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Craniometric variation and subspecific differentiation in *Thrichomys apereoides* in northeastern Brazil (Rodentia: Echimyidae)

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Abstract

Thrichomys apereoides is an echimyid rodent which ranges in distribution from northeastern and central Brazil into Paraguay. Five subspecies are recognized, although each form is not well characterized and diagnosis is based primarily in pelage color variation. In this study we employed procedures from multivariate statistics to assess the systematic status of subspecies described from northeastern Brazil. The results of the craniometric analysis cannot be reconciled with the subspecies currently recognized for northeastern Brazil. Populations assigned to *T. a. laurentius* and *T. a. inermis* form a continuum of variation in cranial size, although they differ in cranial shape from a population from the locality of Bodocó in the state of Pernambuco. The implications of these findings for the systematics of *T. apereoides* are discussed.

Introduction

Thrichomys apereoides (Lund, 1841) is an echimyid rodent commonly found in the savannas of eastern and central Brazil and Paraguay, often associated with rocky habitats (Mares et al. 1981; Alho 1982). This species also inhabits the dry caatingas of northeastern Brazil (Mares et al. 1981; Mares and Ojeda 1982), although it reaches higher densities in mesic refuges. *Thrichomys apereoides* has been the subject of confusing nomenclatural and taxonomic assignements (Petter 1973), and five subspecies are currently recognized (Moojen 1952). The ranges of the subspecies are not well defined and the data available refer primarily to locality records. These are summarized in Moojen (1952), as follows: *T. a. cunicularius* known from the region of Rio São Francisco in Minas Gerais; *T. a. pachyurus* recorded from Paraguay and Mato Grosso and northern São Paulo; *T. a. inermis* described from Jacobina in the state of Bahia; *T. a. apereoides* ranging from western Minas Gerais to Goiás; and *T. a. laurentius* occurring in the states of Ceará through Pernambuco.

The subspecies of *T. a. apereoides* have been described primarily on the basis of pelage color variation (see Moojen 1952), and little is known about patterns of within and among-population variation in other character systems. In this study we employ multivariate morphometric procedures to examine variation in cranial metric traits in population samples of *T. a. apereoides* from northeastern Brazil which were allocated to the two subspecies, viz. *T. a. laurentius* and *T. a. inermis*, recognized for this area. The objectives of this study were (1) to assess the nature, extent, and magnitude of cranial differentiation in *T. apereoides*, and (2) to determine whether the pattern of population differentiation based on multivariate analyses of cranial metric characters is consistent with the subspecific structure established on the basis of pelage variation.

Material and methods

A total of 243 specimens of *T. apereoides* available in the mammal collection of the Museu Nacional (Rio de Janeiro) was examined in this study. All specimens were classified to one of the seven age classes defined in Moojen et al. (1988) on the basis of tooth eruption and occlusal surface wear criteria. Only individuals belonging to age classes 5–7 were selected for the analysis of geographic variation because they were considered adults by the criteria of Moojen et al. (1988). Statistically significant sexual size dimorphism has been detected for a few cranial traits in *T. apereoides* (Moojen et al. 1988), although in this study sexes were pooled to increase samples sizes.

The specimens analyzed in this study represent samples collected at the following localities in northeastern Brazil (Fig. 1): state of Ceará. Itapagé (3°41′ S, 39°35′ W: n = 13), Campos Sales (7°4′ S, 40°22′ W: n = 7); state of Pernambuco. Bodocó (7°42′ S, 39°53′ W: n = 11), Triunfo (7°51′ S, 38°8′ W:

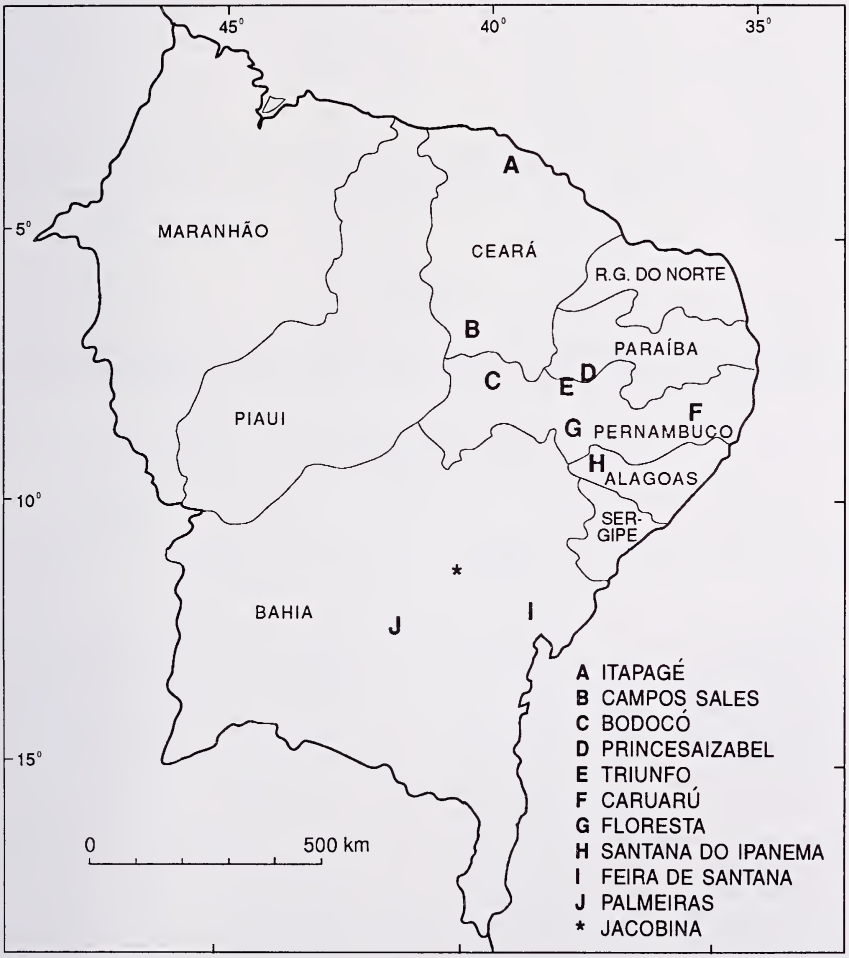

Fig. 1. Population samples of *Thrichomys apereoides* used in this study. Localities as indicated. The star denotes the type locality of *Thrichomys apereoides inermis*

n = 15), Caruaru (8°14′ S, 35°55′ W: n = 9), Floresta (8°36′ S, 38°44′ W: n = 8); state of Paraíba. Princesa Izabel (7°44′ S, 37°59′ W: n = 8); state of Alagoas. Santana do Ipanema (9°20′ S, 37°16′ W: n = 16); state of Bahia. Feira de Santana (12°15′ S, 38°57′ W: n = 9), Palmeiras (12°30′ S, 41°34′ W: n = 7). The population samples from the states of Ceará, Paraíba, and Pernambuco were assigned to *T. a. laurentius*, and the two populations from Bahia were allocated to *T. a. inermis* (Moojen 1952). The population from Santana do Ipanema in the state of Alagoas does not fall into the ranges of either *T. a. laurentius* or *T. a. inermis* and thus was not formally assigned to either of the subspecies.

Thirteen quantitative cranial measurements defined in Smith and Patton (1988) in addition to two mandibular measurements were taken with electronic digital calipers, as follows: occipito-nasal length (ONL), basilar length (BAL), zygomatic breadth (ZB), mastoid breadth (MB), rostral length (RL), nasal length (NL), rostral width (RW), diastema (D), maxillary tooth row length (MTRL), palatal width (PW), bullar length (BUL), rostral depth (RD), cranial depth (CD), mandible length (ML), and mandible height (MH).

Character variation in *T. apereoides* was analyzed by univariate and multivariate statistical procedures (Morrison 1976; Sokal and Rohlf 1981). Cranial size and shape variation among population samples of *T. apereoides* was evaluated using principal components analysis (Morrison 1976), a multivariate statistical procedure designed to summarize major patterns of covariation among metric traits. The values for all characters were transformed to logarithms to equalize variances and produce scale-invariant covariances that linearize allometric relationships (Bookstein et al. 1985). Principal components were extracted from the covariance matrix of log-transformed data. The principal component scores for the first three axes were plotted to assess patterns of cranial size and shape variation within and among populations of *T. apereoides.*

All principal-component variate loadings are expressed as vector correlations (directional cosines; Morrison 1976), estimated for each character by its correlation with projection scores across individuals. Vector plots graphically portray the principal directions of variation of each character within the corresponding principal component space. All statistical analysis were performed with SAS-PC (SAS Institute 1988).

