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Morphology and karyology of two populations of the woodland dormouse *Graphiurus murinus* in the Eastern Cape, South Africa

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A b s t r a c t . We compared cranial, dental, bacular and chromosomal variables between a population of *Graphiurus murinus* collected in riverine forest in the Andries Vosloo Kudu Reserve (AVKR) near Grahamstown (N= 32), and another from Afromontane forest at Hobbiton on Hogsback (HH), in the Amathole Mountains (N=21), Eastern Cape, South Africa. AVKR dormice were significantly larger in 13 out of a total of 23 cranial dimensions and they had a relatively longer rostrum. The 4th upper premolar was clearly longer and the tip of the baculum broader in the sample from HH. Discriminant function analyses of cranial and dental parameters perfectly separated the two samples. The karyotypes were the same at both localities (2n= 46; NFa = 92) but differed from previously reported karyotypes of *Graphiurus* species from Africa.

Key words: African dormice, skull, molars, baculum, morphometrics, karyotype

Introduction

Dormice of the genus *Graphiurus* are restricted to sub-Saharan Africa, where they are widely distributed, both geographically (H o l d e n 1993, R o s s o l i m o et al. 2001) and ecologically (R o s e v e a r 1969). The number of species recognised varies considerably, depending on the authority and the entire genus needs a thorough revision (H o l d e n 1996). G e n e s t - V i l l a r d (1978) recognised six species, but the number reported in more recent compilations is higher, e.g. thirteen in R o s s o l i m o et al. (2001) and fourteen in H o l d e n (1993), K i n g d o n (1997) and N o w a k (1999). The woodland dormouse *Graphiurus murinus* (Desmartes, 1822) has the broadest range in the genus (R o s s o l i m o et al. 2001). In southern Africa, *G. murinus* is one of four *Graphiurus* species currently recognised (M e e s t e r et al. 1986, S k i n n e r & S m i t h e r s 1990), but details of its distribution are not known due to confusion with the lesser savannah dormouse *Graphiurus parvus* (True, 1893); the latter, however, is most likely extralimital (R o s s o l i m o et al. 2001, B r o n n e r et al. 2003). The taxonomy of *G. murinus* is still far from being settled and karyological (D i p p e n a a r et al. 1983) as well as morphological evidence (T a y l o r 1998) suggest further taxonomic division in the southern African subregion (B r o n n e r et al. 2003). M e e s t e r et al. (1986) list 26 synonyms within *G. murinus* (including *G. microtis*) in southern Africa alone and call for taxonomic revision.

Linear cranial and dental measurements, as well as fur colour, tail bushiness and field measurements, have been used to distinguish southern African *Graphiurus* (R o b e r t s 1951), but to the best of our knowledge no detailed study of morphometric variation has ever been conducted. In this paper we report on differences between two woodland dormouse populations originating from two very different ecosystems, but sharing the same standard karyotype.

Material and Methods

Field work. – Material was collected from two localities in the Eastern Cape, South Africa:

1. Riverine forest in the Andries Vosloo Kudu Reserve (AVKR) near Grahamstown (located between 33°04' and 33°09'S and 26°37' and 26°49'E).

2. Afromontane forest at Hobbiton on Hogsback, in the Amathole Mountains (co-ordinates 32°33'S, 26°57'E). Both localities are on the very distributional margin of the *Graphiurus murinus* / *parvus* range (d e G r a a f f 1981).

In total, 55 woodland dormice were collected. The AVKR material (N=32) was obtained between January 30 and February 11, 2002, and the majority of that from Hobbiton (N=21) was from February 14–25, 2002. Two additional specimens were collected from Hobbiton on April 9, 2000.

Specimens were trapped using aluminium Sherman folding traps (23 x 8 x 9 cm) and PVC live traps (W i l l a n 1979). Traps were baited with rolled oats mixed with sunflower oil, or peanut butter. Captured animals were sacrificed and subjected to a standard mammalogical procedure (M o r r i s & W r o o t not dated). Voucher specimens (carded skins, skulls, and skeletons) have been deposited in the Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn (ZFMK).

M o r p h o l o g y . – Three age groups were distinguished on the basis of colour, tail bushiness, cheek-teeth patterns of eruption or abrasion, and on reproductive condition: juveniles, subadults, and adults. Details on ageing will be provided elsewhere.

Twenty-three linear measurements were scored on each skull using a vernier calliper to the nearest 0.1 mm (see Fig. 1). The greatest length (L) and width (W) of crown surfaces were scored on cheek teeth under a dissecting microscope fitted with an eyepiece graticule. The parameters were defined as being mutually orthogonal (Fig. 1). Upper cheek teeth are denoted by capitals (P – premolar, M – molars), and the lower ones by small letters. Position of a tooth in a row is designated by the number (anterior → posterior).

