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Geographic variation in *Aethomys chrysophilus* (Rodentia: Muridae) from southern Africa

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Abstract

Patterns of intraspecific variation in *Aethomys chrysophilus* De Winton, 1897 from southern Africa suggest the recognition of two subspecies: *A. c. chrysophilus* De Winton, 1897 and *A. c. imago* Thomas, 1927, which differ both in cranial size and shape. The morphological discontinuity of the proposed subspecies broadly coincides with an altitudinal limit of either below or above 500 m above sea level in the eastern part of southern Africa.

Key words: *Aethomys chrysophilus*, cranial morphometrics, geographic variation, southern Africa

Introduction

The species conventionally regarded as the red veld rat, *Aethomys chrysophilus* De Winton, 1897 is widely distributed in southern Africa (Meester et al. 1986; Skinner and Smithers 1990; Musser and Carleton 1993). However, the species is apparently composed of two electrophoretically distinct cytotypes ($2n = 44$ and $2n = 50$) that also differ in gross sperm and bacular morphology (Gordon and Rautenbach 1980; Gordon and Watson 1986; Visser and Robinson 1986, 1987; Baker et al. 1988; Breed et al. 1988). The absence of hybrids in areas of sympatry has been suggestive of reproductive isolation between the two chromosomal races (Gordon and Rautenbach 1980; Gordon and Watson 1986; Visser and Robinson 1986). This led to a recent systematic revision of the genus in southern Africa based on morphometric analysis as well as qualitative cranial morphology (Chimimba 1997, 1998; Chimimba et al. 1999).

The morphometric analysis of cytogenetically known and other specimens of *A. chrysophilus* (sensu lato), revealed two sympatric, widely distributed, morphologically similar species referred to the nominate species, *A. chrysophilus* De Winton, 1897 ($2n = 50$) and a newly recognized *A. ineptus* Thomas and Wroughton, 1908 ($2n = 44$) (Chimimba 1997, 1998; Chimimba et al. 1999). This is concordant with observations on qualitative cranial morphology (Chimimba 1997; Chimimba et al. 1999) and the earlier investigations involving cytogenetics, protein electrophoresis, and gross sperm and bacular morphology (Gordon and Rautenbach 1980; Gordon and Watson 1986; Visser and Robinson 1986, 1987; Baker et al. 1988; Breed et al. 1988).

Additional analyses involving type material led to two previously described forms, *acticola* Thomas and Wroughton, 1908, and *imago* Thomas, 1927, to be assigned to *A. chry-*

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sophilus as junior synonyms (Chimimba 1997; Chimimba et al. 1999). Nevertheless, the nature and extent of geographic variation within the currently recognized *A. chrysophilus* from southern Africa remains virtually unknown, and only a few other southern African rodents have been subjected to a rigorous analysis of intraspecific variation (see Chimimba et al. 1998). The present study therefore, represents the first attempt to evaluate both morphometric and morphological patterns of intraspecific variation in *A. chrysophilus* from southern Africa over a more extensive geographical range than has previously been considered for the species.

Material and methods

The analysis of geographic variation in *A. chrysophilus* is based on a subset of data that formed part of the revision of the genus in southern Africa (Chimimba 1997; Chimimba et al. 1999) in which the homogeneity of the sample as representative of a single, widely distributed species was confirmed. This included 365 specimens from 161 localities, which provided an adequate geographical coverage of the species in southern Africa (Fig. 4). Since the data matrix was too large for simultaneous specimen-level analyses, geographically contiguous localities were pooled into 31 operational taxonomic units (OTUs; Sneath and Sokal 1973) (Fig. 4; Chimimba 1997; Chimimba et al. 1999) with reference to phytogeographical zones (Acocks 1988) and vegetation maps (Keay 1959).

Specimens examined are in the American Museum of Natural History, New York (AMNH), The Natural History Museum, London (BMNH), Durban Natural Science Museum, Durban (DM), Kaffrarian Museum, King William's Town (KM), McGregor Museum, Kimberley (MMKM), National Museum, Bloemfontein (NMB), National Museum of Natural History, Washington D. C. (USNM), Natural History Museum of Zimbabwe, Bulawayo (NHMZ), and the Transvaal Museum, Pretoria (TM). Type material examined is listed in the section on taxonomy, while a list of all other specimens examined and a gazetteer are provided in Chimimba (1997).

Eleven cranial measurements were recorded using a pair of Mitutoyo digital callipers and DataQ (D. L. Schultz pers. comm.) for direct data input into Quattro (Borland International 1987). These variables, defined by Chimimba and Dippenaar (1994, 1995) and Chimimba (1997) and selected on the basis of a procedure developed by Taylor (1990), Taylor and Meester (1993), Chimimba and Dippenaar (1995) and Chimimba (1997), are: greatest length of skull, greatest length of frontals, length of nasals to zygomatic arch, greatest width of bulla, foramen magnum height, length of M^1, width of M^2, length of angular process to mandibular condyle, length of mandibular foramen to condyle, length of I_1 to M_3, and width of M_2.

The data set also included four descriptive cranial (breadth of braincase, interorbital breadth, greatest length of bulla, and greatest height of skull), and four external measurements (length of head and body, length of tail, length of hindfoot, and length of ear) recorded from specimen labels. None of these variables were included in multivariate analyses (Chimimba and Dippenaar 1995; Chimimba 1997).

To reduce the effect of age variation, character recording and analyses were based on adult specimens of toothwear classes IV, V, and VI (Chimimba and Dippenaar 1994; Chimimba 1997). The absence of sexual dimorphism in the genus (Chimimba and Dippenaar 1994; Chimimba 1997, Chimimba et al. 1998) resulted in the pooling of sexes.

