	29.21
AFL		9.81***	1.17	0.53		26.46	1.06	1.42	71.06
MAF		11.60***	1.80	2.57		28.21	1.46	6.26	64.07
AFA		6.69***	0.30	0.75		19.75	0.30	2.23	77.72
MRH		13.34***	0.26	0.52		33.12	0.22	1.28	65.38
UJI		16.39***	3.24	2.79*		35.20	2.32	5.94	56.54
LJI		19.12***	1.32	0.94		40.82	0.94	2.01	56.23
WI		20.62***	0.61	1.58		42.30	0.42	3.25	54.03
Mean						37.38	0.80	2.07	59.75

The ANOVA of the older age classes 5–9 (Table 5.6) showed 21 of the 22 measurements to be statistically significant for age (20 at $P < 0.001$ and one at $P < 0.05$), 20 were statistically significant for sexual dimorphism (all at $P < 0.001$) where males are larger than females, and five were statistically significant for the interaction between sex and age (two at $P <$

0.01 and three at $P < 0.05$). Of particular significance is that the ANOVA of the older age classes 5–9 generally had higher *F*-values for sex than for age, and is also evident in the higher %*SSQ* values for sex (*SSQ*: $\bar{x}$ = 14.99%; range = 1.67–22.19%) than that of either the age component (*SSQ*: $\bar{x}$ = 9.97%; range = 2.17–27.46%) or the interaction between age and sex (*SSQ*: $\bar{x}$ = 2.64%; range = 1.44–5.33%) (Table 5.6). Similar to the analysis of the younger age classes 1–4, the analysis of %*SSQ* of the older age classes 5-9 also showed higher mean %*SSQ* values for the error component (%*SSQ*: $\bar{x}$ = 72.40%; range = 62.47–91.55%) than for age (*SSQ*: $\bar{x}$ = 9.97%; range = 2.17–27.46%), sex (*SSQ*: $\bar{x}$ = 2.64%; range = 1.44–5.33%) or the interaction between age and sex (*SSQ*: $\bar{x}$ = 2.64%; range = 1.44–5.33%) (Table 5.6), suggesting that factors other than sexual dimorphism and age variation may be responsible for non-geographic variation in the giant mole-rat.

Table 5.6. *F*-values and percent *SSQ* of each source of variation derived from a two-way analysis of variance (ANOVA) of four age classes (5–9) based on the degree of tooth eruption and wear in male and female giant mole-rats, *Fukomys mechowii*, from Kakalo and Mushishima farm blocks, Chingola, Copperbelt Province of Zambia. Statistical significance: * = $P < 0.05$; ** = $P<0.01$; *** = $P < 0.001$. Measurements are defined and illustrated in Fig. 2.2.

Measurement	*F*-Value			*%SSQ*			
	Age A)	Sex (S)	A x S	Age (A)	Sex (S)	A x S	Error
GLS	12.25***	28.38***	2.05	11.19	19.32	3.24	66.25
ITC	14.09***	34.97***	2.40*	13.00	20.96	3.57	62.47
BCW	7.66***	18.94***	3.06**	8.24	13.33	5.33	73.10
ZMB	14.65***	24.38***	3.28**	9.23	22.19	4.97	63.61
ZYW	13.66***	35.13***	1.80	13.26	20.62	2.72	63.40
IOB	4.66***	18.33***	0.96	8.78	8.94	1.84	80.44
WR	12.99***	34.69***	1.55	13.30	19.92	2.38	64.40
NA	11.89***	25.32***	2.31*	10.12	19.02	3.70	67.16
UTR	2.27**	5.91	0.69	3.18	4.88	1.48	90.46
PAC	3.86***	24.95***	0.84	7.29	11.78	1.58	79.35
NPP	11.29***	29.40***	2.07	11.72	18.00	3.30	66.98
GHS	10.95***	23.64***	1.35	9.81	18.19	2.25	69.75
MLT	11.67***	22.91***	1.69	9.38	19.10	2.77	68.75
MDL	12.30***	15.88***	1.83	6.60	20.47	3.04	69.89
MTR	1.00	10.38***	0.29	2.17	5.65	0.63	91.55
AFL	5.64***	8.00***	0.85	3.95	11.51	1.68	82.86
MAF	8.26***	14.26***	0.90	6.52	15.09	1.64	76.75
AFA	13.13***	24.14***	1.59	9.62	20.92	2.53	66.93
MRH	18.17***	14.39***	2.39*	27.46	5.44	3.62	63.48
UJI	10.52***	11.49***	0.81	5.11	18.72	1.44	74.73
LJI	10.02***	3.58	0.88	18.62	1.67	1.64	78.07
WI	8.10***	24.87***	1.52	10.75	14.01	2.62	72.62
Mean				9.97	14.99	2.64	72.40

