Ontogenetic variation and craniometric sexual dimorphism in the social giant mole-rat, *Fukomys mechowii* (Rodentia: Bathyergidae), from Zambia

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The degree of maxillary molar tooth-row eruption and wear were used to assign samples of the social giant mole-rat, *Fukomys mechowii,* from Zambia, into nine relative age classes in order to assess ontogenetic (age) variation and craniometric sexual dimorphism, with reference to body mass. Univariate and multivariate statistical analyses showed craniometric differences between age classes 1–3 and age classes 5–9, with age class 4 being intermediate between these two age class groupings. This suggests that age class 4 lies at a point on a hypothetical growth curve where growth begins to stabilize. The intermediate placement of age class 4 in multivariate space broadly coincided with body mass categorizations into juveniles (age classes 1–3; <100 g), subadults (age class 4; *c.* 100–150 g), and adults (age classes 5–9; >150 g). The analyses also revealed the absence of sexual dimorphism in the relatively younger age classes 1–4 but its presence in the relatively older age classes 5–9, and these results are supported by data on body mass. These results may have implications in our understanding of the population and social structures, and reproductive strategies in this little-studied giant mole-rat.

Key words: *Fukomys mechowii,* ontogenetic variation, sexual dimorphism, craniometrics, Zambia.

INTRODUCTION

Numerous studies have been undertaken to assess the nature and extent of non-geographic variation in fossorial rodents, particularly with reference to ontogenetic (age) variation and sexual dimorphism. These include studies on mole-rats (*Heterocephalus glaber, Bathyergus suillus, Cryptomys hottentotus* and *Fukomys damarensis*; Davis & Jarvis 1986; Bennett *et al.* 1990; Begall & Burda 1998; O'Riain & Jarvis 1998; Scharff *et al.* 1999); tuco-tucos (*Ctenomys talarum*; Zenuto *et al.* 1999); the highveld mole-rat (*Cryptomys hottentotus pretoriae*; Janse van Rensburg *et al.* 2004); and the Cape dune mole-rat (*Bathyergus suillus*; Hart *et al.* 2007).

Owing to the general paucity of data on absolute ageing of mammals in wild populations, various methods have been used to estimate their relative age (Hart *et al.* 2007). While body mass has been used in the past, for example in subterranean mole-rats (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 1989; Jacobs *et al.* 1991; Wallace & Bennett 1998; Janse van Rensburg *et al.* 2004). The estimation of relative age based on the degree of molar eruption and wear is considered to be at least more reliable, particularly for a homogenous sample that may not potentially be influenced by geographic variation (Chaplin & White 1969; Taylor *et al.* 1985; Dippenaar & Rautenbach 1986; Chimimba & Dippenaar 1994; Janse van Rensburg *et al.* 2004; Hart *et al.* 2007).

Consequently, the degree of molar eruption and wear were used in the present study to assess the nature and extent of ontogenetic (age) variation and craniometric sexual dimorphism in the giant mole-rat, *Fukomys mechowii* (Peters, 1881), from Zambia. Body mass which has previously been

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used to assess the nature and extent of ontogenetic variation and sexual dimorphism in other social mole-rat 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.

The giant mole-rat is a social subterranean rodent (Burda & Kawalika 1993) that is restricted to the subtropical and tropical Miombo woodlands and grasslands of Central Africa (Bennett & Aguilar 1995; Scharff *et al.* 2001; Kawalika & Burda 2007; Sichilima *et al.* 2008a). Generally, its natural history remains unclear and, therefore, there is a critical need to gain insights into the biology of the species which may be threatened because of the spread of agriculture. The data on ontogenetic variation and craniometric sexual dimorphism may have implications in our understanding of the population and social structures, and reproductive strategies in this little-studied species of mole-rat. Given that most studies on mole-rats in Africa have mainly been undertaken in the southern African subregion, our study represents one of the few studies that have been undertaken in central Africa in general and the Zambeziana region in particular.

MATERIALS & METHODS

A total of 265 specimens (114 males and 151 females) were collected between 2005 and 2006 from two geographically proximal and ecologically similar localities, Kakalo and Mushishima Farm Blocks, 25 km south of Chingola, Chingola District, Copperbelt Province, Zambezian region, Zambia (*c.* 10°40′S, 20°58′E) (collection permit number 610946/5). The animals were captured by digging and subsequently sacrificed using halothane inhalation. All animal capture and care procedures followed the guidelines of the American Society of Mammalogists (ASM; Animal Care and Use Committee 1998; http://www.mammalogy.org/committees/index.asp) and the animal ethics committee of the University of Pretoria (Ethics clearance number AUCC 06509/011), Pretoria, South Africa. Standard data recorded included sex and body mass (g), and voucher specimens were prepared and will be deposited in the mammal reference collection of the Natural History Museum, Lusaka, Zambia.

The estimation of relative age was based on the degree of the maxillary molar tooth-row eruption and wear which was used to assign individuals into nine relative age classes (Fig. 1; Appendix 1) adopted and modified from Janse van Rensburg *et al.* (2004) and Hart *et al.* (2007). Ontogenetic variation and sexual dimorphism were assessed using 22 linear cranial measurements (Fig. 2; Appendix 2) adopted and modified from Janse van Rensburg *et al.* (2004) and Hart *et al.* (2007), and have been used traditionally and were selected in order to capture the overall configuration of the cranium. All cranial measurements were recorded by a single observer (A.M.S.) to the nearest 0.05 mm using a pair of Mitutoyo digital callipers (Mitutoyo American Corporation, Aurora, Illinois, U.S.A.).

Initial analyses included standard descriptive statistics and two-way analysis of variance (ANOVA; Zar 1996) of the sexes and age classes. 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 tables were in turn used to estimate the percentage sum of squares (*%SSQ*; Leamy 1983) 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 craniometric data were also subjected to multivariate analyses that included an unweighted pair-group method using arithmetic averages (UPGMA) cluster analysis and principal components 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). The Mann-Whitney *U*-test (Zar 1996) was used to evaluate the body mass data within sexes and age classes. All statistical analyses were based on all the 22 cranial measurements, and were undertaken using the statistical software programme Statistica, version 8.0 (StatSoft Inc. 2008).

RESULTS

Standard descriptive statistics of craniometric data for each sex and age class are presented in Table 1. The ANOVA results showed that all 22 cranial measurements differed significantly with reference to age, while 20 of the 22 measurements differed significantly due to sexual dimorphism (Table 2). Fifteen of the 22 measurements showed statisti-