Multivariate analyses

Multivariate analysis included unweighted pair-group arithmetic average (UPGMA) cluster analysis, principal components analysis (PCA), and minimally connected networks (MST) of the 31 OTU means based on standardized variables (Sneath and Sokal 1973). UPGMA cluster analysis and MST were performed on both average taxonomic distances and product-moment correlation coefficients among OTUs, whereas PCA was computed from product-moment correlation coefficients among characters (Sneath and Sokal 1973). Although sample means were used, the observed major patterns of variation were verified by analyses of specimens (including holotypes) from the entire distributional range of *A. chrysophilus* in southern Africa.

The phenetic groupings obtained were further examined using pairwise canonical variates (discriminant) analysis (CVA; Sneath and Sokal 1973) and multivariate analysis of variance (MANOVA;

Willig et al. 1986; Willig and Owen 1987) based on two groupings of data: 1) all specimens within delineated phena; and 2) specimens from a zone of parapatry of the delineated phena. Diagnostic CVA was used to classify specimens excluded from the analyses.

Univariate analyses

Univariate analysis included Model I analysis of variance (ANOVA; Sokal and Rohlf 1981) of the 31 OTUs. Where significant differences were detected, maximally non-significant subsets were derived by the *a posteriori* sum of squares simultaneous test procedure (SS-STP; Gabriel and Sokal 1969; Sokal and Rohlf 1981) using ranked means (Power 1970).

All statistical procedures were accomplished using algorithms in BIOΣTAT I and II version 2.0 (Pimentel and Smith 1986 a, b), UNIVAR (Power 1970) and NTSYS-pc version 1.01 (Rohlf 1986).

Qualitative morphological variation

After having delineated phena morphometrically, representative specimens (n = 204) of each phenon (including holotypes) from the entire subregion were re-examined for qualitative morphological variation in for example, molar cusp pattern and structures in the basicranial region of the skull. This included the comparison of pelage colouration in natural light using colour standards in Oyama et al. (1967).

Intraspecific nomenclature

The intraspecific nomenclature of the delineated phena was resolved by separate analyses that included the holotypes of *A. chrysophilus* and its two junior synonyms, *acticola* and *imago* (Chimimba 1997; Chimimba et al. 1999).

Results

Multivariate assesment

A distance phenogram showed two discrete geographical clusters, designated A and B (Fig. 1a) which broadly coincide with an altitudinal limit in the eastern part of southern Africa (Clark 1967; Fig. 2). With the exception of OTUs 12, 17, and 26 (indicated by arrows), cluster A comprises OTUs from above 500 m above sea level, whereas cluster B consists of OTUs from below 500 m above sea level.

A correlation phenogram showed similar discrete geographical clusters (A and B; Fig. 1b), but the phenetic relationships were more evident than those shown by the distance phenogram. Except for OTU 12, the other two OTUs (17 and 26) that were of uncertain placement in the distance phenogram fell within a geographically meaningful, altitude-related assemblage of OTUs in the correlation phenogram.

The cluster analysis-derived phena were subsequently used as reference groupings to demarcate clusters in PCA scatterplots. This included the superimposition of MSTs based on both distance and correlation coefficients. There was evidence of two size- and shape-related groups within both the distance (Fig. 3 a) and correlation phenogram-based (Fig. 3 b) PCA scatterplots, which are consistent with the corresponding cluster analyses (Figs. 1 a and 1 b).

Apart from OTU 12, both distance- and correlation-based MSTs connected OTUs 17 and 26, which were of uncertain placement in the distance phenogram, to their geographically meaningful, altitude-related cluster of OTUs in multivariate space. The first component, which accounts for 46.4% of the variance and also has most eigenvector loadings of similar sign (negative) and relative magnitude, shows that overall size accounts for the greatest portion of the variance (Tab. 1). The second component, which is dominated by