The baculum was examined using the technique described by A n d e r s o n (1960). Dry glans penis and the adjoining part of the corpus were removed from museum skins, soaked in water for 24 hours and then macerated for 2 to 4 days in 2–3% potassium hydroxide with a few drops of a saturated alcoholic solution of Alizarin Red S. The stained baculum was placed in glycerine and examined under a dissecting microscope fitted with an eyepiece graticule. Six measurements were taken (see Fig. 1).

C h r o m o s o m e s . – Four specimens from AVKR and seven from Hobbiton were karyotyped using the preparation of *in vivo* bone marrow chromosomes (R o b b i n s & B a k e r 1978). The slides were stained by Giemsa.

S t a t i s t i c s . – Samples were compared by various uni- and multivariate statistical tests. Normality in distribution was tested by Kolmogorov-Smirnov test. Statistical tests were run in Statistica 5.5 (1999).

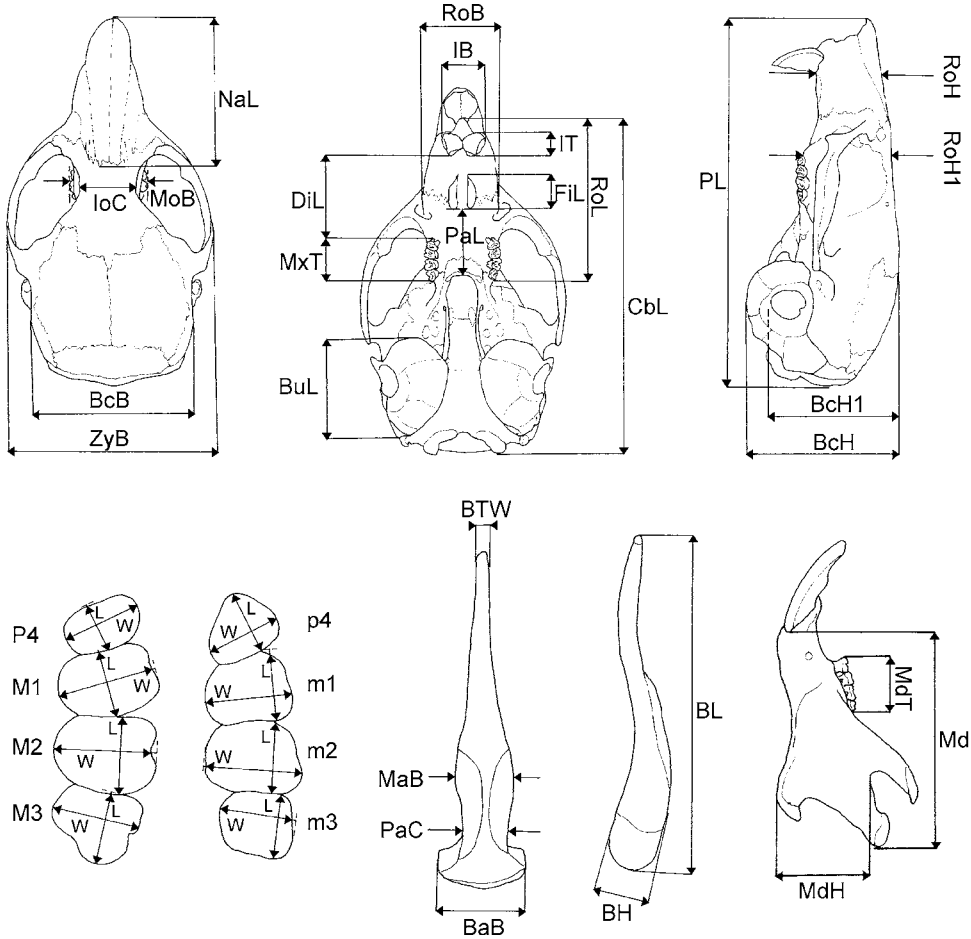

Fig. 1. Acronyms and definitions for cranial, dental and bacular characters used in this study. Cranial and Dental: PL – profile length, CbL – condylobasal length; RoL – length of rostrum; MxT – maxillary tooth-row length (alveolar); DiL – length of diastema; FiL – length of incisive foramen; BuL – length of bullae; PaL – length of palatine; NaL – nasal length; ZyB – zygomatic breadth; BcB – braincase breadth; IoC – interorbital constriction; RoB – rostrum breadth; MoB – upper molar breadth; BcH – braincase height across bullae; BcH1 – braincase height (bullae excluded); RoH – rostrum height behind incisors; RoH1 – rostrum height anterior to maxillary tooth-row; MdL – mandible length; MdT – mandibular tooth-row length (alveolar); MdH – height of mandibular rhamus; IB – combined breadth of upper incisors; IT – thickness of the upper incisor. Bacular: BL – baculum length; BaB – base breadth; PaC – proximal constriction; MaB – medial breadth, BTW – tip width; BH – height of baculum in lateral aspect.