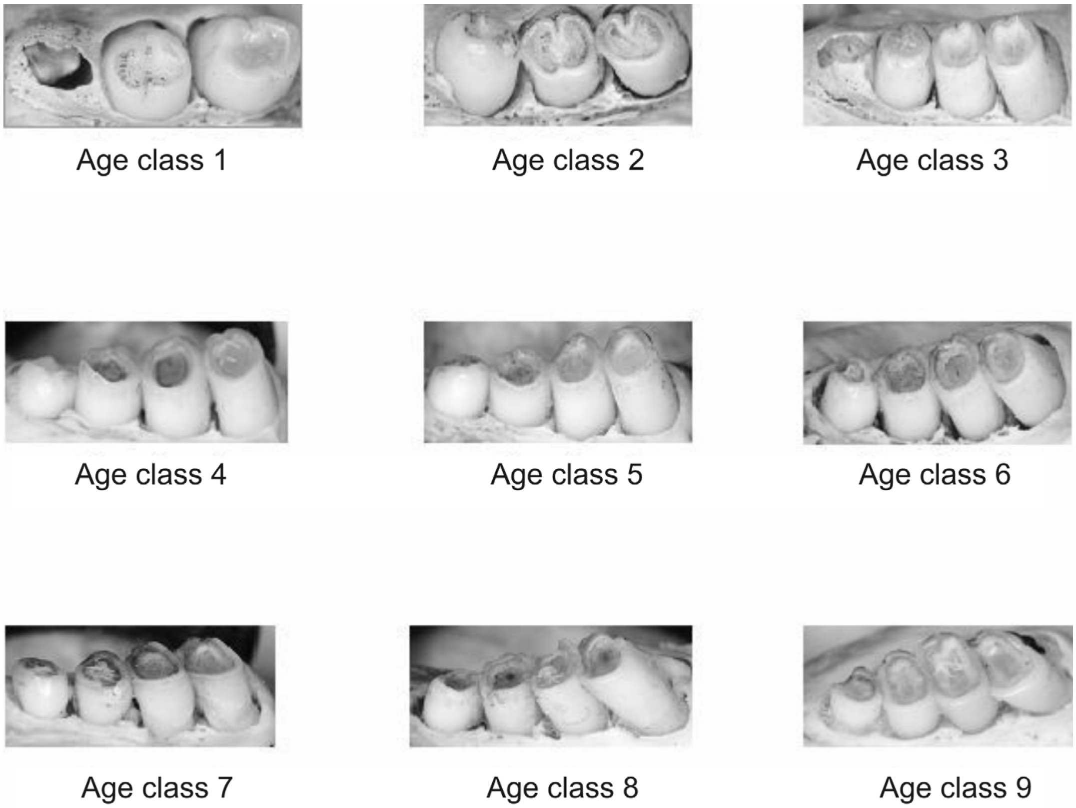

Fig. 1. Right maxillary molar tooth row of the giant mole-rat, *Fukomys mechowii*, illustrating nine tooth-wear classes used to estimate relative age as adopted and modified from Janse van Rensburg *et al.* (2004) and Hart *et al.* (2007), and described in Appendix 1.

cally significant interaction between sex and age class (Table 2) suggesting an interaction between ontogeny and sexual dimorphism. 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 non-geographic variation (Table 2), suggesting a more substantial contribution of ontogenetic variation to the overall degree of non-geographic variation in the giant mole-rat.

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 2). The *%SSQ* values for the error component (= residual) for all 22 measurements and their associated mean values particularly those for sexual dimorphism and its interaction with age were also relatively high (*%SSQ*: $\bar{x}$ = 40.01, range = 13.54–64.98%) (Table 2). This suggests that, apart from the presence of age variation and sexual dimorphism, there are other factors (e.g. different growth trajectories for males and females, and individual variation) that may be influencing the nature and extent of non-geographic variation in the giant mole-rat.

The results of the *post hoc* SNK tests (Table 3) revealed three contrasting patterns of ranked means. The first and major pattern involved 11 of the 22 measurements (BCW, ZMB, IOB, WR, PAC, GHS, MTR, APL, MRH, UJI and LJI), which showed an orderly increase in measurement magnitude with increasing age, a pattern that was also evident in standard descriptive statistics of the craniometric data (Table 1). The second trend involved eight of the 22 measurements (ZYW, NA, UTR, NPP, MDL, CPL, ATP and WI), which grouped individuals of the relatively younger age classes 1–4, and those of the relatively older age classes 5–9 into two different non-overlapping

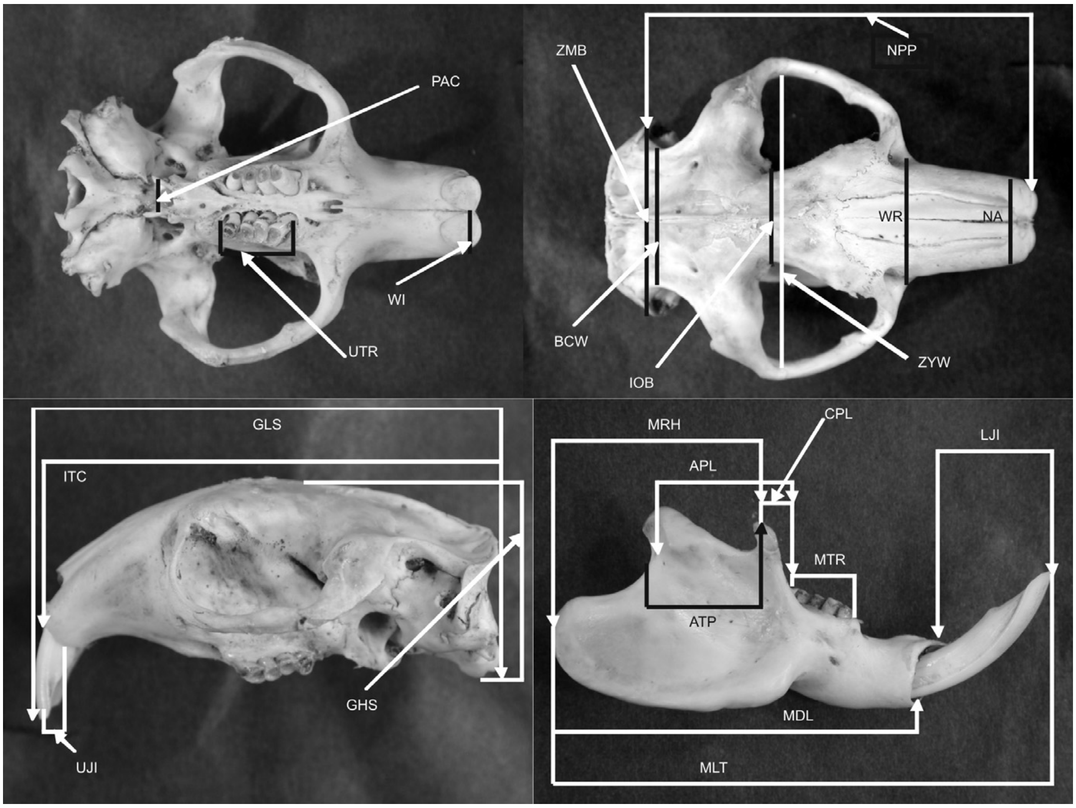

Fig. 2. Abbreviations and reference points of 22 cranial measurements (mm) of the giant mole-rat, *Fukomys mechowii,* used in the present study as adopted and modified from Janse van Rensburg *et al.* (2004) and Hart *et al.* (2007), and as described in Appendix 2.

statistically non-significant ($P > 0.05$) subsets (Table 3). The third pattern, which involved three measurements only (GLS, ITC and MLT), showed statistically significant differences between all the nine age classes (Table 3).

The three contrasting patterns of ranked means revealed by the SNK tests (Table 3) necessitated further assessments of age variation and sexual dimorphism that involved a series of multivariate analyses. A plot of the first two principal components axes (Fig. 3) revealed, that although tooth-wear classes 2 and 3 overlapped extensively, there was a separation between tooth-wear classes 1–3 and those of extensively overlapping tooth-wear classes 5–9 along the first principal components axis. Tooth-wear class 4 was intermediate between tooth-wear classes 1–3 and tooth-wear classes 5–9 (Fig. 3). The intermediate placement of tooth-wear class 4 in multivariate space broadly coincided with body mass categorizations into juveniles (age classes 1–3; <100 g), subadults (age class 4; *c.* 100–150 g), and adults (age classes 5–9; >150 g). The first principal components axis from the PCA explained 77.57% of the total variance and had relatively high negative loadings in all the 22 measurements used in the analysis (Table 4). The second principal components axis which explained 4.05% of the total variance, only two measurements (UTR and MTR) had relatively high positive loadings (Table 4).

