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A morphometric analysis of the skulls of *Xerus inauris* and *Xerus princeps* (Rodentia; Sciuridae)

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Abstract

Studied morphological and morphometrical differences of skulls of *Xerus inauris* and *X. princeps*. Among the qualitative characters, the colour of the incisivi is the best character to differentiate between the two species. Nine more characters turned out to be extremely useful for the identification of the skulls. In fourteen different skull measurements, the condylobasal length, occipitonasal length, interorbital width, postorbital width, nasalia width and incisivi diameter show highly significant differences between the two species. Skulls of *X. inauris* show a tendency to become smaller with narrower nasalia but increasing diameter of the incisivi from the Orange Free State (South Africa) to Namibia.

Introduction

The southern African ground squirrels *Xerus inauris* and *X. princeps* are rather similar in their general appearance: their pelage is cinnamon dorsally with a white lateral stripe and a white and black pattern on the tail. The discriminating characters for the skulls generally used in keys and descriptions (Ellerman et al. 1953; Amtmann 1975; de Graaff 1981; Smithers 1983) are the colour of the incisors (white in *X. inauris*, yellow to orange in *X. princeps*) and the orbit (also called diameter of the orbit or eye orbit) in relation to the occipitonasal length (orbit normally rather less than ⅓ of the occipitonasal length in *X. inauris* and normally more than ⅓ of occipitonasal length in *X. princeps*).

While the first discriminating character (colour of the incisivi) allowed identification of the two squirrel species, the second discriminating character (orbit to occipitonasal length) in use so far seemed very unsatisfactory and will be discussed in more detail later in this paper. Until quite recently even their status as different species seemed debatable (Grubb 1978) and there were doubts whether the skull measurements would withstand a discriminant analysis (de Graaff 1981). Therefore a detailed qualitative and quantitative investigation was initiated, which was coordinated by J. D. Skinner. The aim of this study was to check and measure a sufficient number of skulls, to elaborate and define the differences, and perform a multivariate linear discriminant analysis to answer the question of their species identity.

Material and methods

Skull morphology and morphometry

Altogether 302 skulls of *X. inauris* and 49 of *X. princeps* were examined. The material belonged to the following museums: Museum Alexander Koenig, Bonn; Kaffrarian Museum, King Williamstown; Museum of Natural History, London; Naturhistorisches Museum Wien, Vienna; State Museum of Namibia, Windhoek; Transvaal Museum, Pretoria.

Only skulls with complete definitive dentition were used to discern between the two species since too few skulls of younger specimens of *X. princeps* were available. Eight qualitative characters were established on the cranium and two on the mandible (Tabl. 1; Fig. 1). The form of the proximal end of the nasal bone, parieto-temporal suture and the shapes of the zygomatic process of the temporal bone

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and the maxillar process in front of the first cheek tooth were also examined but did not differentiate well between the two species and hence are not discussed any further. The characters were critically viewed by the senior author and then categorized as either typical for one of the two species or as intermediate.

The skull measurements taken are listed in Tab. 2 and illustrated in Fig. 2. In a smaller series the "orbit" or "orbital length" according to Moore's (1960) definition (the greatest inside distance from the anterior edge of the orbit, in the notch of the lacrimal bone, to the posterior extremity of the orbit on the edge of the zygomatic process of the squamosal) was also measured.

Data analysis

The main tool of the data analysis was a multivariate linear discriminant analysis. This method produces scores which very efficiently discriminate between the groups under study. These scores are linear combinations of the original characters computed for each group and separate the groups better than any of the characters considered on their own. Before the analysis those characters were excluded which did not show significant differences among groups at the 5 % probability level in an univariate F-test.

The analysis compresses the information contained in the full character set from each individual into canonical scores for various combinations of characters (factor) and calculates the value of each factor for separating the population into groups on the basis of the proportion of the total variance accounted for by each factor.