Results

The statistics of variation in cranial dimensions in *T. apereoides* are given in Table 1. Cranial dimensions do not show a clear pattern of variation in population samples from the

Table 1. Mean (± *SE*) and analysis of variance for 15 cranial characters in populations of *Thrichomys apereoides* from ten localities in northeastern Brazil.

Character	Localities		
	Itapagé	Campos Sales	Bodocó
	X ± *SD*	*X* ± *SD*	*X* ± *SD*
Occipito-nasal length	51.48 ± 2.50	49.19 ± 1.61	49.78 ± 1.83
Basilar length	43.90 ± 2.28	42.66 ± 1.20	43.16 ± 1.76
Zygomatic breadth	25.71 ± 1.12	24.66 ± 0.42	25.00 ± 0.86
Mastoid breadth	19.84 ± 0.82	19.11 ± 0.37	19.46 ± 0.50
Rostral length	19.64 ± 1.22	18.90 ± 0.95	19.35 ± 1.11
Nasal length	17.92 ± 1.00	17.05 ± 0.87	16.89 ± 0.91
Rostral width	9.58 ± 0.74	8.92 ± 0.41	10.53 ± 0.58
Diastema	9.98 ± 0.65	9.33 ± 0.44	9.57 ± 0.48
Maxillary tooth row length	9.15 ± 0.25	8.52 ± 0.19	8.61 ± 0.42
Palatal width	2.98 ± 0.52	3.12 ± 0.24	3.43 ± 0.30
Bullar length	11.29 ± 0.47	11.48 ± 0.33	11.62 ± 0.54
Rostral depth	10.61 ± 0.64	9.94 ± 0.51	11.68 ± 0.68
Cranial depth	13.21 ± 0.49	13.13 ± 0.42	14.60 ± 0.62
Mandible length	27.57 ± 1.43	26.06 ± 0.71	26.41 ± 0.86
Mandible height	11.85 ± 0.85	11.33 ± 0.39	11.56 ± 0.54

first four localities, whereas in the remaining populations there is an overall trend of decreasing cranial dimensions from northern to southern localities. The decrease in mean values is more pronounced in the two southernmost populations from Feira de Santana and Palmeiras in the state of Bahia (Tab. 1). Univariate analysis of variation indicates significant heterogeneity among populations in all characters except nasal length (Tab. 1).

Variation in craniometric measurements among populations of *T. apereoides* was assessed by principal components analysis. The first principal component (PC) accounts for

Table 1. Continued

Character	Localities		
	Princesa Izabel	Triunfo	Caruaru
	X ± *SD*	*X* ± *SD*	*X* ± *SD*
Occipito-nasal length	49.49 ± 3.26	52.35 ± 2.09	51.39 ± 1.28
Basilar length	42.30 ± 3.45	45.10 ± 2.14	44.25 ± 1.21
Zygomatic breadth	24.93 ± 1.55	25.91 ± 0.90	26.09 ± 1.15
Mastoid breadth	19.54 ± 0.88	20.22 ± 0.82	20.13 ± 0.43
Rostral length	19.14 ± 1.66	20.37 ± 1.07	19.75 ± 0.60
Nasal length	17.09 ± 1.91	18.29 ± 1.26	17.50 ± 1.03
Rostral width	9.24 ± 0.66	9.82 ± 0.79	9.57 ± 0.69
Diastema	9.40 ± 0.85	10.33 ± 0.45	10.16 ± 0.39
Maxillary tooth row length	8.28 ± 0.75	8.80 ± 0.21	8.79 ± 0.31
Palatal width	2.98 ± 0.43	3.37 ± 0.40	3.48 ± 0.38
Bullar length	11.27 ± 0.47	11.63 ± 0.64	11.75 ± 0.37
Rostral depth	9.99 ± 0.78	11.56 ± 0.59	10.92 ± 0.65
Cranial depth	13.27 ± 0.78	13.99 ± 0.63	13.53 ± 0.52
Mandible length	26.36 ± 1.71	27.76 ± 1.27	27.68 ± 1.24
Mandible height	11.06 ± 0.80	12.30 ± 0.66	11.90 ± 0.64