An Euclidean distance phenogram from a UPGMA cluster analysis (Fig. 4) showed three distinct clusters, with the first mainly comprising a combination of male and female individuals of the younger age classes 1–4, suggesting the absence of sexual dimorphism among these relatively younger age classes. The second cluster largely comprised of an equivocal combination of the sexes and a range of age classes, while, with minor exceptions, the third cluster showed some evidence of sexual dimorphism in the relatively older age classes 5–9. The indications of the general lack of sexual dimorphism in the relatively younger age classes and some evidence of its presence in the

Table 1. Standard descriptive statistics of 22 cranial measurements in nine relative age classes (I–IX; Fig. 1; Appendix 1) of male and female giant mole-rats, *Fukomys mechowii*. *n* = sample size, $\bar{x}$ = mean, S.D. = standard deviation, C.V. = coefficient of variation. Cranial measurements are illustrated in Fig. 2 and described in Appendix 2.

Sex Toothwear class (*n*)		Cranial measurement NPP	ZMB	BCW	IOB	ZYW	WR	NA	WI	PAC	UTR	LJI
Males												
I (7)	$\bar{x}$	27.58	17.69	16.33	9.25	20.57	6.59	4.89	1.29	3.13	4.70	5.16
	S.D.	3.12	1.63	1.10	0.34	1.81	0.76	1.10	0.33	0.27	0.82	0.57
	C.V.	11.12	9.43	7.21	4.11	9.71	12.09	22.45	26.67	9.53	17.32	11.89
II (5)	$\bar{x}$	33.60	19.97	16.74	9.90	26.11	8.06	6.41	2.16	3.36	6.35	8.13
	S.D.	3.13	1.25	0.66	0.61	2.66	0.81	0.87	0.34	0.28	0.15	1.48
	C.V.	9.98	6.35	4.74	6.74	10.22	10.95	14.15	16.18	8.32	2.22	18.45
III (7)	$\bar{x}$	34.73	20.87	17.42	9.80	27.35	8.44	6.59	2.46	3.56	6.71	8.32
	S.D.	2.67	1.41	0.90	0.31	2.11	0.41	0.51	0.27	0.29	0.36	0.97
	C.V.	8.33	7.47	5.72	3.14	8.80	5.15	8.19	11.10	8.11	5.14	12.37
IV (12)	$\bar{x}$	37.77	20.78	17.23	9.93	28.71	9.17	7.41	2.74	3.53	7.37	7.76
	S.D.	4.11	2.40	1.32	0.51	5.20	1.45	1.36	0.68	0.73	0.57	1.13
	C.V.	11.19	12.69	8.38	5.15	18.50	16.42	18.39	25.19	21.21	8.16	15.32
V (10)	$\bar{x}$	43.85	22.64	18.03	10.69	35.23	10.62	8.94	3.45	4.06	8.37	9.02
	S.D.	4.14	2.12	1.03	0.59	3.81	1.37	1.26	0.73	0.59	0.48	1.07
	C.V.	9.31	9.67	6.33	6.19	11.20	13.43	14.40	21.23	15.19	6.15	12.34
VI (14)	$\bar{x}$	45.05	23.58	19.09	11.08	35.20	11.37	9.07	3.38	4.16	9.39	10.61
	S.D.	5.57	2.80	1.50	0.99	5.03	2.03	1.36	0.59	0.48	0.30	1.89
	C.V.	12.49	12.75	8.40	9.27	14.34	18.54	15.36	17.16	12.13	3.08	18.50
VII (6)	$\bar{x}$	46.19	25.54	19.12	11.03	37.74	11.84	9.66	3.63	4.37	9.29	9.81
	S.D.	4.69	2.44	1.16	0.44	5.42	2.07	1.81	0.57	0.73	0.51	2.02
	C.V.	10.92	10.99	6.47	4.18	14.21	17.85	19.74	16.23	17.30	5.21	21.83
VIII (18)	$\bar{x}$	45.57	24.18	18.64	10.69	37.05	11.84	9.44	3.60	4.66	9.73	10.88
	S.D.	4.29	2.31	1.25	0.82	4.80	1.68	1.50	0.60	1.34	0.15	2.65
	C.V.	9.01	10.54	7.29	8.19	13.13	14.40	16.35	17.14	29.32	2.03	25.62
IX (35)	$\bar{x}$	50.97	26.88	19.83	11.63	42.32	13.58	11.26	4.13	4.61	9.87	12.06
	S.D.	4.36	1.86	1.05	1.20	4.52	1.72	1.48	0.53	0.56	0.52	2.14
	C.V.	9.74	7.31	5.18	10.20	11.76	13.29	13.25	13.09	12.09	5.08	18.36

Males (continued)		MLT	MDL	MTR	AFL	AFA	MAF	MRH	GLS	ITC	UJI	GHS
I (7)	$\bar{x}$	31.38	20.07	4.63	4.69	9.18	6.94	10.50	42.27	29.69	3.52	13.32
	S.D.	3.30	1.91	0.65	0.77	0.59	1.01	0.87	6.42	3.19	0.35	1.18
	C.V.	11.25	10.72	14.25	16.29	6.22	15.38	8.33	15.85	11.20	10.13	9.45
II (5)	$\bar{x}$	33.11	28.32	6.56	6.48	12.60	10.21	15.11	47.96	35.80	4.81	15.51
	S.D.	2.86	1.62	0.49	0.21	1.23	1.01	1.57	5.54	3.73	0.28	0.92
	C.V.	9.28	6.72	7.22	3.09	10.55	10.45	10.70	12.75	10.67	6.13	6.41
III (7)	$\bar{x}$	35.36	29.98	6.58	6.51	13.22	12.46	15.56	48.67	40.54	4.71	16.81
	S.D.	2.39	3.70	0.24	0.62	2.34	3.41	2.46	4.88	5.53	0.78	1.80
	C.V.	7.90	12.40	4.09	10.24	18.88	27.05	16.93	10.30	14.09	17.30	11.68
IV (12)	$\bar{x}$	36.30	30.19	7.31	6.85	12.72	10.15	15.95	51.58	40.33	4.71	16.80
	S.D.	2.94	3.03	0.59	1.71	3.14	2.08	3.28	6.04	6.52	0.50	1.78
	C.V.	8.84	10.87	8.17	25.49	25.90	20.60	21.94	12.47	16.88	11.14	11.51

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Table 1 (*continued*)