As in other statistical methods, discriminant analysis depends on certain assumptions, such as multivariate normal distribution of the data and the equality of the group covariance matrices. However, even if these assumptions are not satisfied completely the analysis remains a powerful tool for data analysis. To evaluate the efficiency of an analysis, one can simply look at the graphical representation of the results given as the so-called canonical scores (see below). Furthermore, one can classify the original data according to the results of the group classification analysis. The number of misclassifications is an indication of the degree of overlap between the groups or of some irregularities in the data set.

With canonical functions the information contained in the full character set is compressed into the new scores and a high percentage of the total information is included in a few derived scores. For the graphical representation of the results, we generally use the two most important scores to produce scattergramms if more than two groups were entered for the analysis. An analysis involving two groups produces one-dimensional scores only. In these cases data are presented as probability distribution estimated by a histogram method (van Ryzin 1973).

Results

Skull morphology

The colour of the incisivi (white in *X. inauris* and yellow to orange in *X. princeps*) turned out to be the best discriminant character. The differences in other skull characters of the two species are illustrated in Fig. 1. Additional explanations and comments are given in Tab. 1. Altogether, these characters can be regarded as extremely useful for the identification of skulls (or even certain parts of the skulls) of *X. inauris* and *X. princeps*. The rate of misclassifications is low (0.4–3.0 %); intermediate results occur at a rate of 4.8–22.9 %.

Skull morphometry

Fourteen different measurements were taken from each skull (Fig. 2). Occasionally skulls were damaged and hence only some of their characters could be measured. The results are listed in Tab. 2. An univariate F-test for single characters reveals highly significant differences between the two species in condylobasal length, occipitonasal length, interorbital width, postorbital width, nasalia width and the incisivi diameter (Tab. 3). The most discriminating character is the nasalia width.

The orbital length in 30 skulls of *X. inauris* was shorter than or equal to (0.3 mm–0.0 mm) one third of the occipitonasal length in three cases only and from 0.3 mm to 1.9 mm longer than one third of the occipitonasal length in the remaining 27

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cases. In seven *X. princeps*, however, the orbital length was 0.87 mm to 2.3 mm longer than one third of the occipitonasal length.

Discriminant analysis

As the number of skulls (especially of *X. princeps*) examined is rather low, we tested whether males and females had to be analysed separately or could be lumped together. It is apparent from Fig. 3 that there is a large overlap among sexes in both species. Because of