Results

Sexual dimorphism

Significant sexual dimorphism was detected only on two cranial variables in the Hobbiton sample (at $p<0.05$): maxillary tooth row (males 3.90 ± 0.173; females 3.70 ± 0.076, t=2.80) and length of palate (males 5.20 ± 0.200 females 4.83 ± 0.255, t=2.27). Secondary sexual dimorphism is exceptional or entirely absent in dormice as demonstrated in *Dryomys nitedula*

(Kryštufek 1985), *Eliomys quercinus* (Grulich & Jurík 1994), *Graphiurus lorraineaus* (Holden 1996), and *Glis glis* (Kryštufek 2001). Being such a rare phenomenon, this source of variation is ignored in subsequent analyses.

Cranial dimensions

Adult dormice from AVKR were significantly larger than those from Hobbiton, in 13 out of 23 cranial dimensions (see Table 1). Greatest variation was found in RoL, DiL, Bc, RoH1, and IT. Bivariate comparisons revealed that Hobbiton dormice were not simply a smaller version of the AVKR ones. The two populations were characterised by differences in skull size and proportions (Fig. 2). Consequently, the 23 cranial dimensions were subjected to multivariate analyses.

Principal Components Analysis (PCA) was used to assess the overall cranial variation. Prior to analysis, data were $\log_{10}$-transformed to allow the application of linear statistics. The first two principal components combined explained slightly over half of the variance in the original data set (= 55.6%), suggesting a fairly low degree of inter-correlation among variables. Principal Component 1 (PC1) had high and positive character loadings for the majority of variables. Correlation analysis between PC1 scores and eight variables (PL,

Table 1. Cranial dimensions (mean, standard deviation, minimum–maximum) of two adult *Graphiurus murinus* populations. Values for t-test are given only for significantly different pairwise comparisons. P levels: * p<.05, ** p<.01. *** p<.001, **** p<.0001. See Fig. 1 for character designations.

	AVKR (N=19)		HH (N=11)		t-value
	mean ± SD	min–max	mean ± SD	min–max	
PL	29.04 ± 0.572	28.2–29.9	28.74 ± 0.522	27.9–29.6	
CbL	26.52 ± 0.529	25.5–27.7	26.03 ± 0.490	25.0–27.0	2.50*
RoL	12.47 ± 0.235	12.1–13.1	11.98 ± 0.189	11.6–12.3	5.91****
MxT	3.78 ± 0.205	3.4–4.1	3.75 ± 0.137	3.6–4.0	
DiL	6.062 ± 0.261	5.5–6.6	5.68 ± 0.154	5.4–5.9	4.41***
FiL	3.28 ± 0.242	2.6–3.6	3.15 ± 0.294	2.5–3.5	
PaL	5.23 ± 0.286	4.6–5.6	4.93 ± 0.290	4.3–5.4	2.74*
NaL	10.99 ± 0.394	10.4–11.7	10.82 ± 0.271	10.4–11.3	
BuL	7.57 ± 0.243	7.1–8.0	7.61 ± 0.278	7.3–8.1	
ZyB	16.18 ± 0.464	15.4–17.2	15.62 ± 0.449	14.9–16.3	3.21**
BcB	12.92 ± 0.335	12.2–13.6	12.51 ± 0.226	12.2–12.8	3.62**
IoC	4.72 ± 0.118	4.6–5.0	4.57 ± 0.131	4.3–4.8	3.28**
RoB	5.99 ± 0.166	5.6–6.3	5.86 ± 0.186	5.6–6.2	
MoB	6.12 ± 0.102	6.0–6.3	6.10 ± 0.201	5.8–6.5	
BcH	11.02 ± 0.252	10.5–11.6	10.72 ± 0.301	10.4–11.2	2.86**
BcH1	8.39 ± 0.161	8.1–8.7	8.15 ± 0.192	7.9–8.4	3.68***
RoH	6.01 ± 0.217	5.7–6.5	5.92 ± 0.183	5.6–6.2	
RoH1	7.48 ± 0.128	7.2–7.7	7.32 ± 0.060	7.2–7.4	3.89***
MdL	13.26 ± 0.310	12.6–13.9	13.14 ± 0.338	12.7–13.9	
MdT	3.37 ± 0.116	3.2–3.6	3.43 ± 0.129	3.2–3.7	
MdH	5.50 ± 0.180	5.2–5.8	5.27 ± 0.290	4.8–5.8	2.69*
IB	3.00 ± 0.139	2.7–3.2	2.78 ± 0.198	2.4–3.1	3.59**
IT	1.61 ± 0.058	1.5–1.7	1.53 ± 0.47	1.5–1.6	3.91***