Table 1. Continued

Character	Localities		
	Floresta	Santana do Ipanema	Feira de Santana
	X ± *SD*	*X* ± *SD*	*X* ± *SD*
Occipito-nasal length	50.77 ± 2.02	51.38 ± 2.53	49.47 ± 2.09
Basilar length	43.85 ± 1.66	44.28 ± 2.40	42.24 ± 1.77
Zygomatic breadth	25.41 ± 0.65	25.26 ± 0.98	24.51 ± 0.97
Mastoid breadth	20.04 ± 0.48	19.79 ± 0.77	18.83 ± 0.66
Rostral length	19.59 ± 0.83	20.11 ± 1.25	19.38 ± 1.26
Nasal length	17.64 ± 0.74	17.77 ± 1.22	17.49 ± 1.28
Rostral width	9.89 ± 0.89	9.13 ± 0.61	9.60 ± 0.47
Diastema	10.01 ± 0.45	10.15 ± 0.92	9.20 ± 0.55
Maxillary tooth row length	8.41 ± 0.41	8.80 ± 0.30	8.14 ± 0.30
Palatal width	3.54 ± 0.33	3.24 ± 0.58	3.24 ± 0.39
Bullar length	11.39 ± 0.56	11.87 ± 0.57	11.08 ± 0.53
Rostral depth	10.29 ± 0.29	10.84 ± 0.67	10.03 ± 0.62
Cranial depth	13.38 ± 0.46	13.32 ± 0.58	12.88 ± 0.60
Mandible length	27.70 ± 1.27	27.20 ± 1.36	25.54 ± 1.12
Mandible height	11.38 ± 0.67	11.55 ± 0.95	11.39 ± 0.63

Table 1. Continued

Character	Localities		
	Palmeiras		
	X ± *SD*	*F*	*P*
Occipito-nasal length	47.35 ± 1.65	4.33	0.0001
Basilar length	41.50 ± 1.62	2.93	0.0042
Zygomatic breadth	23.66 ± 0.74	4.85	0.0001
Mastoid breadth	18.26 ± 0.69	7.17	0.0001
Rostral length	18.63 ± 0.79	2.26	0.0243
Nasal length	16.75 ± 0.53	1.99	0.0496
Rostral width	8.67 ± 0.56	6.09	0.0001
Diastema	9.22 ± 0.26	5.08	0.0001
Maxillary tooth row length	8.16 ± 0.36	8.45	0.0001
Palatal width	3.24 ± 0.32	2.08	0.0388
Bullar length	10.66 ± 0.41	4.40	0.0001
Rostral depth	9.60 ± 0.48	12.96	0.0001
Cranial depth	13.65 ± 0.51	7.89	0.0001
Mandible length	25.03 ± 0.85	5.72	0.0001
Mandible height	10.03 ± 0.51	6.40	0.0001

82.7% of the total variation, whereas PC-2 and PC-3 explain 4.3% and 3.0% of the variation, respectively. Because all cranial characters were positively and significantly ($P < 0.0001$) correlated with the first pooled among-group principal component extracted from the covariance matrix of log-transformed character values, the first axis can be used as a general variable expressing overall cranial size. All populations overlap extensively in the space defined by the first two principal components (Fig. 2 A, B). On the other hand, the plot of PC-2 against PC-3 indicates the existence of two cranial shape morphologies; one represented by the population of Bodocó (state of Pernambuco) and the other by a major cluster including all other populations (Fig. 3 A). The vector plot (Fig. 3 B) indicates that individuals in the population from Bodocó differ by having higher skulls and shorter rostra relative to individuals in the other populations.