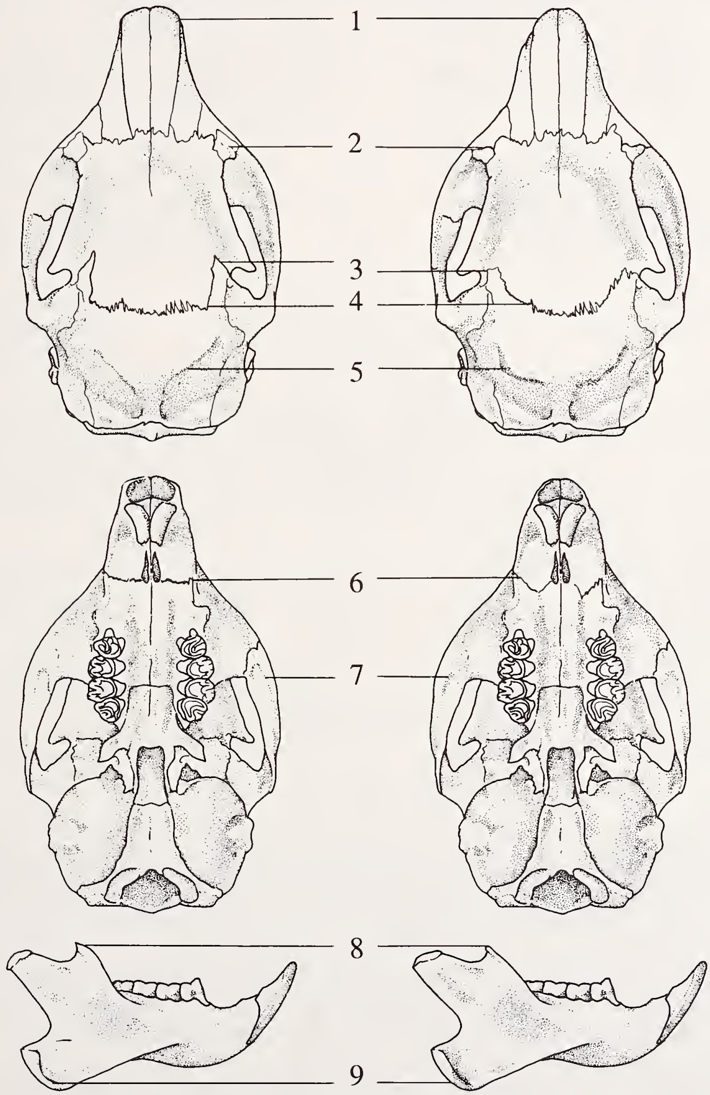

Fig. 1. Skulls of *X. inauris* (left) and *X. princeps* (right). Differences in qualitative characters on cranium and mandible (1-nasalia; 2-lacrimal bone; 3- and 4-fronto-parietal suture; 5-temporal crest; 6-maxillo-praemaxillar suture; 7-base of musculus masseter on zygomatic arch; 8-coronoid process; 9-angular process). See Tab. 1 for further explanations

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Table 1. **Differences in qualitative skull characters**
(see also Fig. 1)

Character	*Xerus inauris*	*Xerus princeps*	Comments
Incisivi colour	white; intermediate: yellow tinge	yellow to orange	a good character with no misclassifications
Nasalia – form of the distal end	clearly broader than the proximal end; intermediate: just sligthly widened Fig. 1:1	narrow, not essentially broader than the proximal end Fig. 1:1	a good character; 1,3 % misclassification in *X. i.*; intermediate results in 7.7 % of *X. i.* and 11.4 % of *X. p.*
Shape of lacrimal bone	roundish Fig. 1:2	longish Fig. 1:2	a fairly good character; 0.4 % misclassification in *X. i.* and 2.9 % in *X. p.*; intermediate results in 4.8 % of *X. i.* but in 22.9 % of *X. p.*
Form of fronto-parietal suture – lateral end	pointed Fig. 1:3	rounded Fig. 1:3	a good character; 1.8 % misclassification in *X. i.*; intermediate results in 13.5 % of *X. i.*
Form of fronto-parietal suture – middle part	see Fig. 1:4	see Fig. 1:4	a good character; 0.4 % misclassification in *X. i.*; intermediate results in 4.4 % of *X. i.* and 11.8 % of *X. p.*
Form of temporal crest	see Fig. 1:5	see Fig. 1:5	a good character; 0.4 % misclassification in *X. i.* and 3 % in *X. p.*; intermediate results in 7.7 % of *X. i.* and 12.1 % of *X. p.*
Maxillo-praemaxillar suture	see Fig. 1:6	see Fig. 1:6	a good character
Base of musculus masseter on the zygomatic arch	pointed end Fig. 1:7	roundish end Fig. 1:7	a good character
Shape of coronoid process	see Fig. 1:8	see Fig. 1:8	a good character
Shape of angular process	see Fig. 1:9	see Fig. 1:9	a good character

this and despite the fact that the second axis represents statistically significant ($p < 1$ %) differences between the four groups, the further analysis were performed with all specimens (with complete definitive teeth) irrespective of sex. These individuals of the two species are clearly separated along axis 1 (Fig. 3); within this factor the nasalia width is the character with the highest correlation coefficient and the greatest weight. The variation of scores along axis 2 reflects the differences between different populations and between the different age classes. The main characters within factor 2 are the condylobasal length, occipitonasal length and the orbital width, i.e., measures which reflect growth and differences in growth.