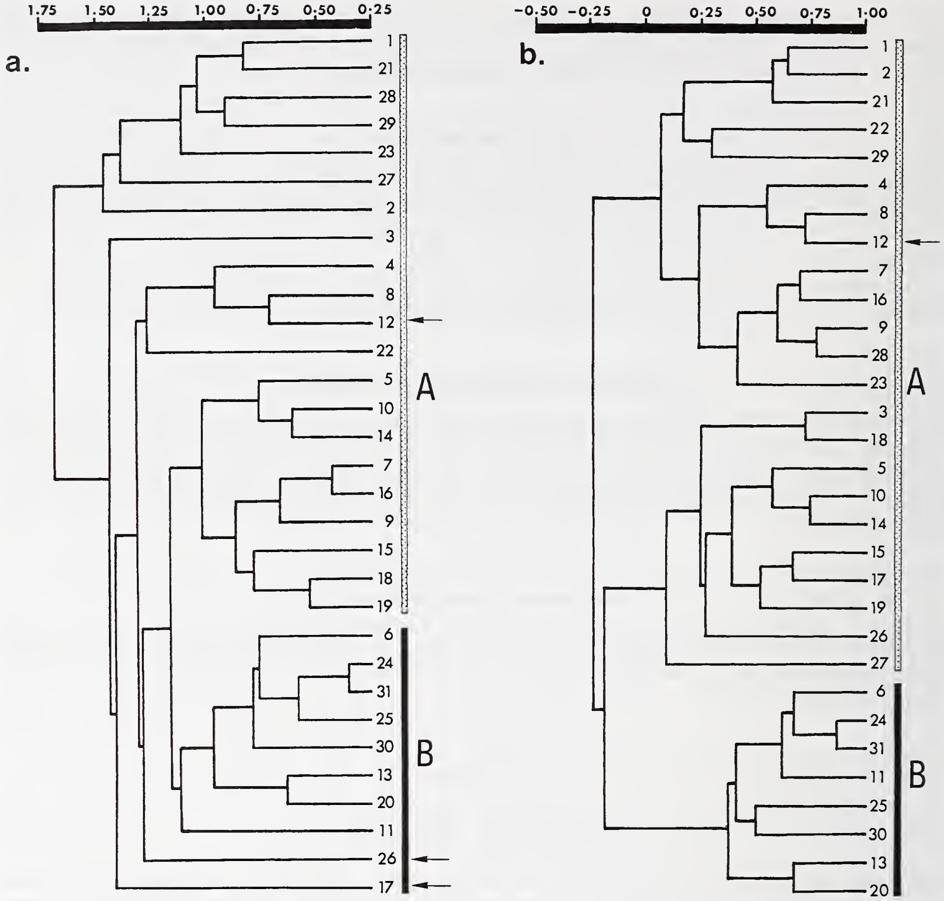

Fig. 1. Distance (a) and correlation (b) phenograms from UPGMA cluster analyses of pooled samples (OTUs) of *Aethomys chrysophilus* from southern Africa. OTUs correspond to those in Fig. 4, while arrows indicate OTUs of uncertain placement. Cophenetic correlation coefficients = 0.66 and 0.69, respectively.

greatest width of bulla and foramen magnum height (positive eigenvector loadings), and width of M^2 (negative loading), accounts for 14.9% of the variance (Tab. 1). These results indicate that cranial shape configuration of the bulla, foramen magnum region, and maxillary dental characteristics are also intraspecifically important in *A. chrysophilus* from southern Africa. The phenetic affiliation of specimens excluded from all multivariate analyses because of small sample sizes were verified by additional distance- and correlation-based UPGMA cluster analysis and MST, and PCA.

A geographical summary of these results (Fig. 4) suggests two cranially distinct, size- and shape-related phena which broadly coincides with an altitudinal limit of either below or above 500 m above sea level in the eastern part of southern Africa. OTU 12 is tentatively referred to the OTU assemblage from below 500 m above see level since the majority of OTUs clustered with their geographically meaningful groupings of OTUs.

Pairwise CVAs based on two groupings of data were broadly similar. Results presented are those based on specimens from zones of parapatry of the two delineated phe-

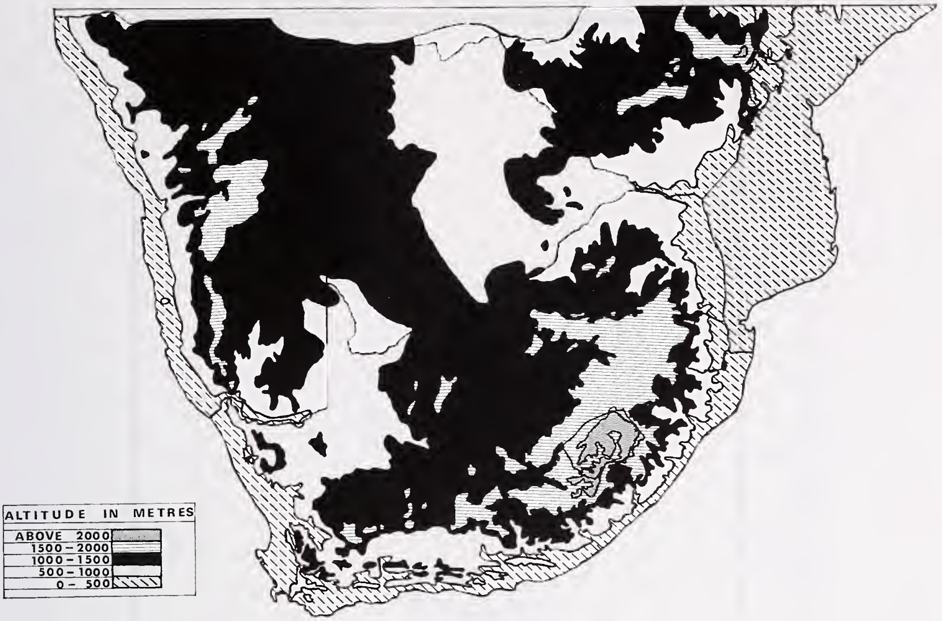

Fig. 2. Topographic map of southern Africa (after Clark 1967).

na. Despite overlaps in discriminant score ranges, pairwise CVA of the two delineated phena produced a 74% correct *a posteriori* classification (n = 365). A MANOVA indicated significant differences between group centroids (F = 6.90; P < 0.001: group centroid of OTUs from above 500 m above see level = –0.80; score range: –3.01 – 1.42; OTUs from below 500 m above see level: centroid = 0.52; range = –1.96 – 2.63).

Univariate assessment

Model I ANOVA of the 31 OTUs revealed statistically significant differences (P < 0.05) in 14 of the 15 measurements examined. The order of ranked means revealed three contrasting patterns as illustrated by selected measurements (Tab. 2).

The first pattern involved four measurements with F-values ranging from 3.22 to 5.44. As is evident in greatest width of bulla (Tab. 2 a), there is a trend in the order of ranked means for larger values to be associated with low-altitude OTUs and lower values with high-altitude OTUs. The uniqueness of high- and low-altitude OTUs was also evident in all multivariate analyses (Figs. 1 and 3).