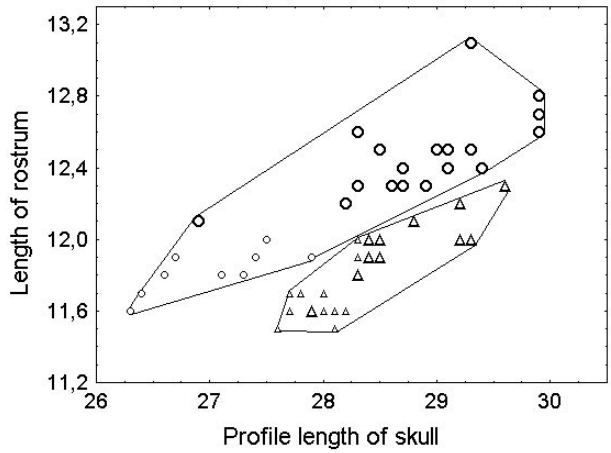

Fig. 2. Bi-variate plot of rostral length (RoL) against the profile length of skull (PL) for *Graphiurus murinus*. Circles – AVKR, triangles – HH; large symbols represent adults and small symbols refer to subadults.

CbL, RoL, NaL, ZyB, RoB, MdL, and IT) resulted in high correlation coefficients ($r>0.78$, $p<<0.0001$). Weak correlations were found for FiL, IoC, BcH, and MdT ($r<0.370$, $p<0.05$), while the correlations with MxT and BcH1 did not differ significantly from zero.

Maxillary and mandibular tooth-row lengths showed negative character loadings for PC1. Evidently, after the cheek-teeth row is formed early during postnatal development, it is not subject to further growth, thus it is independent of variation in the majority of other cranial parameters.

It was clear that PC1 explained mainly the size component, however more than half of the variance in the original data set (= 56.7 %) was due to a residual variance (i.e. size-out or shape) in skull structure (see L e m e n 1983).

Projection of specimens onto the first two principal components revealed reasonably good separation between the samples (Fig. 3). Subadults were separated from the adults along PC1, i.e. mainly according to their smaller size, while the two geographic samples differed in PC2 with AVKR dormice attaining lower scores. Principal Component 2 had high loading only for BcH1. A plot of PC2 against PC6 (a component with the highest character loading for BcB) provided even better separation between the two samples (Fig. 4). A bivariate plot of BcB against any of the variables with high character loadings for PC2 (BcH, BcH1, IoC, RoH1), however, did not separate satisfactorily between the two samples.

To achieve the best possible separation between the groups, the cranial data were subjected to Discriminant Function Analysis (DFA). Low Wilks' lambda (=0.0024) suggested high predictability. The first two discriminant functions (DF) explained 95.5 % of the variance in the original data set. First discriminant function (DF1) separated between the geographic samples, while DF2 distinguished between the age groups (Fig. 5). Surprisingly, the first two DFs explained nearly the same amount of the variance suggesting that interpopulation differentiation was of a similar magnitude as was the distance between the age groups. All squared Mahalanobis distances among the four groups were highly significant ($p<0.0001$).

When age variation was ignored and DFA run on combined adult-subadult samples from the two localities, the specimens were still classified into their actual group. The analysis,