Fig. 4 displays the separation of various *X. inauris* populations and *X. princeps*. The discriminant factor 1 consists mainly of the differences in nasalia width and incisivi diameter (see Tab. 4a). The *X. princeps* skulls are obviously different from all the *X. inauris* skulls. *X. princeps* skulls have the narrowest nasalia width (7.77 mm) and show the largest incisivi diameter (3.9 mm). The *X. inauris* skulls from Namibia are closest to the ones of *X.*

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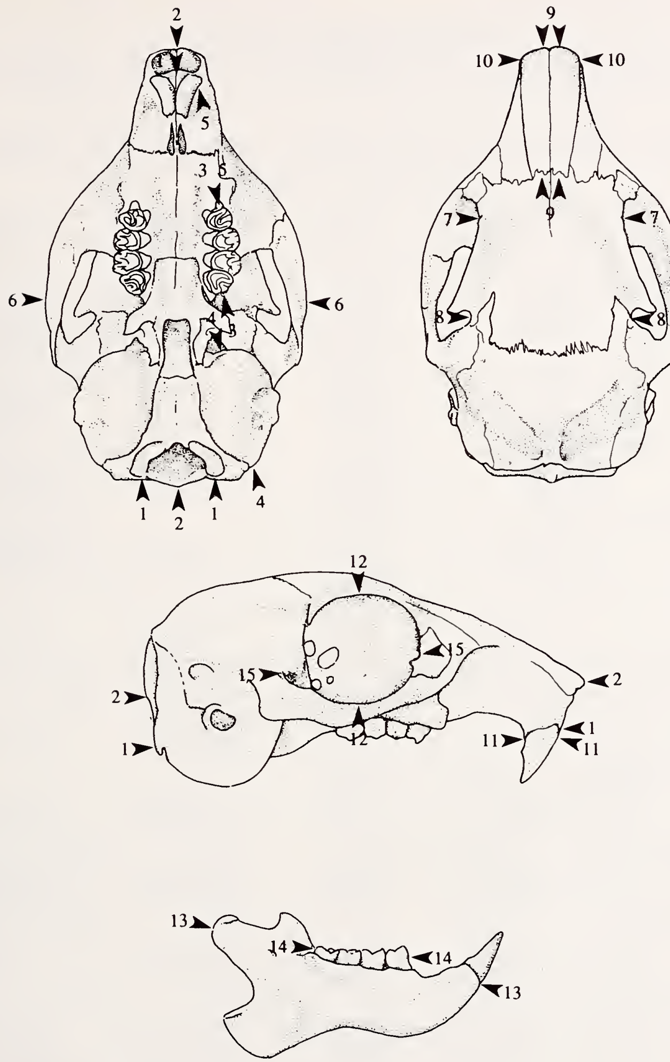

Fig. 2. Measurements taken on cranium and mandible of *Xerus* skulls (1-condylobasal lenth; 2-occipitonasal length; 3-length of upper tooth row; 4-length of bulla; 5-diastema length; 6-zygomatic breadth; 7-interorbital width; 8-postorbital width; 9-nasalia length; 10-nasalia width; 11-incisivi diameter; 12-orbital width; 13-mandible length; 14-length of lower tooth row; 15-orbital length)

princeps (i.e., 8.45 mm and 3.61 mm, respectively). *X. inauris* from Bloemhof (western Transvaal) and the Orange Free State show the greatest distance from *X. princeps* along this axis. Their nasalia width is much larger (9.22 mm and 9.61 mm, respectively) and their incisivi diameter significantly smaller (3.54 mm and 3.49 mm, respectively).