The second pattern involved width of M^2 (F-value = 2.04; Tab. 2 b), in which a trend opposite to that in greatest width of bulla (Tab. 2 a) was revealed. There was a tendency for lower values to be associated with low-altitude OTUs and larger values with high-altitude OTUs. These two assemblages are also consistent with the two major patterns revealed by all multivariate analyses (Figs. 1 and 3).

Variation involving nine measurements with F-values ranging from 1.68–5.62, was not meaningful geographically. This is exemplified by breadth of braincase and greatest height of skull (Tabs. 2 c and 2 d). A similar pattern was also evident in foramen magnum height, the measurement with the lowest, and the only statistically non-significant F-value (F-value = 1.45; P > 0.05) among the 15 measurements examined.

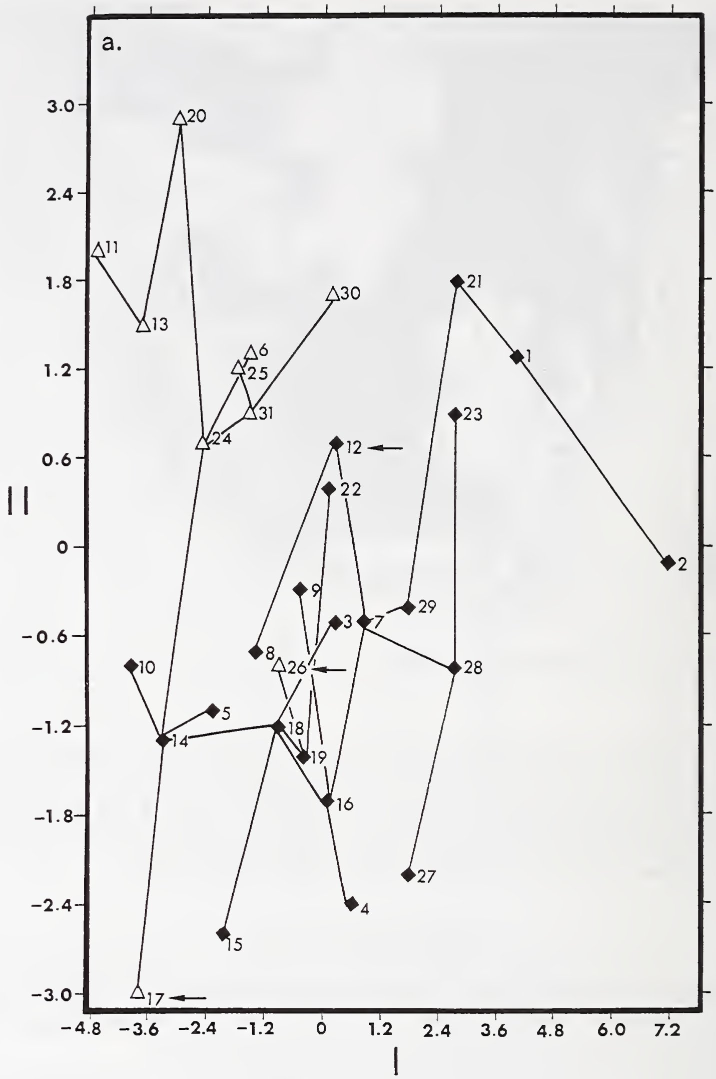

Fig. 3 a.

Taxonomic status of delineated phena

The phenetic difference between the two delineated phena and their association with an altitudinal limit of either below or above 500 m above sea level in the eastern part of southern Africa, provides support for their recognition as distinct subspecies. To further resolve the intraspecific nomenclature, the phenetic affiliations of holotypes of *A. chrysophilus* and the two described forms, *acticola* and *imago* (Chimimba 1997; Chimimba et al. 1999), were verified by UPGMA cluster analyses, PCA, MST and CVA.

All holotypes phenetically associated with their geographically meaningful assemblages of OTUs (Fig. 4). As is convention, the earliest described taxa within OTU assemblages were considered senior synonyms of the two delineated phena. Consequently, the