Males (continued)		MLT	MDL	MTR	AFL	AFA	MAF	MRH	GLS	ITC	UJI	GHS
V (10)	$\bar{x}$	41.83	38.04	8.26	8.76	14.73	12.57	19.87	50.41	46.96	6.15	18.87
	S.D.	2.06	5.17	0.42	1.99	1.83	2.36	2.69	4.98	4.47	0.68	1.42
	C.V.	5.65	14.64	5.13	23.63	12.58	19.75	14.85	10.17	10.41	11.21	8.45
VI (14)	$\bar{x}$	45.08	36.92	9.45	8.17	15.20	11.85	18.17	56.36	46.73	5.44	19.21
	S.D.	4.49	5.04	0.29	1.17	2.07	1.68	3.82	4.08	5.40	0.78	1.99
	C.V.	10.20	14.35	3.08	14.31	14.55	14.45	21.02	7.69	12.44	14.21	10.53
VII (6)	$\bar{x}$	50.14	38.36	9.36	8.48	15.54	12.85	21.07	31.60	49.31	6.02	20.03
	S.D.	5.18	4.23	0.52	1.59	2.33	1.73	2.90	3.17	5.94	1.08	2.28
	C.V.	10.12	11.73	6.21	19.65	15.95	13.71	14.18	10.75	12.43	18.44	11.93
VIII (18)	$\bar{x}$	49.42	42.25	9.66	8.97	16.41	13.33	21.05	36.71	48.25	6.58	19.28
	S.D.	5.06	5.99	0.19	1.89	2.52	3.34	3.86	2.99	4.86	0.84	1.96
	C.V.	10.19	14.41	2.04	21.45	15.60	25.79	18.91	8.64	10.14	13.20	10.46
IX (35)	$\bar{x}$	55.80	44.07	9.77	9.84	18.52	14.37	24.70	39.35	54.19	6.79	21.70
	S.D.	4.96	4.75	0.54	1.57	2.58	1.42	2.82	3.77	4.40	1.14	2.80
	C.V.	9.84	11.80	6.09	16.27	14.44	10.24	11.48	10.74	8.74	17.19	13.47
Females		NPP	ZMB	BCW	IOB	ZYW	WR	NA	WI	PAC	UTR	LJI
I (11)	$\bar{x}$	28.35	17.40	14.93	9.39	27.71	6.55	4.78	1.65	2.99	4.49	6.14
	S.D.	3.02	1.87	1.40	0.88	3.48	0.62	0.92	0.42	0.34	0.68	0.84
	C.V.	11.21	11.33	9.01	13.11	13.62	9.98	19.27	25.13	11.10	15.20	14.25
II (17)	$\bar{x}$	33.40	18.73	16.20	9.78	26.33	8.17	6.53	2.33	3.54	6.30	8.31
	S.D.	2.06	1.28	0.90	0.83	3.60	1.02	1.06	0.47	0.49	0.44	1.42
	C.V.	6.50	7.31	6.22	8.20	14.88	12.25	16.26	20.12	14.12	7.10	17.35
III (19)	$\bar{x}$	35.03	19.77	16.18	9.73	26.15	8.56	6.71	2.58	3.46	6.84	8.02
	S.D.	2.16	0.91	2.05	0.46	3.16	0.99	0.96	0.58	0.38	0.69	1.13
	C.V.	6.50	5.21	13.47	5.11	12.72	12.23	14.22	22.13	11.08	10.16	14.26
IV (9)	$\bar{x}$	36.84	20.82	17.11	9.74	27.61	8.58	6.83	2.45	3.65	7.53	8.16
	S.D.	1.91	1.44	0.83	0.43	2.57	0.52	0.98	0.25	0.57	0.72	1.47
	C.V.	5.64	7.48	5.28	4.14	9.85	6.17	14.32	10.08	16.19	10.24	18.49
V (31)	$\bar{x}$	40.99	22.33	18.15	10.21	31.55	9.73	8.11	2.91	3.82	8.28	8.88
	S.D.	5.02	2.09	1.29	1.06	3.55	1.06	1.14	0.51	0.45	0.79	1.58
	C.V.	12.90	9.38	7.23	10.19	11.64	11.19	14.21	18.09	12.08	10.14	18.28
VI (14)	$\bar{x}$	41.27	21.93	17.51	10.09	32.15	9.94	8.25	3.18	3.76	8.27	9.40
	S.D.	4.04	1.40	0.92	0.67	4.06	1.05	1.07	0.45	0.46	0.38	1.45
	C.V.	10.08	6.37	5.24	7.18	13.08	11.28	13.29	14.12	12.12	5.10	15.38
VII (9)	$\bar{x}$	38.84	22.04	17.65	10.10	30.93	9.31	7.83	2.95	3.49	8.04	9.33
	S.D.	2.76	1.65	0.91	0.60	2.33	0.61	0.74	0.36	0.40	0.45	2.05
	C.V.	7.92	7.45	5.30	6.20	8.78	7.21	9.25	12.12	11.13	6.15	22.68
VIII (15)	$\bar{x}$	44.38	23.68	18.40	10.47	34.97	10.78	4.98	3.35	4.00	8.65	10.86
	S.D.	4.50	2.27	0.93	0.68	4.34	1.36	1.35	0.52	0.47	0.49	2.10
	C.V.	10.16	10.59	5.24	6.18	12.12	13.35	27.35	16.13	12.12	6.13	19.54
IX (26)	$\bar{x}$	45.03	24.11	18.76	10.76	36.07	11.31	9.26	3.44	4.07	8.88	10.79
	S.D.	4.45	1.76	1.02	0.96	4.45	2.19	1.60	0.58	0.42	0.55	1.65
	C.V.	10.87	7.34	5.20	9.19	12.87	19.43	17.31	17.11	10.08	6.11	15.32

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Table 1 (*continued*)

Females (continued)		MLT	MDL	MTR	AFL	AFA	MAF	MRH	GLS	ITC	UJI	GHS
I (11)	$\bar{x}$	32.03	22.53	4.45	4.88	10.26	7.46	11.19	40.53	30.13	4.10	13.62
	S.D.	2.20	3.23	0.36	0.48	2.20	1.13	1.44	3.22	2.69	0.70	1.00
	C.V.	7.65	14.97	8.10	10.15	21.66	15.34	13.43	8.07	9.81	17.21	7.30
II (17)	$\bar{x}$	33.94	28.04	6.66	6.21	11.69	9.80	14.75	43.98	34.66	4.61	15.61
	S.D.	2.17	4.75	0.87	1.29	2.20	1.68	2.91	6.96	3.13	0.47	1.37
	C.V.	6.53	17.15	13.21	21.31	19.53	17.41	20.71	16.25	9.76	10.11	9.33
III (19)	$\bar{x}$	34.27	28.30	6.76	6.16	12.29	9.62	14.17	45.96	36.24	4.63	15.82
	S.D.	2.18	4.57	0.65	1.05	2.63	1.32	2.99	3.61	2.40	0.52	0.99
	C.V.	6.50	16.04	10.15	17.24	21.60	14.31	21.69	8.97	7.55	11.12	6.23
IV (9)	$\bar{x}$	35.44	28.16	7.44	6.16	12.29	10.26	15.78	43.93	38.54	5.33	16.37
	S.D.	2.56	3.46	0.75	0.86	1.13	1.53	2.25	2.17	2.89	0.57	0.69
	C.V.	7.85	12.15	10.25	14.29	9.38	15.51	14.75	5.72	7.96	11.19	4.23
V (31)	$\bar{x}$	39.86	34.12	8.19	7.55	13.89	11.30	17.71	48.63	42.78	5.39	17.66
	S.D.	3.35	4.51	0.76	1.04	1.38	1.30	2.82	4.99	3.70	0.75	1.46
	C.V.	8.60	13.80	9.14	14.19	10.24	12.23	16.51	10.29	9.66	14.13	8.26
VI (14)	$\bar{x}$	40.99	35.01	8.36	7.60	13.82	11.45	18.02	49.41	43.68	5.40	17.56
	S.D.	3.35	4.71	0.51	1.86	2.31	1.76	2.54	4.39	4.43	0.71	1.08
	C.V.	8.89	13.26	6.13	24.50	17.62	15.47	14.68	9.86	10.16	13.19	6.29
VII (9)	$\bar{x}$	41.79	32.94	8.13	6.80	13.24	10.70	17.77	31.09	41.90	5.26	17.31
	S.D.	2.80	3.38	0.49	0.70	0.96	1.15	1.78	3.37	2.78	0.50	0.83
	C.V.	7.94	10.13	6.16	10.23	7.32	11.38	10.59	11.27	7.93	10.17	5.28
VIII (15)	$\bar{x}$	45.80	38.50	8.69	9.04	14.95	12.70	20.57	38.09	46.88	6.20	18.81
	S.D.	4.48	4.66	0.51	1.42	2.31	1.61	2.52	2.88	4.71	0.91	1.79
	C.V.	10.15	12.20	6.13	16.37	15.60	13.41	12.65	8.89	10.22	15.23	10.46
IX (26)	$\bar{x}$	48.23	37.50	8.81	8.91	15.60	12.82	21.20	42.11	47.66	6.20	19.55
	S.D.	4.49	4.75	0.60	2.89	1.85	1.70	2.75	5.94	4.25	0.77	1.86
	C.V.	9.88	13.93	7.12	32.57	12.36	13.33	13.54	14.24	9.83	12.15	10.36

relatively older age classes was further assessed by two independent ANOVAs and *%SSQ* analyses of individuals of age classes 1–4 and age classes 5–9.