Obvious differences within *X. inauris* skulls occur along the discriminant axis 2 (Fig. 4). The main characters within factor 2 are condylobasal length, occipitonasal length, mandible length, postorbital width, orbital width, interorbital width and zygomatic breadth (see Tab. 4a). *X. inauris* from the Orange Free State show the largest skulls (occipitonasal length 58.28 mm); those from Namibia the smallest ones (occipitonasal

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Table 2. **Skull measurements (mm) of *X. inauris* (n = 157) and *X. princeps* (n = 22); specimens with complete permanent dentition**

Mean ($\bar{x}$), standard deviation (± S.D.), 95 % confidence limits (± 95 % C.L.) and range of measurements

	Mean	±S.D.	95 % C.L.	Range
Condylobasal length				
inauris	53.1	1.82	52.8–53.4	47.9–56.9
princeps	54.6	1.38	54.0–55.2	51.4–57.0
Occipitonasal length				
inauris	56.4	1.99	56.1–56.7	51.1–61.3
princeps	58.2	1.53	57.6–58.9	54.6–61.4
Upper tooth row				
inauris	11.4	0.53	11.3–11.5	10.0–12.6
princeps	11.2	0.40	11.0–11.4	10.3–11.9
Zygomatic breadth				
inauris	35.2	1.51	35.0–35.4	31.1–38.6
princeps	35.4	1.02	34.9–35.8	33.4–37.1
Interorbital width				
inauris	17.0	0.86	16.9–17.2	15.1–19.9
princeps	17.9	0.83	17.6–18.3	16.2–19.2
Diastema				
inauris	12.8	0.86	12.7–13.0	11.1–18.8
princeps	13.5	0.59	13.2–13.7	12.4–14.5
Bulla				
inauris	13.2	0.56	13.2–13.4	12.0–14.4
princeps	13.7	1.37	13.1–14.3	12.8–15.1
Postorbital width				
inauris	21.4	0.84	21.3–21.6	19.7–25.2
princeps	22.5	0.39	22.4–22.7	21.8–23.1
Nasalia length				
inauris	19.4	1.01	19.2–19.5	16.2–21.6
princeps	20.1	1.02	19.6–20.5	18.0–22.0
Nasalia width				
inauris	9.0	0.71	8.9– 9.2	7.0–10.5
princeps	7.8	0.28	7.6– 7.9	7.2– 8.4
Incisivi diameter				
inauris	3.6	0.23	3.5– 3.6	3.1– 4.2
princeps	3.9	0.26	3.8– 4.0	3.4– 4.4
Orbital width				
inauris	15.8	0.77	15.7–15.9	14.1–17.5
princeps	16.2	0.58	16.0–16.4	15.2–17.5
Mandible length				
inauris	36.1	1.49	35.9–36.3	32.8–39.4
princeps	36.9	1.29	36.4–37.5	33.5–39.1
Lower tooth row				
inauris	12.2	0.55	12.2–12.3	10.9–13.4
princeps	12.2	0.41	12.0–12.3	11.5–12.9

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length 54.91 mm). The overall skull size of *X. princeps* (occipitonasal length 58.25 mm) is very much the same as the measure of *X. inauris* from the Orange Free State. The classification of the original data according to the results of the discriminant analysis reveals an extremely low number of misclassifications (see Tab. 4b). That means one can

Table 3. **Univariate F-test for single characters of the skull (*X. inauris* – n = 157; *X. princeps* – n = 22)**
(* significant, ** highly significant)

Variable	F-value	P	
Condylobasal length	14.7124	0.00039	**
Occipitonasal length	17.9930	0.00015	**
Upper tooth row	3.9820	0.04472	*
Zygomatic breadth	0.3447	0.056505	
Interorbital width	21.0348	0.00007	**
Diastema	11.4186	0.00127	*
Bulla	6.6380	0.01049	*
Postorbital width	36.1449	0.00000	**
Nasalia length	8.9001	0.00359	*
Nasalia width	69.2131	0.00000	**
Incisivi diameter	38.9516	0.00000	**
Orbital width	4.8454	0.02723	*
Mandible length	6.2139	0.01303	*
Lower tooth row	0.4726	0.50016	