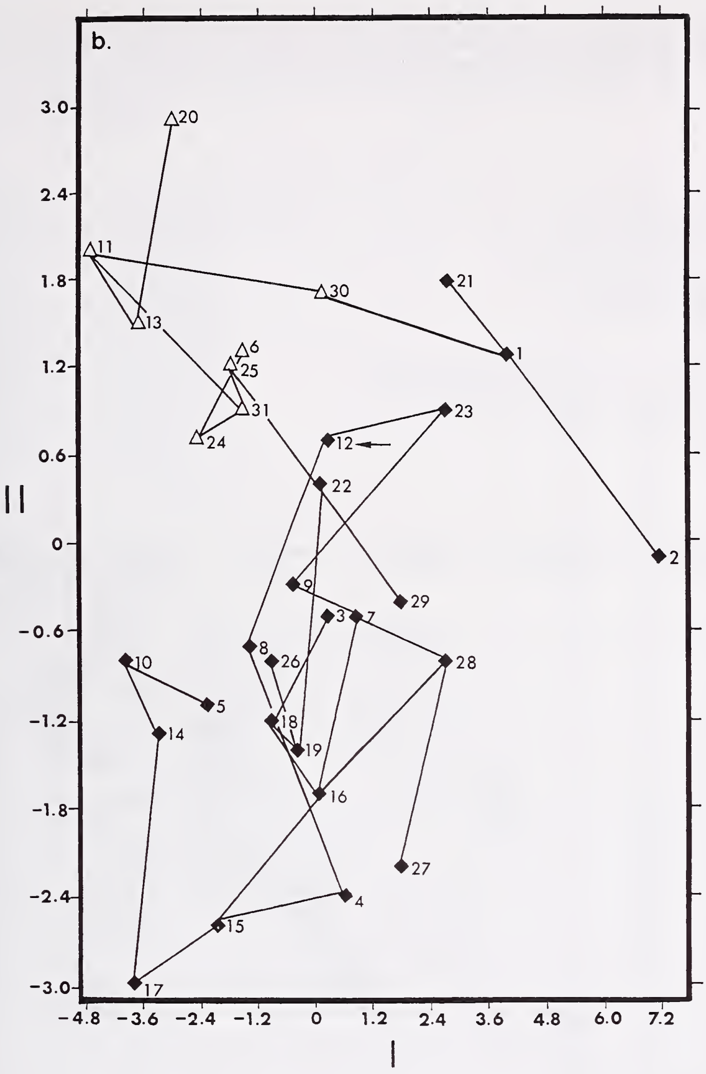

Fig. 3b.

Fig. 3. Components I and II from a principal components analysis of *Aethomys chrysophilus* from southern Africa. A minimum spanning tree is superimposed. Symbols indicate OTUs from major clusters A (solid diamonds) and B (open triangles) delineated by (a) distance (Fig. 1 a) and (b) correlation (Fig. 1 b) phenograms. Arrows indicate OTUs of uncertain placement. OTUs correspond to those in Fig. 4.

nominate subspecies, *chrysophilus* De Winton, 1897, is assigned to low-altitude OTUs from the eastern part of southern Africa, with *acticola* Thomas and Wroughton, 1908, as a junior synonym. *Aethomys chrysophilus* was described from Mazoe in eastern Zimbabwe (De Winton 1897), which falls within the low-altitude assemblage of OTUs. High-altitude OTUs are allocated to *A. c. imago* Thomas, 1927.

Table 1. Loadings of variables on components I and II from a principal components analysis of pooled samples (OTUs) of *Aethomys chrysophilus* from Southern Africa. The percent variance contributions appear in brackets. Measurements are defined in Chimimba and Dippenaar (1994,1995) and Chimimba (1997).

Variable	Principal components	
	I	II
Greatest length of skull	–0.423 (91.11)	–0.032 (0.16)
Greatest length of frontals	–0.314 (50.16)	–0.063 (0.65)
Length of nasals to zygomatic arch	–0.426 (92.44)	–0.013 (0.03)
Greatest width of bulla	0.158 (12.79)	0.548 (49.34)
Foramen magnum height	0.040 (0.83)	0.421 (29.13)
Length of M^1	–0.269 (37.01)	0.025 (0.11)
Width of M^2	–0.108 (6.00)	–0.606 (60.45)
Length of angular process to mandibular condyle	–0.394 (79.18)	0.124 (2.53)
Length of mandibular foramen to condyle	–0.294 (44.23)	–0.186 (5.67)
Length of I_1 to M_3	–0.369 (69.34)	0.227 (8.48)
Width of M_2	–0.230 (27.06)	–0.218 (7.79)
% Trace	46.4%	14.9%

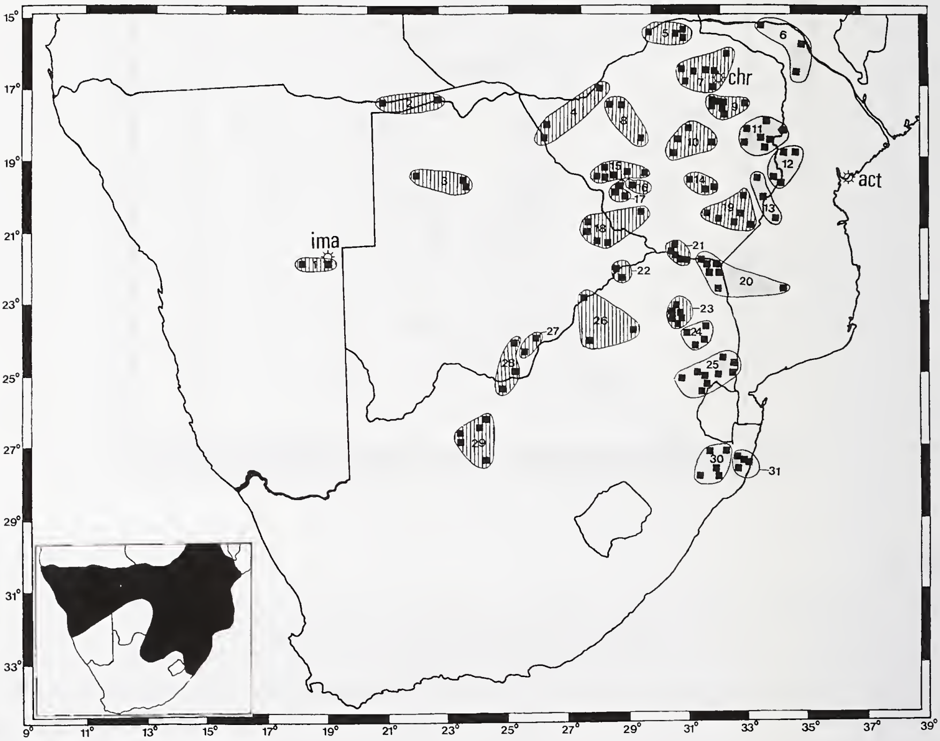

Fig. 4. Collecting localities and pooled samples (OTUs) of *Aethomys chrysophilus* from southern Africa and a geographical representation of delineated phena based on collation of UPGMA clustering, minimum spanning trees and principal components analysis results, and the tentative placement of OTU 12 into a geographically meaningful assemblage of OTUs. Samples represent phenetic assemblages that coincide with localities from the eastern (shaded) part of southern Africa, below 500 metres above sea level, and western (horizontal lines) part of this region (cf. Clark 1967; Fig. 2). Abbreviations represent type localities of *A. chrysophilus* (chr) and its two described subspecies in southern Africa, *acticola* (act) and *imago* (ima). Insert represents the distribution of the species in southern Africa.