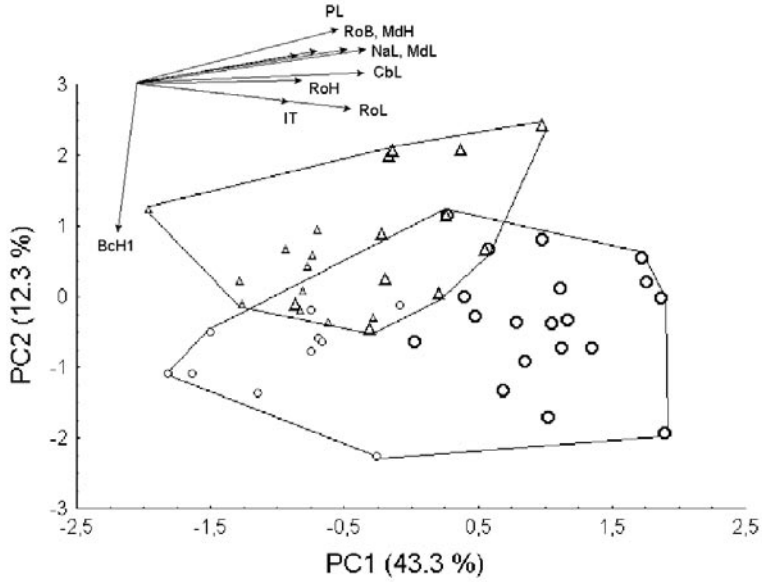

Fig. 3. Projection of specimens onto the first two principal components derived from a PCA on 23 log-transformed cranial variables. Share of variance explained by a particular PC is in parentheses. Character vectors are given only for variables with loadings for at least one of the two DFs of > 0.70. See Fig. 1 for character designations.

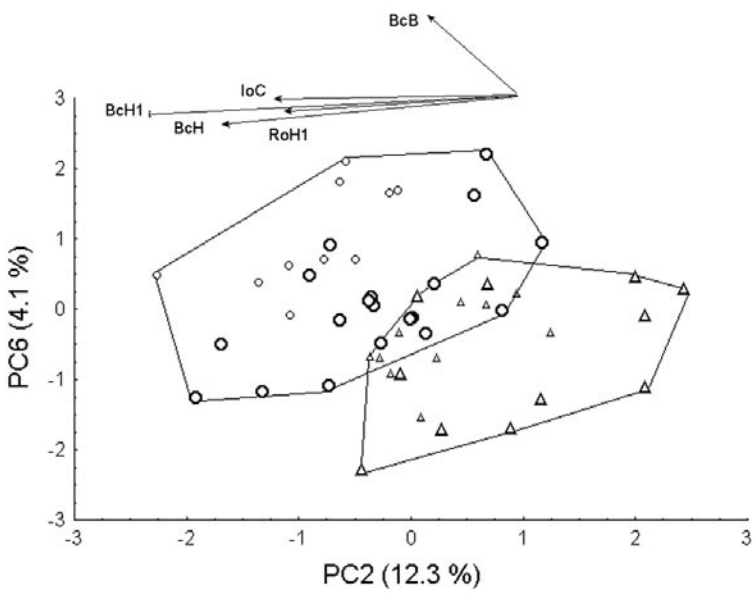

Fig. 4. Projection of specimens onto the principal components 2 and 6, derived from a PCA on 23 log-transformed cranial variables. Share of variance explained by a particular PC is in parentheses. Character vectors are given only for variables with loadings for at least one of the two DFs of > 0.50. See Fig. 1 for character designations.

however, lost some of its discriminatory power (Wilks' lambda = 0.074) and the resulting discriminant function achieved its highest loadings for PL, RoL, and BcB.

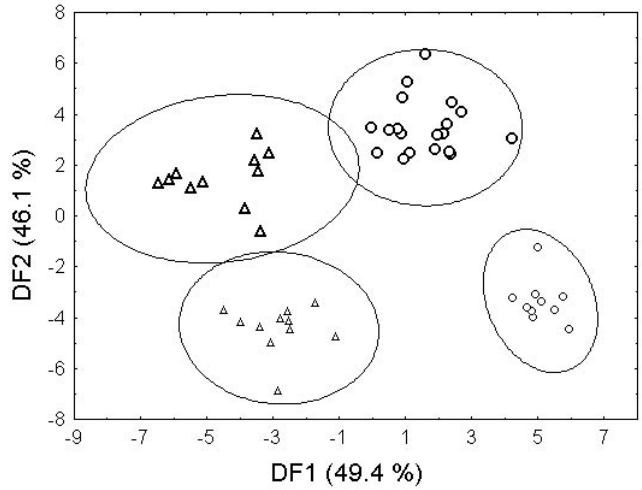

Fig. 5. Projection of specimens onto the first two discriminant functions derived from a DFA on 23 log-transformed cranial variables. Share of variance explained by a particular DF is in parentheses. See Fig. 1 for character designations.

Dental dimensions

Eight out of 16 cheek-teeth measurements differed significantly between the geographic samples (Table 2). The 3rd molars, both maxillary and mandibular, where the only teeth to show almost no variation. Hobbiton specimens, which had smaller cranial dimensions, exhibited significantly higher means in six dental parameters. The difference was particularly

Table 2. Cheek teeth dimensions (mean, standard deviation, minimum–maximum) in two *Graphiurus murinus* populations. See Table 1 for further explanation and Fig. 1 for character designations.