Table 4a. **Correlations between 14 characters and the discriminant axis 1 and 2, the corresponding weights and F-values of univariate test ($p < 0.05$ for all characters)**

Variable	F-value	Discriminant factor 1		Discriminant factor 2	
		Correlation coefficient	Weight	Correlation coefficient	Weight
Condylobasal length	33.89	−0.088	−0.06601	0.768	−0.08000
Occipitonasal length	36.44	−0.050	0.09359	0.776	0.26067
Upper tooth row	26.08	−0.543	−0.19576	0.425	−0.17675
Zygomatic breadth	39.85	−0.410	−0.04403	0.654	0.03297
Interorbital width	20.38	0.114	0.20683	0.652	0.15982
Diastema	5.44	0.144	0.04152	0.363	−0.13890
Bulla	2.86	0.077	0.01025	0.281	−0.08083
Postorbital width	28.37	0.121	0.01781	0.712	0.23792
Nasalia length	12.94	−0.061	0.02647	0.560	−0.09580
Nasalia width	84.18	−0.880	−0.71432	0.125	−0.35457
Incisivi diameter	16.25	0.550	0.60673	0.145	−0.58604
Orbital width	30.60	−0.272	−0.02983	0.696	0.29341
Mandible length	34.21	−0.234	−0.01852	0.727	0.10528
Lower tooth row	29.22	−0.464	−0.14626	0.554	0.45808

Table 4b. **Classification of the original data according to the above analysis**

Species/Population	Number of Cases	Number of Missclassifications	Correct classifications (%)
Xerus inauris, Bloemhof	34	4	88.2
Xerus inauris, Orange Free State	38	3	92.1
Xerus inauris, Namibia	34	1	97.1
Xerus princeps	22	0	100.0

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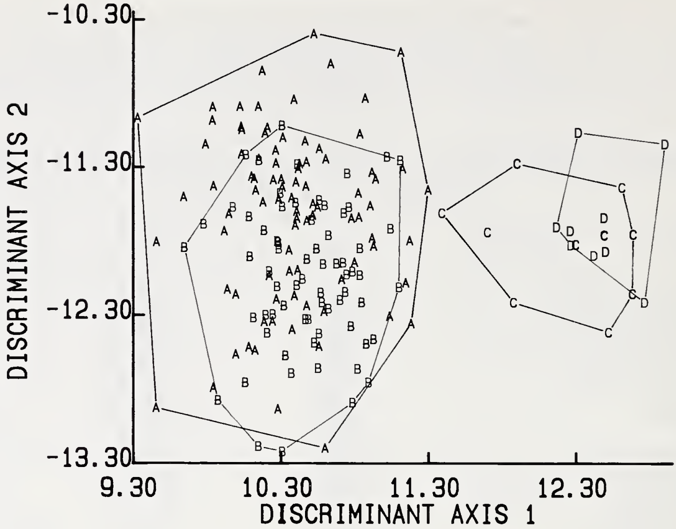

Fig. 3. Separation of *X. inauris* (A – females, n = 88; B – males, n = 69) and *X. princeps* (C – females, n = 10; D – males, n = 9). Analysis is based on 10 characters (multivariate F-test, $p < 0.05$). 98.1 % of the total variance are explained by two discriminant factors