The ANOVA of the relatively younger age classes showed that all 22 measurements differed significantly among age classes (Table 5). None of the measurements differed significantly between the sexes, but one measurement only (UJI) showed significant interaction between sexual dimorphism and age. 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 either sex (*%SSQ*: 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). The *%SSQ* computations of age classes 1–4 also showed higher mean *%SSQ* values for the error component than for either age (*%SSQ*: $\bar{x}$ = 59.75, range = 26.06–89.25), sex or the interaction between age and sex (Table 5) suggesting that other factors may be responsible for non-geographic variation in the giant mole-rat rather than age variation and sexual dimorphism alone.

The ANOVA of the relatively older age classes 5–9 (Table 6) showed 21 of the 22 measurements to differ significantly among age classes, 20 differed significantly for sexual dimorphism with males being larger than females, and five showed significant interaction between sex and age. Of particular significance is that the ANOVAs 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 6). Similar to the analysis of the younger age classes 1–4, the *%SSQ*

Table 2. *F*-values and percentage sum of squared (%*SSQ*) of each source of variation derived from a two-way analysis of variance (ANOVA) of nine relative age classes (1–9; Fig. 1; Appendix 1) based on the degree of tooth eruption and wear in male and female giant mole-rats, *Fukomys mechowii.* Statistical significance: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; $n = 265$; d.f. = 1,8. Cranial measurements are illustrated in Fig. 2 and described in Appendix 2.

Cranial measurement	*F*-value			%*SSQ*			
	Age (A)	Sex (S)	A × S	Age (A)	Sex (S)	A × 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
CPL	23.11***	7.20**	0.77	41.52	1.62	1.39	55.47
ATP	24.33***	12.38***	1.62	41.67	2.65	2.79	52.89
APL	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

computations 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 either 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 6), suggesting that other factors may be responsible for non-geographic variation in the giant mole-rat rather than sexual dimorphism and age variation alone.

Evidence for the lack of sexual dimorphism in the relatively younger age classes and its presence in the relatively older age classes is apparent in independent PCAs of these age class groupings (Figs 5 and 6, respectively). This is also evident if these results are compared with the PCA of the total sample (Fig. 3), standard descriptive statistics of craniometric data (Table 1), and in results of the Mann-Whitney *U*-tests of body mass data (Fig. 7) which showed statistically significant differences in overall body size between the sexes in the older age classes, with males being larger and heavier than females.

DISCUSSION

Both univariate and multivariate analyses undertaken in the present study showed the presence of statistically significant age variation within the giant mole-rat, but a lack of sexual dimorphism in younger individuals of relative age classes 1–4. While these analyses also showed the presence of statistically significant age variation in the older relative age classes 5–9, these age classes also showed sexual dimorphism with males being larger than females. The absence of sexual dimorphism in the relatively younger age classes, and its presence in the relatively older age classes, is also supported by data on body mass.

Overall, the relatively younger and older age class groupings are also craniometrically 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,

Table 3. Multiple range Student-Newman-Keuls (SNK) tests of tooth-wear classes 1–9 (I–IX) of giant mole-rats, *Fukomys mechowii*. Non-significant subsets ($P > 0.05$) of ranked means ± standard deviation are indicated by horizontal lines; NS = not significantly different; AS = all means significantly different; the sample size (n) is indicated in barckets. Measurements are described in Appendix 2 and illustrated in Fig. 2.

Measurement	Tooth-wear class (*n*)								
	I (18)	II (22)	III (26)	IV (21)	V (41)	VI (28)	VII (15)	VIII (33)	IX (61)
NPP	28.05 ± 2.99	33.45 ± 2.56	34.95 ± 2.26	37.37 ± 3.31	41.7 ± 4.93	43.16 ± 5.14	41.78 ± 5.11	45.03 ± 4.36	48.44 ± 5.27
NAS	4.82 ± 0.96	6.5 ± 1.00	6.67 ± 0.86	7.16 ± 1.22	8.31 ± 1.21	8.66 ± 1.27	8.56 ± 1.53	9.23 ± 1.43	10.41 ± 1.82
ZMB	17.52 ± 1.74	19.01 ± 1.36	20.07 ± 1.15	20.79 ± 2.00	22.41 ± 2.07 AS	22.75 ± 2.33	23.44 ± 2.61	23.96 ± 2.27	25.70 ± 2.27
WI	1.51 ± 0.41	2.29 ± 0.45	2.55 ± 0.51	2.62 ± 0.55	3.05 ± 0.61	3.28 ± 0.53	3.22 ± 0.56 AS	3.48 ± 0.57	3.83 ± 0.65
BCW	15.08 ± 1.27	16.33 ± 0.87	16.51 ± 1.88	17.17 ± 1.11	18.12 ± 1.21	18.30 ± 1.46	18.24 ± 1.23	18.53 ± 1.11	19.37 ± 1.16
PAC	3.00 ± 0.32	3.50 ± 0.45	3.49 ± 0.36	3.58 ± 0.65	3.88 ± 0.49 NS	3.96 ± 0.5	3.84 ± 0.69	4.36 ± 1.08	4.38 ± 0.56
IOB	9.34 ± 0.70	9.81 ± 0.77	9.75 ± 0.41	9.85 ± 0.48	10.33 ± 0.99	10.58 ± 0.97	10.47 ± 0.7	10.59 ± 0.76	11.26 ± 1.18
UTR	4.57 ± 0.72	6.31 ± 0.39	6.81 ± 0.62	7.44 ± 0.62	8.30 ± 0.72	8.83 ± 0.66	8.54 ± 0.78	9.24 ± 0.64	9.45 ± 0.72
ZYW	21.88 ± 3.07	26.28 ± 3.35	26.48 ± 2.92	28.24 ± 4.22	32.45 ± 3.91 AS	33.68 ± 4.75	33.66 ± 5.04	36.10 ± 4.65	39.66 ± 5.43
LJI	5.76 ± 0.88	8.27 ± 1.40	8.10 ± 1.08	7.93 ± 1.27	8.91 ± 1.46	10.00 ± 1.76	9.52 ± 1.98	10.88 ± 2.38	11.52 ± 2.03
WR	6.57 ± 0.66	8.15 ± 0.96	8.52 ± 0.87	8.91 ± 1.16	9.95 ± 1.19	10.66 ± 1.75	–	11.36 ± 1.61	12.61 ± 2.23
MLT	31.78 ± 2.59	33.75 ± 2.30	34.56 ± 2.25	35.93 ± 2.75	40.34 ± 3.18	43.04 ± 5.66	–	47.77 ± 5.07	52.57 ± 6.05
MDL	21.57 ± 3.00	28.10 ± 4.21	28.75 ± 4.35	29.31 ± 3.30	35.07 ± 4.91	35.97 ± 4.88 AS	35.10 ± 4.53	40.55 ± 5.67	41.27 ± 5.74
GLS	31.60 ± 3.17	36.71 ± 3.00	39.35 ± 3.77	41.53 ± 5.25	44.95 ± 6.80 AS	47.31 ± 4.44	47.00 ± 5.55	49.60 ± 5.00	53.40 ± 5.43
MTR	4.52 ± 0.48	6.63 ± 0.79	6.71 ± 0.57	7.36 ± 0.65	8.21 ± 0.68	8.90 ± 0.69	8.62 ± 0.79	9.22 ± 0.61	9.36 ± 0.74
ITC	30.00 ± 2.81	34.92 ± 3.21	37.39 ± 3.91	39.57 ± 5.25	43.80 ± 4.25	45.21 ± 5.09	44.86 ± 5.58	47.63 ± 4.77	51.41 ± 5.39
AFL	4.81 ± 0.60	6.27 ± 1.13	6.26 ± 0.95	6.55 ± 1.42	7.85 ± 1.41	7.89 ± 1.55	7.47 ± 1.38	9.00 ± 1.67	9.44 ± 2.55
UJI	3.87 ± 0.64	4.66 ± 0.44	4.65 ± 0.59	4.97 ± 0.60	5.58 ± 0.80 NS	5.42 ± 0.74	5.56 ± 0.85	6.41 ± 0.88	6.54 ± 1.04
AFA	9.84 ± 1.81	11.89 ± 2.03	12.54 ± 2.55	12.53 ± 2.45	14.10 ± 1.52 AS	14.51 ± 2.26	14.16 ± 1.95	15.75 ± 2.50	17.28 ± 2.71
GHS	13.51 ± 1.05	15.59 ± 1.26	16.09 ± 1.30	16.61 ± 1.41	18.00 ± 1.53 AS	18.39 ± 1.78	18.40 ± 2.04	19.06 ± 1.87	20.78 ± 2.65
MAF	7.26 ± 1.09	9.89 ± 1.54	10.39 ± 3.15	10.19 ± 1.82	11.61 ± 1.68	11.65 ± 1.7	11.56 ± 1.73	13.04 ± 2.67	13.71 ± 1.72
MRH	10.92 ± 1.26	14.83 ± 2.64	14.55 ± 2.88	15.88 ± 2.82	18.23 ± 2.91	–	19.09 ± 2.76	20.83 ± 3.28	23.2 ± 3.27