	AVKR (N=29-32)		HH (N=22-23)		t-value
	mean ± SD	min–max	mean ± SD	min–max	
P4W	1.07 ± 0.051	0.98–1.18	1.07 ± 0.049	0.98–1.18	
P4L	0.71 ± 0.048	0.62–0.82	0.81 ± 0.037	0.72–0.85	7.51****
M1W	1.32 ± 0.038	1.27–1.47	1.33 ± 0.052	1.24–1.44	
M1L	1.04 ± 0.054	0.92–1.14	1.11 ± 0.065	0.98–1.24	4.27****
M2W	1.38 ± 0.043	1.31–1.47	1.44 ± 0.044	1.34–1.54	4.97****
M2L	1.13 ± 0.047	0.98–1.24	1.12 ± 0.062	0.98–1.24	
M3W	1.18 ± 0.043	1.08–1.24	1.18 ± 0.057	1.08–1.27	
M3L	0.98 ± 0.048	0.92–1.08	0.99 ± 0.056	0.85–1.08	
p4W	0.94 ± 0.047	0.82–1.05	0.97 ± 0.059	0.85–1.08	2.25*
p4L	0.85 ± 0.039	0.78–0.95	0.93 ± 0.048	0.82–0.98	5.99****
M1W	1.28 ± 0.042	1.14–1.34	1.22 ± 0.051	1.11–1.31	4.56****
M1L	1.00 ± 0.036	0.92–1.08	1.04 ± 0.051	0.92–1.11	3.52**
M2W	1.32 ± 0.033	1.24–1.37	1.28 ± 0.038	1.21–1.37	3.84**
M2L	1.08 ± 0.050	0.98–1.18	1.06 ± 0.048	0.98–1.14	
M3W	1.01 ± 0.047	0.92–1.08	1.00 ± 0.059	0.88–1.14	
M3L	0.90 ± 0.035	0.85–0.98	0.92 ± 0.059	0.82–0.98	

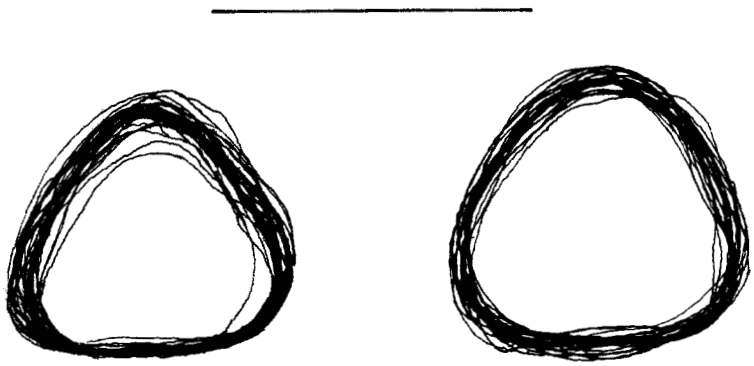

Fig. 6. Superimposition of the upper premolar outlines, separately for AVKR (left) and HH (right) *Graphiurus murinus*. Scale bar = 1 mm.

evident in the upper cheek-teeth, all of which were larger in the Hobbiton sample. The 1st and the 2nd lower molars were broader in AVKR dormice. The greatest dental difference was evident on the 4th upper premolar, which was longer in both absolute and relative terms, in Hobbiton animals (Fig. 6). The width / length ratio in the AVKR sample varied between 1.32–1.65 (mean = 1.50) and that from Hobbiton between 1.15–1.50 (mean = 1.34).

Discriminant Function Analysis on log-transformed cheek teeth parameters perfectly separated the two samples (Fig. 7). The length of both premolars had the highest character loadings.

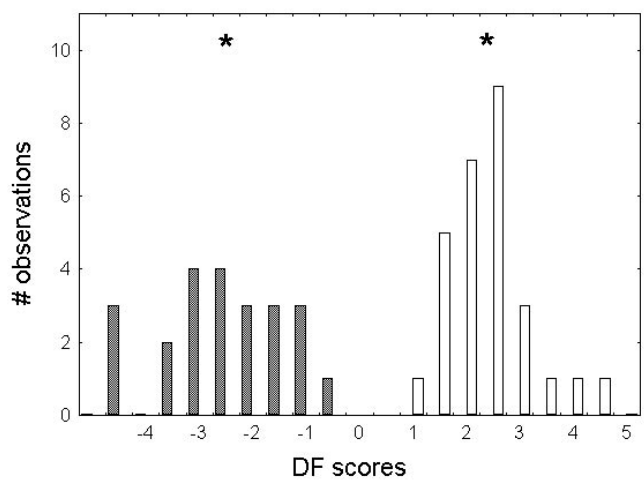

Fig. 7. Projection of specimens onto the dicriminant function derived from a DFA on 16 log-transformed cheek-teeth variables. HH – shaded; AVKR – blank. Asterisk is placed on a group centroid.