Evidence for the lack of sexual dimorphism in the younger age classes 1–4 and its presence in the older age classes 5–9 is apparent in independent PCAs of these age class groupings (Figs 5.3 and 5.4, respectively). This is also evident if these results are compared with the

PCA of the total sample indicated in Fig. 5.1 and also in standard descriptive statistics (Table 5.3) where there are differences in size between the sexes in the older age classes.

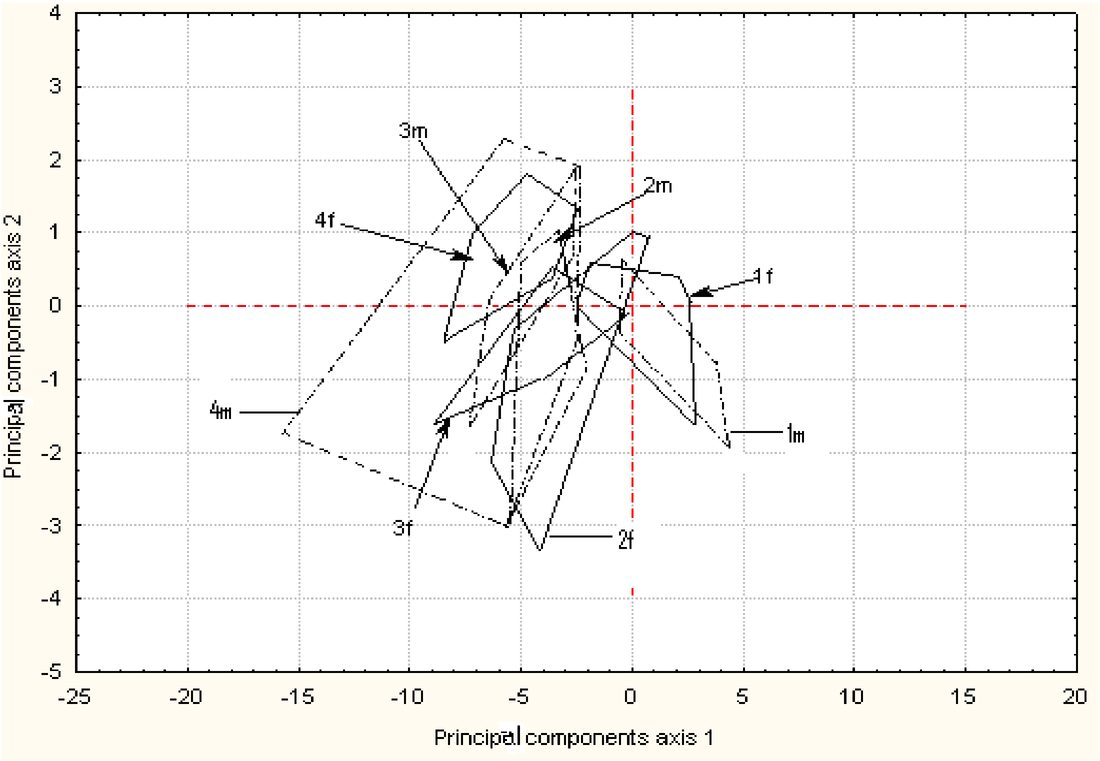

Figure 5.3. A plot of the first two principal components from a principal components analysis of giant mole-rats, *Fukomys mechowii* of younger tooth-wear classes 1–4 from Kakalo and Mushishima Farm Blocks, Chingola, Copperbelt Province of Zambia. Dashed and continuous minimum convex polygons enclose male (m) and female (f) individuals of each age class (1–4), respectively.