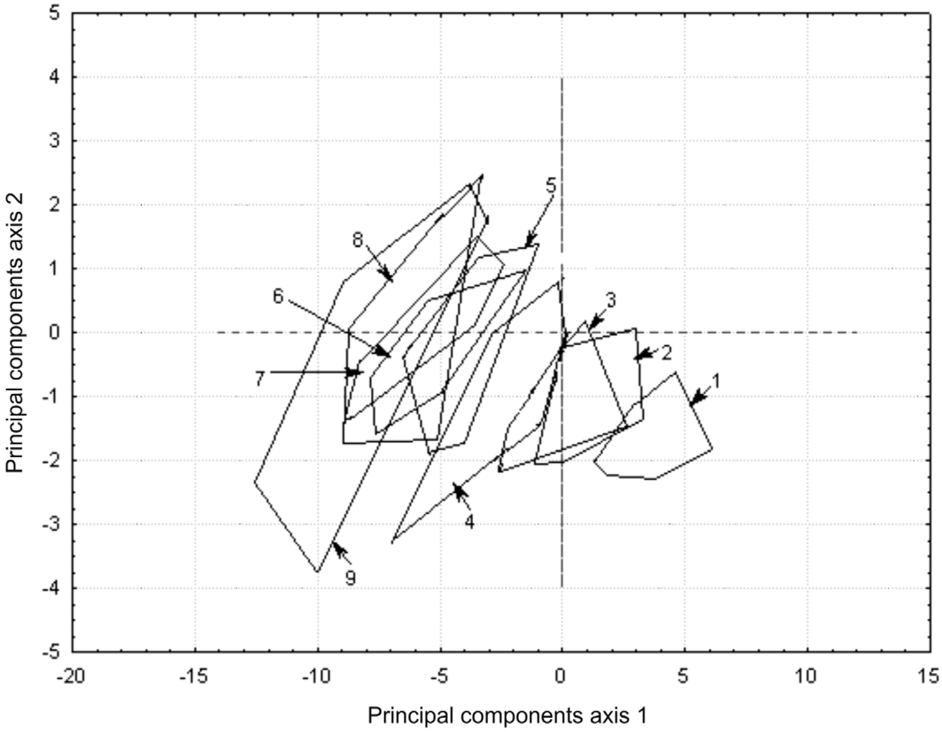

Fig. 3. A plot of the first two principal components from a principal components analysis of giant mole-rats, *Fukomys mechowii*, of tooth-wear classes 1–9 (Fig. 1; Appendix 1). Minimum convex polygons enclose individuals of each tooth-wear class, which together with their associated sexes have been omitted for clarity.

suggesting that age class 4 lies at a point on a hypothetical growth curve where growth begins to stabilize. The intermediate placement of age class 4 in multivariate space broadly coincided with body mass categorizations of individuals into juveniles (age classes 1–3; <100 g), subadults (age class 4; *c.* 100–150 g), and adults (age classes 5–9; >150 g). In addition, sexual dimorphism in relatively older age classes 5–9 was also evident in body mass data with males being heavier than females.

Sichilima *et al.* (2008b) found that among adult females of age classes 5–9, breeding females were generally the heaviest in the colony, and a follow-up study is evaluating how breeding females compare in body size with males in this species. The results in the present study are broadly similar to the pattern found in the Zambian mole-rat, *Fukomys anselli* where Begall & Burda (1998) found that the growth rate in both sexes was similar until the 18–20th week, after which males were observed to grow faster than females. Similarly, Hart *et al.* (2007) reported that body length and body mass in the Cape dune mole-rat, *Bathyergus suillus* was also sexually dimorphic, with males being larger than females in relatively older rather than relatively younger individuals, suggesting that in mole-rats, the sexes may have different growth trajectories depending on reproductive, dominance hierarchy, and/or other strategies that need to be investigated further.

Sexual dimorphism, regardless of age class, has been demonstrated in other subterranean rodents such as the 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 & Jarvis 1986). Conversely, the absence of sexual dimorphism regardless of age class has been reported in other subterranean rodents such as 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*; Šumbera *et al.* 2007).

The results of the present study reveal that

Table 4. Relative loadings of cranial measurements from the first two principal components (I and II) of a principal components analysis of the giant mole-rat, *Fukomys mechowii,* of tooth-wear classes 1–9 (Fig. 1; Appendix 1). Cranial measurements are illustrated in Fig. 2 and described in Appendix 2.

	Principal components axes	
Cranial 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
CPL	–0.85	–0.22
ATP	–0.83	–0.06
APL	–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	77.57	4.05

differences between males and females are mainly due to overall body size and body mass, with males being larger and heavier than females. Similar results were found in the social Damaraland mole-rat (*F. damarensis*; Bennett & Faulkes, 2000) as well as in the solitary Cape dune mole-rat (*Bathyergus suillus*; Hart *et al.* 2007). These authors suggested that the increased size of older males in the Cape dune mole-rat may be due to an increase in male–male interactions during reproduction when males compete for reproductive opportunities. Hart *et al.* (2007) further suggested that massive fat deposits around the necks of male Cape dune mole-rats may act as a cushion for 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 interactions (A.M.S., pers. obs.).