Table 2. Results of sum of squares simultaneous test procedure (SS-STP) of selected cranial measurements of pooled samples (OTUs) of *Aethomys chrysophilus* from Southern Africa. Non-significant subsets ($P > 0.05$) are indicated by vertical lines to the right of each array of means. OTUs correspond to those in Fig. 4. Measurements are defined in Chimimba and Dippenaar (1994, 1995) and Chimimba (1997).

(a)

Locality code	Sample size	Standard deviation	Arithmetic mean	Non-significant subsets
Greatest width of bulla				
($F = 4.28$; $P < 0.05$)				
20	22	0.11	5.8	
25	11	0.27	5.7	
12	7	0.09	5.7	
6	4	0.25	5.7	
21	6	0.27	5.7	
22	10	0.14	5.7	
13	6	0.19	5.7	
11	15	0.16	5.6	
31	8	0.12	5.6	
24	11	0.19	5.6	
26	4	0.20	5.6	
30	7	0.18	5.6	
3	4	0.32	5.6	
9	9	0.17	5.6	
29	6	0.32	5.6	
10	10	0.24	5.6	
19	11	0.16	5.5	
18	13	0.20	5.5	
14	46	0.22	5.5	
23	5	0.21	5.5	
7	29	0.23	5.5	
16	12	0.16	5.5	
5	6	0.35	5.4	
15	23	0.18	5.4	
17	9	0.17	5.4	
28	5	0.07	5.4	
1	5	0.11	5.4	
2	8	0.20	5.3	
27	6	0.14	5.3	
8	4	0.30	5.3	
4	4	0.08	5.3	

(b)

Locality code	Sample size	Standard deviation	Arithmetic mean	Non-significant subsets
Width of M^2				
($F = 2.04$; $P < 0.05$)				
15	23	0.08	2.0	
16	12	0.07	2.0	
17	9	0.08	2.0	
9	9	0.08	2.0	
4	4	0.13	2.0	
5	6	0.05	2.0	
11	15	0.06	2.0	
18	13	0.06	2.0	
7	29	0.07	2.0	
14	46	0.07	2.0	
3	4	0.06	2.0	
8	4	0.06	2.0	
19	11	0.07	2.0	
28	5	0.02	2.0	
10	10	0.05	2.0	
29	6	0.07	1.9	
27	6	0.05	1.9	
25	11	0.06	1.9	
6	4	0.04	1.9	
22	10	0.06	1.9	
23	5	0.05	1.9	
13	6	0.05	1.9	
31	8	0.03	1.9	
20	22	0.03	1.9	
24	11	0.05	1.9	
21	6	0.06	1.9	
30	7	0.03	1.9	
1	5	0.05	1.9	
12	7	0.06	1.9	
26	4	0.02	1.9	
2	8	0.05	1.9	

Diagnostic morphological and morphometric characters

Variation in qualitative morphological and pelage colouration was not geographically meaningful. Both within and among the two delineated phena, upper parts ranged from brown (7.5 YR 4/3) to dark brown (7.5 YR 3/4), sprinkled with brownish black (7.5 YR 3/1) to very dark brown (7.5 YR 2/3) hairs; cheek, sides and thighs from light grey (7.5 YR 8/2) to light brown-grey (7.5 YR 7/2); underparts and feet from light yellow-orange (7.5 YR 8/4) to orange (7.5 YR 6/8); the few scattered hairs on ears from yellow-orange

Table 2. Continued

(c)

Locality code	Sample size	Standard deviation	Arithmetic mean	Non-significant subsets
Breadth of braincase				
(F = 4.93; P < 0.05)				
11	15	0.61	15.5	
13	6	0.37	15.3	
14	46	0.44	15.2	
6	4	0.33	15.1	
15	23	0.40	15.1	
8	4	0.60	15.1	
24	11	0.62	15.0	
4	4	0.38	15.0	
17	9	0.41	15.0	
10	10	0.49	15.0	
18	13	0.55	15.0	
9	9	0.39	15.0	
5	6	0.76	14.9	
7	29	0.39	14.9	
12	7	0.35	14.9	
3	4	0.56	14.8	
22	10	0.42	14.8	
20	22	0.34	14.8	
16	12	0.54	14.8	
30	7	0.38	14.8	
26	4	0.53	14.8	
25	11	0.46	14.7	
19	11	0.43	14.7	
21	6	0.37	14.6	
28	5	0.20	14.6	
31	8	0.25	14.5	
27	6	0.34	14.4	
1	5	0.38	14.3	
29	6	0.29	14.2	
2	8	0.40	14.2	
23	5	0.29	14.1	

(d)

Locality code	Sample size	Standard deviation	Arithmetic mean	Non-significant subsets
Greatest height of skull				
(F = 1.68; P < 0.05)				
8	4	0.29	11.9	
11	15	0.25	11.8	
3	4	0.40	11.8	
10	10	0.42	11.7	
5	6	0.61	11.7	
6	4	0.17	11.7	
4	4	0.27	11.7	
15	23	0.27	11.7	
16	12	0.37	11.6	
9	9	0.43	11.6	
31	8	0.26	11.6	
7	29	0.31	11.6	
13	6	0.25	11.5	
24	11	0.33	11.5	
25	11	0.41	11.5	
17	9	0.27	11.5	
28	5	0.25	11.5	
20	22	0.30	11.5	
14	46	0.32	11.5	
29	6	0.48	11.4	
23	5	0.22	11.4	
18	13	0.30	11.4	
27	6	0.27	11.4	
12	7	0.38	11.4	
30	7	0.36	11.4	
2	8	0.39	11.4	
19	11	0.39	11.4	
21	6	0.35	11.4	
26	4	0.11	11.4	
22	10	0.25	11.4	
1	5	0.30	11.3	