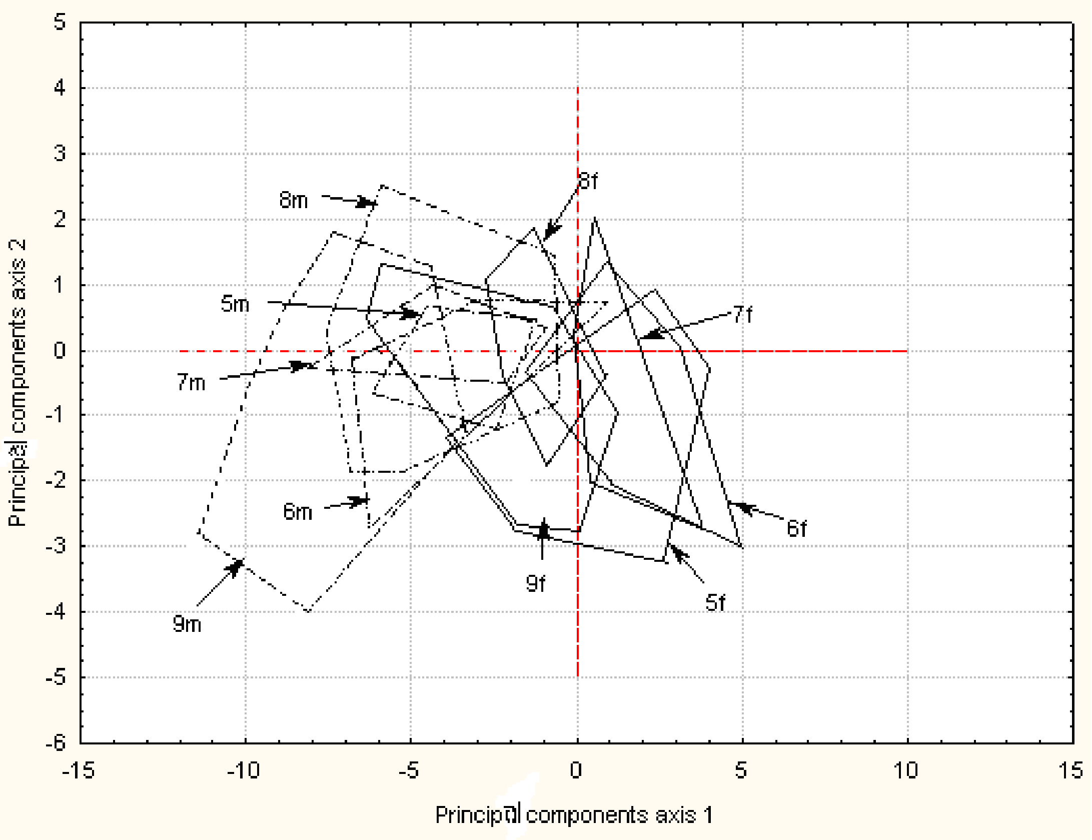

Figure 5.4. A plot of the first two principal components from a principal components analysis of the giant mole-rat, *Fukomys mechowii* of older tooth-wear classes 5–9 from Kakalo and Mushishima farm blocks, Chingola, Copperbelt Province of Zambia. Dashed and continuous minimum convex polygons enclose male (m) and female (f) individuals of each age class, respectively.

The absence of sexual dimorphism in younger age classes 1–4 and its presence in older age classes 5–9 of the giant mole-rat shown by the craniometric data in the present study was independently tested using data on body mass. There is a distinct increase in body mass as a function of relative age in both sexes (Fig. 5.5). Of particular relevance however, is that in broad similarity with craniometric data in the present study, individuals of the younger age classes 1–5 showed no sexual dimorphism in body mass, while males and females of the older age classes 6–9 differed statistically significantly in body mass