O'Riain *et al.* (1996) found that dispersing male

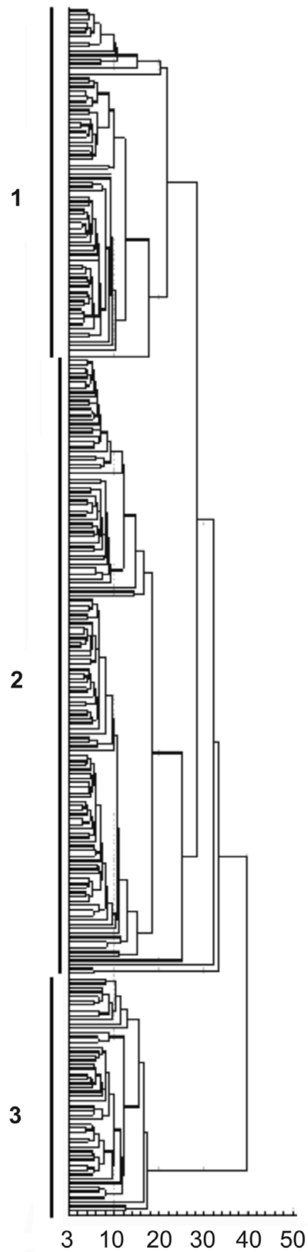

Fig. 4. An Euclidean distance phenogram from an unweighted pair-group method using arithmetic averages (UPGMA) cluster analysis of male and female giant mole-rats, *Fukomys mechowii,* of tooth-wear classes 1–9 (Fig. 1; Appendix 1) showing three distinct clusters of individuals comprising the following sample sizes, toothwear 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.

Table 5. *F*-values and percentage sum of squares (%*SSQ*) of each source of variation derived from a two-way analysis of variance (ANOVA) of four relative age classes (1–4; Fig. 1; Appendix 1) based on the degree of tooth eruption and wear in male and female giant mole-rats, *Fukomys mechowii.* Statistical significance: **P* < 0.05; ***P* < 0.01; ****P* < 0.001; *n* = 87; d.f. = 1,3. Cranial measurements are illustrated in Fig. 2 and described in Appendix 2.

Cranial measurement	*F*-value			%*SSQ*			
	Age (A)	Sex (S)	A × S	Age (A)	Sex (S)	A × 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
CPL	9.81***	1.17	0.53	26.46	1.06	1.42	71.06
ATP	11.60***	1.80	2.57	28.21	1.46	6.26	64.07
APL	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

Table 6. *F*-values and percentage sum of squares (%*SSQ*) of each source of variation derived from a two-way analysis of variance (ANOVA) of five relative age classes (5–9; Fig. 1; Appendix 1) based on the degree of tooth eruption and wear in male and female giant mole-rats, *Fukomys mechowii.* Statistical significance: **P* < 0.05; ***P* < 0.01; ****P* < 0.001; *n* = 127; d.f. = 1,4. Cranial measurements are illustrated in Fig. 2 and described in Appendix 2.

Cranial measurement	*F*-value			%*SSQ*			
	Age (A)	Sex (S)	A × S	Age (A)	Sex (S)	A × 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
CPL	5.64***	8.00***	0.85	3.95	11.51	1.68	82.86
ATP	8.26***	14.26***	0.90	6.52	15.09	1.64	76.75
APL	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

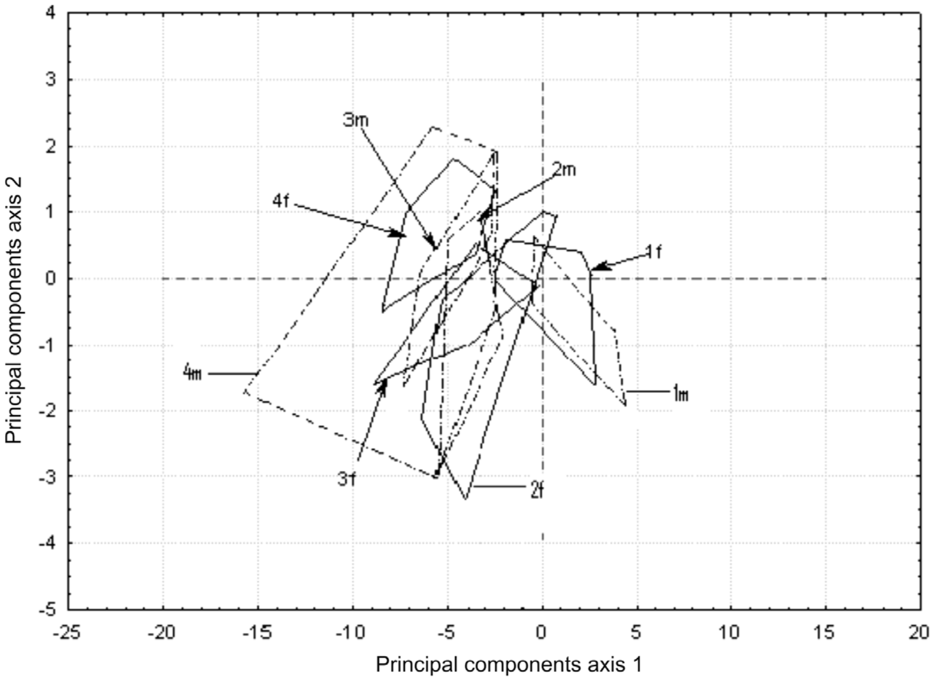

Fig. 5. A plot of the first two principal components from a principal components analysis of giant mole-rats, *Fukomys mechowii*, of relatively younger tooth-wear classes 1–4 (Fig. 1; Appendix 1). Dashed and continuous minimum convex polygons enclose male (m) and female (f) individuals of each relative age class (1–4), respectively.

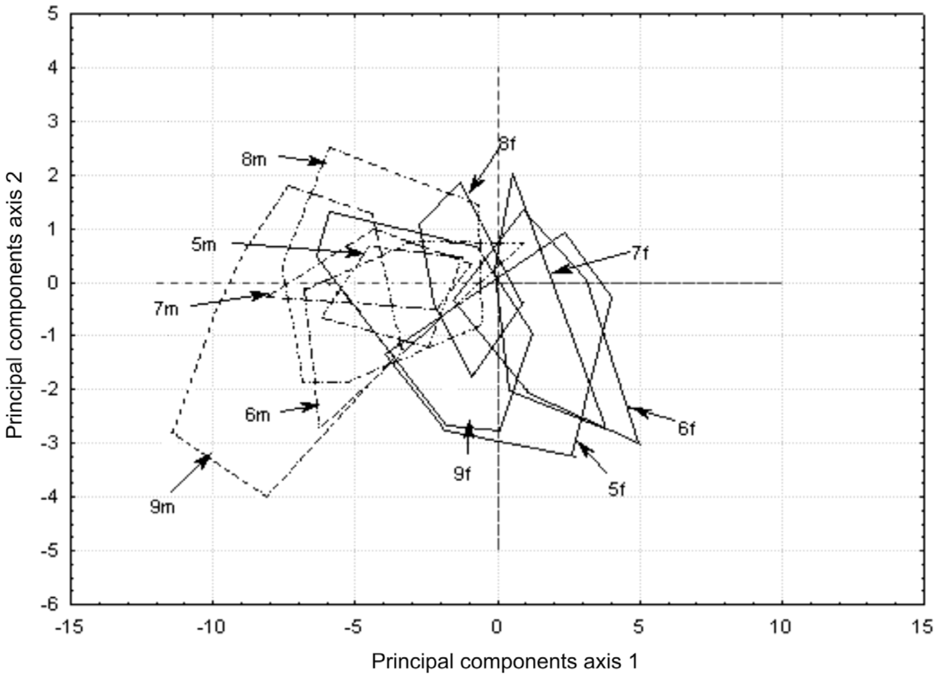

Fig. 6. A plot of the first two principal components from a principal components analysis of giant mole-rats, *Fukomys mechowii*, of relatively older tooth-wear classes 5–9 (Fig. 1; Appendix 1). Dashed and continuous minimum convex polygons enclose male (m) and female (f) individuals of each relative age class (5–9), respectively.