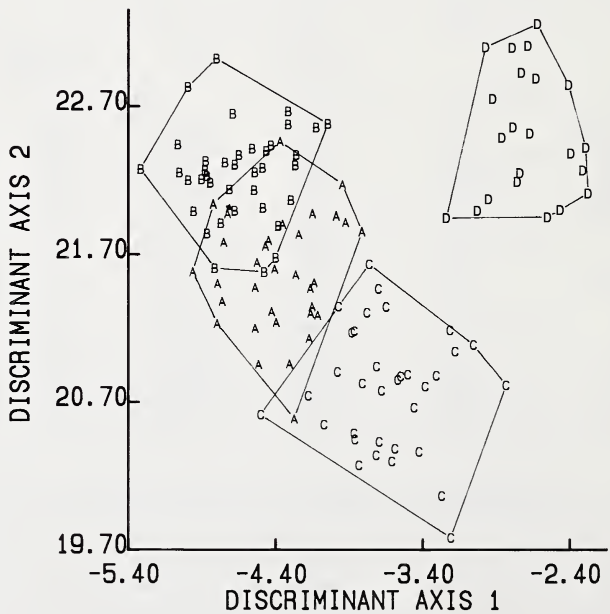

Fig. 4. Separation of various *X. inauris* populations (A – Bloemhof [western Transvaal], n = 34; B – Orange Free State, n = 38; C – Namibia, n = 34) and *X. princeps* (D, n = 22). Analysis is based on 14 characters (univariate F-test, $p < 0.05$); 95.44 % of the total variance are explained by 2 discriminant factors

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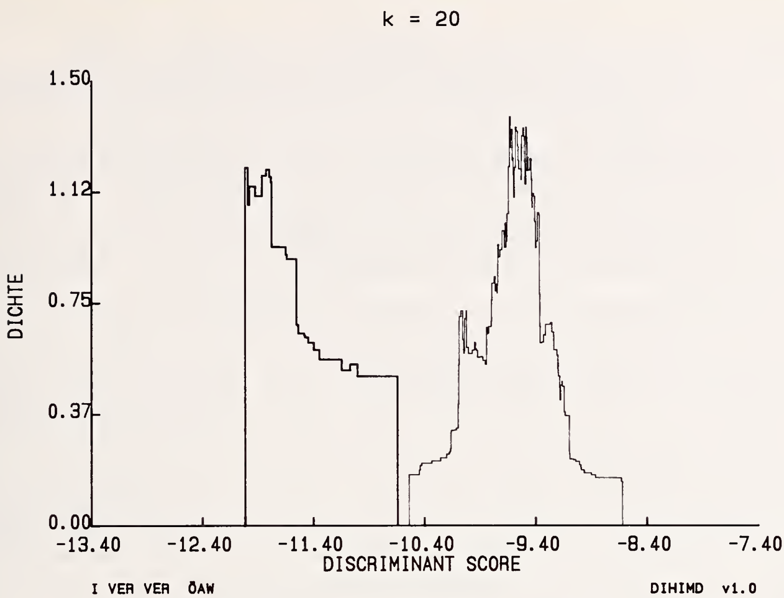

Fig. 5. Separation of *X. inauris* (n = 157; thin line) and *X. princeps* (n = 22, thick line); analysis is based on 12 characters (univariate F-test, $p < 0.05$)

easily discriminate between the skulls of *X. inauris* and *X. princeps*, and the discrimination between the skulls of various *X. inauris* populations is highly successful too.

Finally, the multivariate linear discriminant analysis was applied to all specimens with 12 characters which were significantly different between *X. inauris* and *X. princeps* in the univariate F-test (Tab. 3). As is apparent from Fig. 5, the two species are clearly separated. Within the only discriminant factor nasalia width, incisivi diameter and postorbital width are the characters with the highest correlation coefficients and the greatest weight; the most discriminating measure is the nasalia width (Tab. 5). A reclassification of the data according to this analysis produces not a single misidentification.

Table 5. **Correlations between 12 characters and the canonical discriminant axis and the corresponding weights**

(F-values of the univariate test see Table 3)

Variable	Correlation coefficient	Weight
Condylobasal length	−0.320	0.06115
Occipitonasal length	−0.351	−0.14454
Upper tooth row	0.171	0.19787
Interorbital width	−0.377	−0.18208
Diastema	−0.284	0.00791
Bulla	−0.220	−0.00704
Postorbital width	−0.476	−0.21190
Nasalia length	−0.253	0.00767
Nasalia width	0.613	0.87515
Incisivi diameter	−0.491	−0.23103
Orbital width	−0.188	−0.16309
Mandible length	−0.213	0.11016

Discussion

Although the species identity of *X. inauris* and *X. princeps* has sometimes been questioned in the past recent studies have already supported their recognition as two different species: Robinson et al. (1986) showed a subtle heterochromatic difference between them, Haim et al. (1987) found several significant physiological differences

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between them, and recently Herzig-Straschil and Herzig (1989) illustrated differences between the two species with regard to habitat selection and social structure.