(7.5 YR 7/8) to orange (7.5 YR 6/8); the bicoloured basal half of tail from brown (7.5 YR 4/6) to dark brown (7.5 YR 3/4) above and orange (7.5 YR 6/8) to bright brown (7.5 YR 5/8) below, and the unicoloured terminal portion from yellow-orange (7.5 YR 7/8) to orange (7.5 YR 6/8). This suggests that intraspecific variation in qualitative morphology and pelage colour within *A. chrysophilus* from southern Africa is either subtle or does not form part the delineated patterns of cranial and dental morphological variation.

As an additional aid to subspecies identification, a search was made for simple ratios from standard statistics of the 11 basic cranial, four descriptive cranial and four external measurements examined (Tab. 3). Cranial ratios, using all specimens from the subregion, were computed for characters with high negative (width of M^2) and positive (greatest width of bulla and foramen magnum height) loadings in the shape-related axes II of PCA

Table 3. Standard statistics of external and cranial measurements in millimetres of subspecies of *Aethomys chrysophilus* from southern Africa: *A. c. chrysophilus* and *A. c. imago*. $\overline{X}$ = arithmetic mean; SD = standard deviation; n = sample size; CV = coefficient of variation; Range = observed range of variation. External measurements were obtained from specimen labels. Measurements are defined in CHIMIMBA and DIPPENAAR (1994, 1995) and CHIMIMBA (1997).

Variable	*A. c. chrysophilus*					*A. c. imago*				
	$\overline{X}$	SD	n	CV	Range	$\overline{X}$	SD	n	CV	Range
Length of head and body	143.5	10.85	47	7.57	125.0–169.0	143.1	10.01	79	7.00	120.0–165.0
Length of tail	167.7	10.64	47	6.34	144.0–185.0	160.5	12.93	79	8.06	135.0–190.0
Length of hind foot	29.7	2.47	47	8.32	21.0–35.0	29.0	2.19	79	7.54	20.0–33.0
Length of ear	20.9	1.65	47	7.94	16.0–25.0	20.4	1.94	79	9.53	15.0–27.0
Greatest length of skull	36.6	1.36	91	3.71	33.7–39.8	36.3	1.40	235	3.87	32.1–40.6
Greatest length of frontals	11.4	0.39	91	3.42	10.0–12.1	11.2	0.53	235	4.72	9.6–12.1
Length of nasals to zygomatic arch	25.6	1.02	91	3.98	23.5–28.1	25.2	1.09	235	4.32	21.8–27.7
Breadth of braincase	15.0	0.52	91	3.46	14.0–16.5	14.9	0.52	235	3.48	13.6–16.1
Interorbital breadth	5.2	0.24	91	4.66	4.7–6.0	5.1	0.25	235	4.94	4.5–5.9
Greatest length of bulla	7.7	0.23	91	3.02	7.0–8.5	7.5	0.31	235	4.13	6.7–8.6
Greatest width of bulla	5.7	0.18	91	3.09	5.2–6.3	5.5	0.22	235	4.04	4.8–6.2
Greatest height of skull	11.6	0.33	91	2.86	10.7–12.2	11.5	0.35	235	3.01	10.4–12.7
Foramen magnum height	4.9	0.22	91	4.46	4.4–5.4	4.8	0.25	235	5.15	4.1–5.5
Length of M^1	2.9	0.11	91	3.96	2.6–3.4	2.9	0.16	235	5.65	2.5–3.4
Length of M^2	1.9	0.05	91	2.57	1.8–2.1	2.0	0.07	235	3.53	1.8–2.2
Length of angular process to mandibular condyle	7.6	0.33	91	4.38	6.4–8.7	7.4	0.44	235	5.97	7.0–8.4
Length of mandibular foramen to condyle	5.6	0.30	91	5.34	5.0–6.4	5.5	0.38	235	6.88	4.4–6.6
Length of I_1 to M_3	10.6	0.37	91	3.50	9.7–11.9	10.4	0.36	235	3.52	9.0–11.3
Width of M_2	1.8	0.05	91	2.97	1.7–2.0	1.8	0.07	235	3.63	1.7–2.1

(Tab. 1). Greatest length of skull, one of the two highly negative size-related character on PC Axis I was also included, but all combinations, including external ratios were not informative.

Discussion

The present study represents the first analysis of intraspecific variation in *A. chrysophilus* from southern Africa over a more extensive geographical coverage than has previously been considered for the species. Morphometric analysis revealed the presence of two major assemblages of OTUs within *A. chrysophilus* from southern Africa.

A taxonomic interpretation of the detected variation suggests that *A. chrysophilus* in southern Africa is polytypic and can be separated into two subspecies: *A. c. chrysophilus* De Winton, 1897 and *A. c. imago* Thomas, 1927. These results presented a classical intraspecific taxonomic problem of having to decide whether the two delineated phena were sufficiently different to justify the recognition of subspecies (Mayr and Ashlock 1991).