B a c u l u m

The baculum of *Graphiurus murinus* did not differ essentially from the condition seen in the European members of Gliridae (K r a t o c h v í l 1973, S i m s o n et al. 1994). The baculum was approximately of the same length as the *glans penis* and nearly reached the tip of the

ostium urethrae externum. It was a single bone of simple structure, composed of a prolonged distal shaft and of two basal expansions. Longitudinal crests were obvious along the proximal half of the bone on the ventral and dorsal side. The baculum was curved dorsally in its proximal part but the shape of the distal portion varied considerably among specimens (Fig. 8).

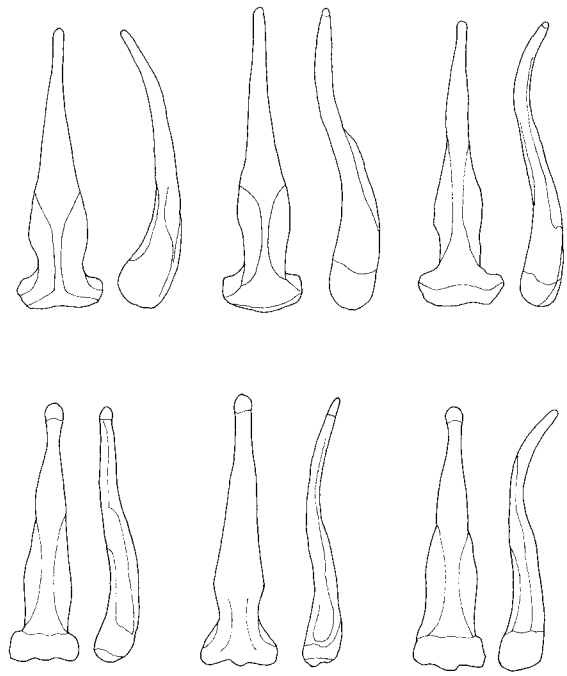

Fig. 8. Baculum (dorsal and lateral aspect) in *Graphiurus murinus* from AVKR (upper row) and Hobbiton (lower row).

Bacular dimensions are shown in Table 3. Three out of six parameters showed significant differences. No differences were found with respect to proximal constriction (PaC), medial breadth (MaB) and bacular height (BH). Dormice from the AVKR had a longer baculum but those from Hobbiton had a wider tip. Basal breadth (BaB) and bacular tip width (BTW) showed no overlap between populations thus allowing complete separation. Bias due to small sample sizes, however, is possible.

Table 3. Baculum dimensions (mean, standard deviation, minimum-maximum) in two *Graphiurus murinus* populations. See Table 1 for further explanation and Fig. 1 for character designations.

	AVKR (N=8)		HH (N=3)		t-value
	mean SD	min-max	mean ± SD	min-max	
BL	7.91 ± 0.342	7.37-8.51	7.37 ± 0.052	7.32-7.42	2.67*
BaB	2.33 ± 0.106	2.22-2.47	2.01 ± 0.089	1.96-2.11	4.65**
PaC	1.13 ± 0.101	0.98-1.23	1.16 ± 0.093	1.06-1.24	
MaW	1.51 ± 0.095	1.39-1.65	1.40 ± 0.083	1.34-149	
BtW	0.31 ± 0.040	0.26-0.39	0.49 ± 0.026	0.46-0.52	7.27****
BH	1.26 ± 0.117	1.13-1.44	1.14 ± 0.127	1.06-1.29	

K a r y o t y p e

The diploid number of chromosomes was 2N=46 in all the specimens studied. There were two large submetacentric pairs, five medium-sized and two small metacentric pairs. As all the chromosomes possessed a short arm, the number of chromosomal arms in the female karyotype was therefore NF=92. Eleven pairs of autosomes were submeta- and subtelocentric, with their size ranging from medium to small. The last two pairs of autosomes were distinctly smaller than the others, and apparently biarmed. The Y-chromosome was a dot-like element while the X-chromosome was one of the medium-sized metacentrics (Fig. 9).