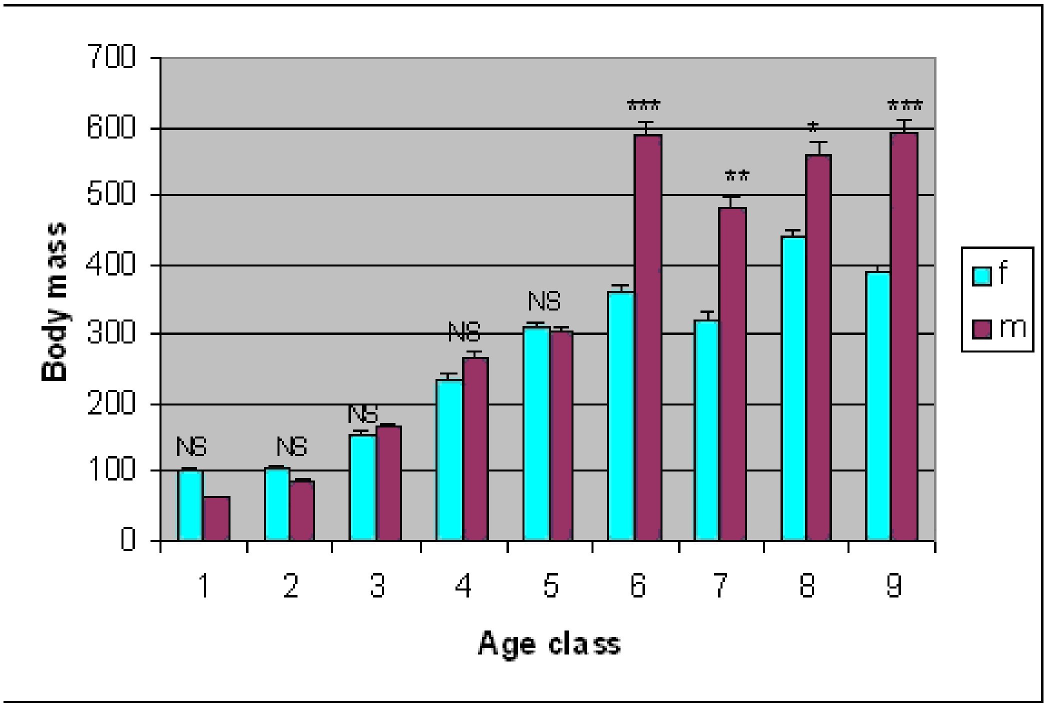

Figure 5.5. A plot of nine relative age classes (1–9) defined and illustrated in Fig. 2 and body mass (g) (± 2 standard errors of the mean (*SE*)) of male (m) and female (f) giant mole-rats, *Fukomys mechowii* from Kakalo and Mushishima farm blocks, Chingola, Copperbelt Province of Zambia. Statistical significance: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not statistically significant.

Discussion

Both the univariate (ANOVA, *post hoc* SNK tests, and %*SSQ*) and multivariate (UPGMA cluster analysis and PCA) analyses undertaken in the present study showed the presence of statistically significant age variation, but a lack of sexual dimorphism in younger individuals of age classes 1–4 within the giant mole-rat. However, while these analyses also showed the presence of statistically significant age variation in the older age classes 5–9, these age class groupings also revealed the presence of sexual dimorphism. Overall, these two age class groupings (i.e., age classes 1–4 vs 5–9) are also morphometrically distinct from each other in multivariate space, where individuals of age class 4 lie intermediate between those of age classes 1–3 and age classes 5–9. This suggests that intermediately placed individuals of age class 4 lie at a point on a hypothetical growth curve where it begins to stabilize.

The results in the present study are similar to those found in the Zambian mole-rat, *Fukomys anselli* where Begall & Burda (1998) demonstrated that the growth rate in both sexes was constant up until 18th–20th weeks, after which, males were observed to grow faster than females. Similarly, Yu & Lin (1999) showed that the body mass of the spiny rat, *N. coxingi* was sexually dimorphic in older individuals than in juveniles and sub-adults. In addition, Hart *et al.,* (2007) also reported that the body mass and length of the Cape dune mole-rat, *Bathyergus suillus* was also sexually dimorphic in older rather than young individuals.

In contrast, body mass and sexual dimorphism has been demonstrated in other small mammals regardless of age. These include the subterranean social [Damaraland mole-rat, *Fukomys damarensis*; (Bennett *et al*., 1990)], the [Talas, tuco-tuco *Ctenomys talarum* (Zenuto *et al*., 1999)] and the solitary [Namaqua dune mole-rat, *Bathyergus janetta* (Davies & Jarvies, 1986)]. Other studies on subterranean rodents in which sexual dimorphism occurs regardless of age include the bushy-tailed wood rat (*Neotoma cinerea*), the deer mouse (*Peromyscus maniculatus*), and the red-backed *Clethionomys gapperi* Schulte-Hostedde *et al*., (2001). In contrast, a lack of sexual dimorphism has also been reported in other subterranean rodents. These include the social common mole-rat [*Cryptomys hottentotus hottentotus* Bennett *et al*., (1990)], the highveld mole-rat, [*C. h. pretoriae* Janse van Rensburg *et al*., (2004)], the solitary Cape mole-rat [*Georychus capensis* Taylor *et al*., (1985)] and the silvery mole-rat [*Heliophobius argenteocinereus* Scharff *et al*., (1999)].