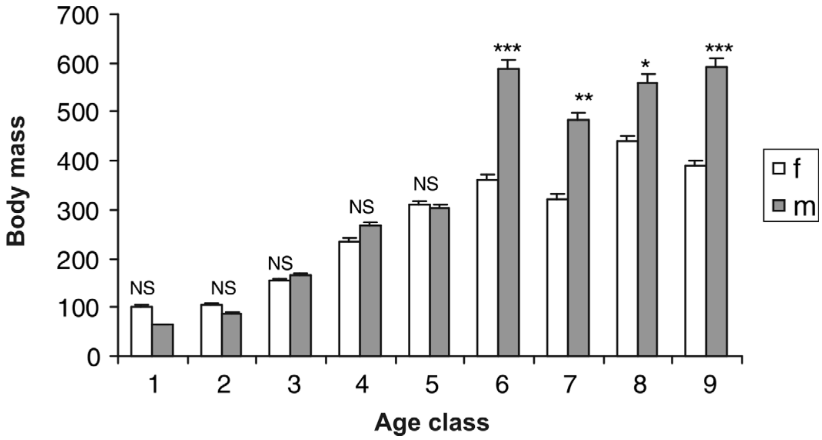

Fig. 7. A plot of nine relative age classes (1–9; Fig. 1; Appendix 1) and body mass (g) (± 2 standard errors of the mean) and results of Mann-Whitney *U*-tests of male (m) and female (f) giant mole-rats, *Fukomys mechowii*. Statistical significance: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; NS = not statistically significant; d.f. = 1,8; sample sizes (*n*) for each sex and age class are as indicated in Table 1.

naked mole-rats (*Heterocephalus glaber*) were usually larger than non-dispersing males of similar age. The lone dispersing males of the giant mole-rat have similarly been observed to be usually large in body size, with body mass ranging between *c.* 850 g and *c.* 1000 g (A.M.S., pers. obs.) which may skew the results in an analysis. 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. Sexual dimorphism in older and more dominant males may be a necessity for ensuring that pair-bonding in mole-rat colonies is maintained. Furthermore, dispersing male giant mole-rats need to be strong in order to either secure a mate or if they enter into existing colonies, to be able to entice and mate with one of the females. Indeed, giant mole-rats often show plural breeding within colonies and this may be the result of immigration of a large male transiently into the colony (Sichilima *et al.* 2008b).

Although other studies have argued that the estimation of age in mammals based on molar eruption and wear may not be suitable for 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 1970), studies on bathyergids including *Bathyergus suillus* (Hart *et al.* 2007), and indeed our study on *F. mechowii*, show that these estimators of absolute age can be informative. Our data suggest that in the absence of data on absolute ageing, the estimation of age based on molar eruption and wear in the giant mole-rat can provide useful ontogenetic data that can be related to other independent data (e.g. reproductive data; Sichilima *et al.* 2008a,b) to better understand the biology of this poorly-known species.

In addition, the use of body mass to estimate absolute age in mammals has also been considered inappropriate (Chaplin & White 1969). Similar to the findings in the study on the solitary Cape dune mole-rat (Hart *et al.* 2007), however, the results of our study show a general trend of greater body mass with increasing age. More importantly, similar to the craniometric data, sexual dimorphism in body mass in both the Cape dune mole-rat (Hart *et al.* 2007) and the giant mole-rat in the present study was absent in the younger age classes, but present in the older age classes. It is worth noting 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 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 relatively very large error (= residual) component in the derived *%SSQ* values. This suggests that, apart from the presence of ontogenetic (age) variation and sexual dimorphism in the giant mole-rat, there are other factors (such as different growth trajectories of males and females, or individual variation) that may be influencing non-geographic variation, and which need to be investigated further. Some of the important questions that need to be addressed include: 1) whether age- and sex-related craniometric variation is substantial enough to confound patterns of geographic and inter-specific variation, and 2) the nature of the interactive effect between ontogeny and sexual dimorphism which could allow other insights than explored in the present study. As in the case of the results in the present study, these additional studies will allow a better insight into our understanding of the population and social structures, and reproductive strategies in this little-studied mole-rat species.

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Appendix 1. Descriptions of the degree of the maxillary molar tooth-row eruption and wear used to assign individuals of the giant mole-rat, *Fukomys mechowii,* into nine (I–IX) relative age classes (Fig. 1) adopted and modified from Janse van Rensburg *et al.* (2004) and Hart *et al.* (2007).

Tooth-wear class	Description
I	Only two cheek teeth fully erupted, an emerging third cheek tooth still in a cavity, little sign of tooth-wear.
II	Three cheek teeth fully erupted, only the first two cheek teeth showing signs of tooth-wear.
III	Three cheek teeth fully erupted, an emerging fourth cheek tooth still in a cavity.
IV	Three cheek teeth fully erupted, with the fourth cheek tooth starting to surface.
V	All four cheek teeth erupted with no sign of tooth-wear on the fourth cheek tooth.
VI	All four cheek teeth erupted, fourth cheek tooth showing little signs of wear.
VII	All four cheek teeth erupted, fourth cheek tooth showing a fair amount of wear.
VIII	All four cheek teeth erupted, with deeply scooped dentine on all four cheek teeth.
IX	All four cheek teeth erupted with deeply scooped dentine on all four cheek teeth that are also deformed and reduced in height due to heavy tooth-wear.

Appendix 2. Abbreviations, descriptions and reference points of 22 cranial measurements (mm) of the giant mole-rat, *Fukomys mechowii,* used in the present study as adopted and modified from Janse van Rensburg *et al.* (2004) and Hart *et al.* (2007).

Abbreviation	Description and measurement reference points
GLS	Greatest length of skull, from the tip of the front of the incisors to the posterior part of the skull.
ITC	Incisor to condyle length, from the anterior surface of the incisor at alveolus to the most posterior projection of the occipital condyle.
BCW	Widest braincase breadth.
ZMB	Zygomatic breadth–parietal width.
ZYW	Greatest zygomatic width, between inner margins of the zygomatic arches, perpendicular to longitudinal axis of the skull.
IOB	Least breadth of the interorbital constriction.
WR	Width of the rostrum.
NA	Anterior width of nasals where they join with the premaxillae.
UTR	Crown length of maxillary tooth row, from the anterior edge of the first molar to the posterior edge of the last molar.
PAC	Hard palate width at point of constriction immediately posterior to the last molar.
NPP	The distance from anterior edge of nasals to the anterior edge of posterior part of the zygomatic arch.
GHS	Greatest height of skull, perpendicular to horizontal plane through bullae.
MLT	Greatest length of mandible, including teeth, from the posterior surface of condylar process to the tip of incisor.
MDL	Greatest length of mandible (excluding teeth), from the posterior surface of condylar process to anteroventral edge of the incisor alveolus.
MTR	Mandibular toothrow length, from the anterior edge of the first molar alveolus to the posterior edge of the last molar alveolus.
CPL	Coronoid process length to posterior edge of fourth molar.
ATP	Articular process length, from the ventral edge of mandibular foramen to mid-posterodorsal edge of the coronoid process.
APL	Angular process length at the middle of the mandible.
MRH	Mandibular-ramus height, from the dorsal edge of the coronoid process to the ventral edge of angular process.
UJI	Upper jaw incisor length, from the tip of the incisors to the base, where the teeth connect to the skull.
LJI	Lower jaw incisor length, from the tip of the incisor to the base, where the teeth connect to the skull.
WI	Width of the incisor where the incisor meets the premaxillae.