In this study, however, one of the prerequisites considered for recognizing the two subspecies within *A. chrysophilus* from southern Africa was the pattern of variation which was both size- and shape-related. More importantly, the phenetic discontinuity broadly coincides with an altitudinal limit (Clark 1967) of either below or above 500 m above sea level in the eastern part of southern Africa. The subspecies *A. c. chrysophilus* occurs below 500 m above sea level in the eastern part of southern Africa, whereas *A. c. imago* occurs outside this region. It is possible that the altitudinal limit in geographical distribution may act as a potential barrier to gene flow. Subspecies as units of evolution are expected to be represented by transitional zones that coincide with partial or complete, present or past, geographical or ecological barriers (Endler 1977; Barton and Hewitt 1985).

Of additional importance is that the recognition of subspecies was supported by a variety of both size- and shape-related morphometric characters, which also showed no evidence of clinal variation. The identification key below, however, is based only on geographical distributions because the characters were so subtle to be useful for practical diagnostic purposes.

An examination of pelage colouration in *A. chrysophilus* showed considerable and geographically discordant variation. This was also evident in *A. namaquensis*, *A. ineptus*, and *A. granti* from southern Africa (Chimimba 1997; Chimimba et al. 1998, 1999), and may be interpreted as an adaptive response to local climatic conditions. In Botswana, Smithers (1971) considered specimens of *A. chrysophilus* (sensu lato) with pure white or nearly pure white underparts to occur on the fringes of the Kalahari but refrained from recognizing subspecies. These pelage colour forms were not discernible in the present study.

Key to subspecies of *Aethomys chrysophilus* from southern Africa

1. Restricted to the eastern part of southern Africa, below 500 m above sea level (Figs. 2 and 4) .... *A. c. chrysophilus*
2. Occurring outside the above region .... *A. c. imago*

Taxonomy

Aethomys chrysophilus chrysophilus (De Winton, 1897)
Mus chrysophilus De Winton, 1897: Proc. Zool. Soc. Lond. 1896: 801.

Mus chrysophilus acticola Thomas and Wroughton, 1908: Proc. Zool. Soc. Lond. 1908: 547.

Holotype: BM 95.11.3.23 (original No. 54); adult female; Mazoe, Mashonaland, eastern Zimbabwe (17°31′S, 30°58′E). Both the holotype of *A. c. chrysophilus* and that of its junior synonym, *A. c. acticola* (BM 7.6.2.59; male; Beira, Mozambique: 19°50′S, 34°55′E) were examined.

Distribution: Occurring in the eastern part of southern Africa, below 500 m above sea level, including Mozambique, eastern Zimbabwe, eastern Northern Province, eastern Mpumalanga and eastern KwaZulu-Natal (Figs. 2 and 4).

Diagnosis: Medium-sized (observed range: length of head and body: 125–169 mm; greatest length of skull: 33.7–39.8 mm); dorsal and ventral colour clearly demarcated; upper parts brown (7.5 YR 4/3), sprinkled with brownish black (7.5 YR 3/1) hairs; cheek, sides, and thighs light grey (7.5 YR 8/2); underparts and feet light yellow-orange (7.5 YR 8/4); ears naked apart from a few scattered yellow-orange (7.5 YR 7/8) hairs; apart from a few short adpressed hairs that increase in number and length towards the tip, tail almost naked and more coarsely scaled; shiny, mica-like scales present; basal half bicoloured, brown (7.5 YR 4/6) above and orange (7.5 YR 6/8) below; terminal portion unicoloured yellow orange (7.5 YR 7/8).

Etymology: A combination of two Latin words, *chrysos* = gold and *philos* = having affinity for, to denote the golden dorsal surface.

Aethomys chrysophilus imago Thomas, 1927

Aethomys chrysophilus imago Thomas, 1927: Proc. Zool. Soc. Lond. 1927: 387.

Holotype: BM 26.12.7.220 (original No. 1832); adult male; Stampriet, eastern Gobabis, east-central Namibia (22°29′S, 19°32′E), was examined.

Distribution: Occurring widely in southern Africa above 500 m above sea level, from northern and central Namibia, northern and eastern Botswana to western Zimbabwe, western Northern Province and the northern sector of the Northern Cape Province around Kuruman (Figs. 2 and 4).

Diagnosis: Medium-sized (observed range: length of head and body: 120–165 mm; greatest length of skull: 32.1–40.6 mm); dorsal and ventral colour clearly demarcated; upper parts yellowish brown (10 YR 5/6), sprinkled with dark brown (10 YR 3/4); underparts, thighs light grey (10 YR 8/1); ears naked apart from a few scattered bright yellowish brown (10 YR 6/8) hairs; basal half of tail bicoloured, brown (10 YR 4/4) above and bright yellowish brown (10 YR 7/6) below; terminal portion unicoloured dark brown (10 YR 3/3).

Etymology: The subspecies name is probably derived from a Latin root, imago meaning "image, copy, likeness, similarity", perhaps reflecting its resemblance to the nominate subspecies.

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Zusammenfassung

Geographische Variation von Aethomys chrysophilus (Rodentia: Muridae) aus dem südlichen Afrika

Muster intraspezifischer Variation bei *Aethomys chrysophilus* De Winton, 1897, aus dem südlichen Afrika legen die Unterscheidung zweier Unterarten nahe: *A. c. chrysophilus* De Winton, 1897 und *A. c. imago* Thomas, 1927. Diese zwei Unterarten unterscheiden sich sowohl in Cranium-Größe als auch Form. Die morphologische Diskontinuität der vorgeschlagenen Unterarten deckt sich weitgehend mit einer Höhengrenze von über oder unter 500 m NN im östlichen Teil des südlichen Afrika.

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