The results of the PCA in the present study showed that the difference between males and females in the social giant mole-rat was mainly due to overall size rather than shape. Similar results were found in the social [Damaraland mole-rat *F. damarensis* (Bennett & Faulkes, 2000)] as well as in solitary Cape dune mole-rat [*Bathyergus suillus* Hart *et al.,* (2007)]. However, these authors suggested that this may be due to an increase in male–male interactions during reproduction when males compete for reproductive opportunities. Hart *et al*., (2007) suggested that massive fat deposits around the necks of male Cape dune mole-rats may act as a cushion from incisor bites during aggressive interactions between males which have been observed under laboratory conditions and from inter-locked skulls in the wild. Giant mole-rats have also been observed fighting aggressively during male–male contacts (A.M. Sichilima, pers. obs).

Dispersing males of naked mole-rats (*Heterocephalus glaber*) are usually found larger than non-dispersing males of similar age (O'Riain *et al.,* (1996). The lone dispersing male of the giant mole-rat has similarly been observed to be usually large in body size (A. M. Sichilima, pers. obs). O'Riain *et al*., (1996) suggested that fat reserves associated with dispersing large body-sized male naked mole-rats may serve a nutritional function in order to avoid starvation during dispersal and the establishment of colonies.

It is interesting to note that in monogamous social mole-rats, two reproductive pairs have been reported to be responsible for procreation within a colony (Jarvis & Bennett, 1993; Gayland *et al.,* 1998), while in polygamous systems, two potential reproductive males are responsible for controlling the recruitment of unrelated pups into the colony Greenwood, (1980). Consequently, the monogamous system has either none or insignificant male–male competition for mates while in the polygamous system, there is male–male competition for mates among older males and possibly among younger unrelated maturing males. However, evidence of the presence of: (1) a single male and a single queen, (2) 2–5 adult males, and (3) two queens in some colonies (A. M. Sichilima, pers. obs.) suggests that the social *F. mechowii* may be both monogamous and polygamous.

Although other studies have argued that the estimation of age in mammals based on molar eruption and wear may not be suitable in some species such as bats *Myotis lucifugus* Hall *et al.,* (1957), the elk *Cervus elephus* Keiss (1969) and white tailed deer *Odocoileus virginianus* (Gilbert & Stolt, 1990), our study suggests that this may not be the case in *F. mechowii*. Our data suggest that in the absence of data on absolute ageing, the estimation of age based on molar eruption and wear may be appropriate for the giant mole-rat.

In addition, the use of body mass to estimate absolute age in mammals has also been considered to be inappropriate. However, similar to the results found in the solitary Cape dune mole-rat Hart *et al*., (2007), the results in our study on the social giant mole-rat also found a general trend of an increasing body mass with increasing age. More importantly, similar to the cranial morphometric data, sexual dimorphism in body mass was absent in the younger age classes but present in the older age classes. It is interesting to note that body mass can be a good indicator of sexual dimorphism and relative age in both the social giant mole-rat (the present study) as well as in the solitary Cape dune mole-rat where Hart *et al.,* (2007) argued that there may not be an additional constraint on body mass (and body length) due to the social rank of an individual as has been reported in other social mole-rats Bennett *et al*., (1990).

Of additional relevance in the present study is that the results of our variance partitioning showed a very large error (= residual) component in the derived %*SSQ* values. This suggests that apart from the presence of sexual dimorphism and age variation in the giant mole-rat, there are other factors that may be influencing non-geographic variation within the species. These other potential influences of non-geographic variation in the giant mole-rat need to be investigated further in order to allow a better insight into the understanding of the population and social structures, and reproductive strategies in this little-studied mole-rat species.

Conclusion

Sexual dimorphism and relative age variation in nine age classes estimated from the degree of molar tooth-row eruption and wear in the giant mole-rat, *Fukomys mechowii* from Zambia, Central Africa were assessed using traditional cranial morphometric data and body mass, and a range of univariate and multivariate analyses. All analyses revealed craniometric differences between individuals of age classes 1–3 and those of age classes 5–9, with those of age class 4 being intermediate between these two age class groupings, suggesting that age class 4 is at a point on a hypothetical growth curve where it begins to stabilize. In contrast, the analyses revealed the absence of sexual dimorphism in the younger individuals of the giant mole-rat of age classes 1–4 and its presence in older age classes 5–9, and these results are supported by the analysis of the data on body mass. The sexual dimorphish in giant mole-rasts has therefore, demonstrated that there are different growth curves in males versus females, whereby males attain much larger size (skull size and body mass) than females after puberty. In conclusion, it is this factor that has been responsible for ANOVA significant interaction results in the older age classes 5-9.