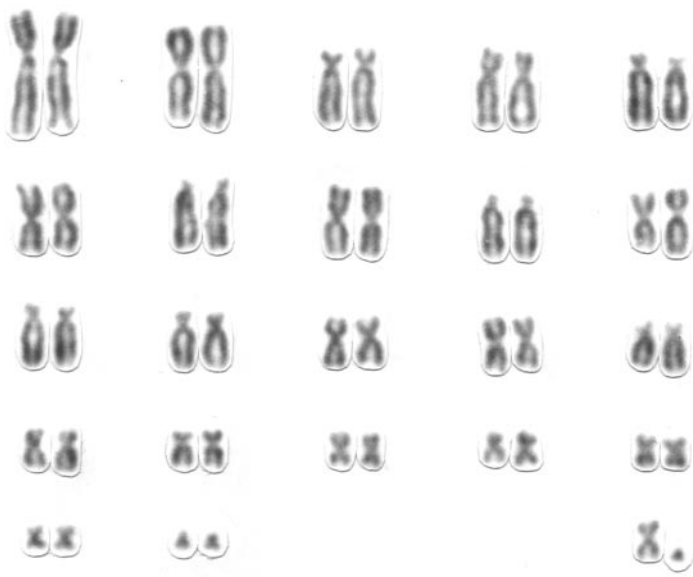

Fig. 9. Male karyotype of *Graphiurus murinus* from Hobbiton.

Discussion

The two samples studied came from different elevations and, although both shared the same karyotype, they differed significantly in several aspects of their morphology. It was difficult to interpret the karyotypic data due to a shortage of information on karyotypes of *Graphiurus* in the literature. R o b b i n s & B a k e r (1978) did not list any glirid species in their review of karyotypic data for African mammals. D i p p e n a a r et al. (1983) reported three diploid chromosomal types within *Graphiurus murinus s. lat*. throughout its range in southern Africa, but provided no details.

Previous chromosomal studies of *Graphiurus* were made in west and central Africa. T r a i n e r & D o s s o (1979) reported 2N=40 and NF=66 for *G. hueti*, and 2N=70 for *G. murinus* from Ivory Coast; D o b i g n y et al. (2002) reported 2N=70 for a single specimen provisionally referred to *G. parvus*, while C h i t a u k a l i et al. (2001) found 52 chromosomes in *G. microtis* from the Nyika Plateau in Malawi. These data indicate that there may be considerable karyotypic variation within African species of *Graphiurus*.

While the findings reported here are different from the diploid numbers reported for other African species of *Graphiurus*, the same diploid number of chromosomes has been reported

in the karyotypes of other glirids from Europe and Asia (certain populations of *Eliomys quercinus, E. melanurus, Muscardinus avellanarius* and *Glirulus japonicus* – see Z i m a et al. 1995 for a review; *Dryomys laniger* – K i v a n ç et al. 1997). This suggests that the diploid number of 46 may be ancestral within the family.

The karyotypes of *Eliomys* species were distinctly different in the detailed chromosome morphology from those of *Graphiurus murinus* (present study) while those of *Glirulus japonicus* and *Dryomys laniger* were not described in sufficient details to enable comparisons with other species. Remarkable similarity, however, can be found between the chromosomal sets of *Muscardinus avellanarius* (Z i m a 1987) and *Graphiurus murinus* (this study). The unexpected homology between karyotypes of these distantly related species should be further confirmed in chromosome banding studies.

Because of the fundamentally different ecological conditions between the lowland Valley Thicket vegetation (with riverine forest vegetation in seasonal river beds) on one hand and the Afromontane Forest on the other, at least some of the morphological difference might simply reflect adaptations to local environment. B r o w n et al. (1999) found that the Hogsback population of the vlei rat *Otomys irroratus* from moist Alpine grassland differed from its lowland (savanna) conspecific at Alice in having longer hair and relatively shorter tail. This was explained as an eco-morphological adaptation, enabling a lower minimum thermal conductance in the high altitude animals. Noteworthy, the two vlei rat samples differed also in karyotype (T a y l o r et al. 1994). The eco-morphological response of small mammals along the elevational gradient in southern Africa was also shown in the forest shrew *Myosorex varius* (body size) and the striped mouse *Rhabdomys pumilio* (relative tail length) in the Natal Drakensberg (R o w e - R o w e & M e e s t e r 1982) but B a x t e r (in press) questions the *M. varius* data. Contrary to the cited case studies, however, the observed interpopulation variation in the woodland dormouse is unlikely to be entirely due to a response to the local environment. *G. murinus* does show phenotypic differences which are presumably not subject to selective pressures (e.g. in tooth shape) and are of phylogenetic and taxonomic significance.

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