The above results on the morphology and morphometry of skulls of the two species now again show clear differences between these two ground squirrels which look so very much alike at first sight.

Generally the size of skulls and especially the width of the nasalia and the diameter of the incisivi show some gradient from E (SE) to W (NW) in *X. inauris*: while skulls get smaller and nasalia narrower from the Orange Free State (South Africa) to Namibia, the diameter of the incisivi increases. Skulls of *X. princeps* from Namibia are large (comparable to those of *X. inauris* from the Orange Free State), but also have narrow nasalia and strong incisivi (one could speculate about a correlation of this feature with an arid environment).

Finally, it is amazing that the best discriminating factor apart from the colour of the incisivi, the width of the nasalia, a difference previously recognized by Thomas (1929) and illustrated by de Graaff (1981), was never used in identification keys, while the relationship of orbital length (also merely called orbit or orbit diameter or eye orbit) to occipitonasal length appeared in most of the keys (e.g., "orbit normally rather less than one third of occipitonasal length in *X. inauris* and normally more than one third of occipitonasal length in *X. princeps*" [Ellerman et al. 1953]). The measurement "orbit" is defined by Ellerman et al. (1953) and described in more detail as "orbital length" by Moore (1960), while other keys lack any explanation. The results of some measurements, however, showed that there are differences between the two species but not in the procedures used thus far. This disagreement is probably the result of a still not standardized way of measuring the orbital length.

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Zusammenfassung

Morphometrische Analyse der Schädel von Xerus inauris und Xerus princeps (Rodentia, Sciuridae)

Der Artstatus von *Xerus inauris* und *X. princeps*, die einander äußerlich sehr ähnlich sehen, wurde in der Vergangenheit zeitweise angezweifelt. Um eine Klärung in der Unterscheidbarkeit der beiden Arten herbeizuführen, wurden insgesamt 302 Schädel von *X. inauris* und 49 Schädel von *X. princeps* untersucht. Deutliche qualitative Unterschiede ergaben sich in der Farbe der Incisivi (weiß bei *X. inauris*; gelb bis orange bei *X. princeps*) sowie neun weiteren morphologischen Merkmalen, deren Gebrauch zur Unterscheidung der beiden Arten nur geringe Fehlbestimmungen (0.4–3 %) ergaben.

Schädelmaße von Tieren mit kompletter Bezahnung wurden anschließend einer multivariaten linearen Diskriminanzanalyse unterzogen. Ein univariater F-Test für einzelne Maße zeigt hochsignifikante Unterschiede zwischen den beiden Arten in der Codylobasalllänge, der Occipitonasallänge, dem Interorbitalabstand, Postorbitalbreite, der Breite der Nasalia und dem Durchmesser der Incisivi. Das am stärksten trennende Merkmal ist die Nasaliabreite.

Eine abschließende multivariate lineare Diskriminanzanalyse mit 12 Merkmalen, die im univariaten F-Test signifikant waren, zeigt eine deutliche Differenzierung zwischen diesen beiden Arten, wobei Nasaliabreite, Incisividurchmesser und Postorbitalbreite die stärkste Gewichtung zukommt.

Schädel von *X. inauris* zeigen Unterschiede vom Orange Free State und Western Transvaal bis Namibia: die Schädel werden von Ost nach West kleiner, die Nasalia schmäler und die Incisividurchmesser größer. *X. princeps* in Namibia haben große Schädel, aber ebenfalls schmale Nasalia und große Incisividurchmesser.

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