To further clarify the ordination of *T. apereoides* we performed canonical discriminant function analysis (Morrison 1976). The pattern of ordination is similar to that uncovered with principal components analysis (Fig. 4 A), in that the population from Bodocó is fully discriminated. Ordination of the remaining populations is more informative in the canonical discriminant analysis. The populations from Itapagé, Campos Sales, Triunfo, Caruaru, Floresta, Princesa Izabel, Santana do Ipanema, Feira de Santana, and Palmeiras are distributed along an axis (CV-2) of increasing cranial size starting with the population from Itapagé and ending with the population from Palmeiras (Fig. 4 A). Canonical variate 2 is clearly an axis of size since all cranial characters have positive correlations with this vector (Fig. 4 B).

Discussion

The statistical analysis of cranial metric traits in *T. apereoides* in northeastern Brazil revealed the existence of two groups of populations which lie in discrete regions in multivariate character space and differ in cranial shape. One major group is widespread in distribution and includes population samples assigned to *T. a. laurentius* and *T. a. inermis* from the localities of Itapagé, Campos Sales, Triunfo, Caruaru, Floresta, Princesa Iza-

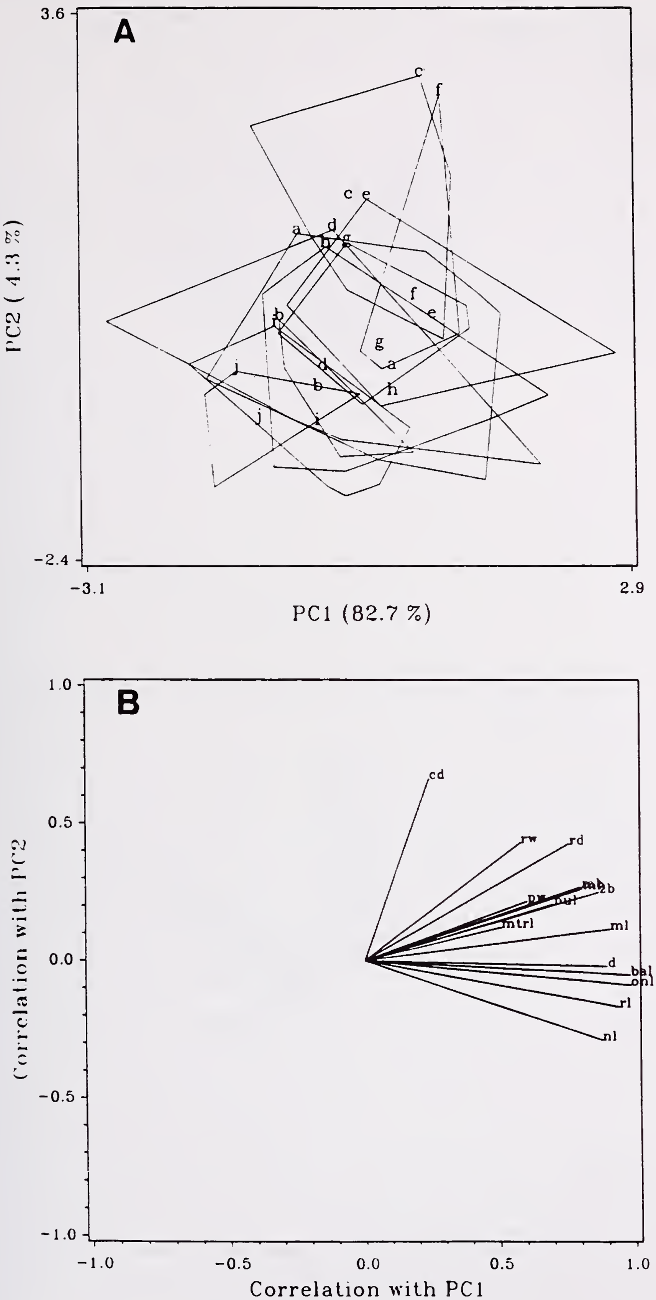

Fig. 2. Principal components analysis for ten populations of *Thrichomys apereoides*. (A) Bivariate plots of projection scores on principal components 1 and 2. Letters at the tip of polygons indicate sample locality and letters at the middle of polygons indicate sample centroids. (B) Vectors portraying the principal directions of character variation in the plane of the first two principal components

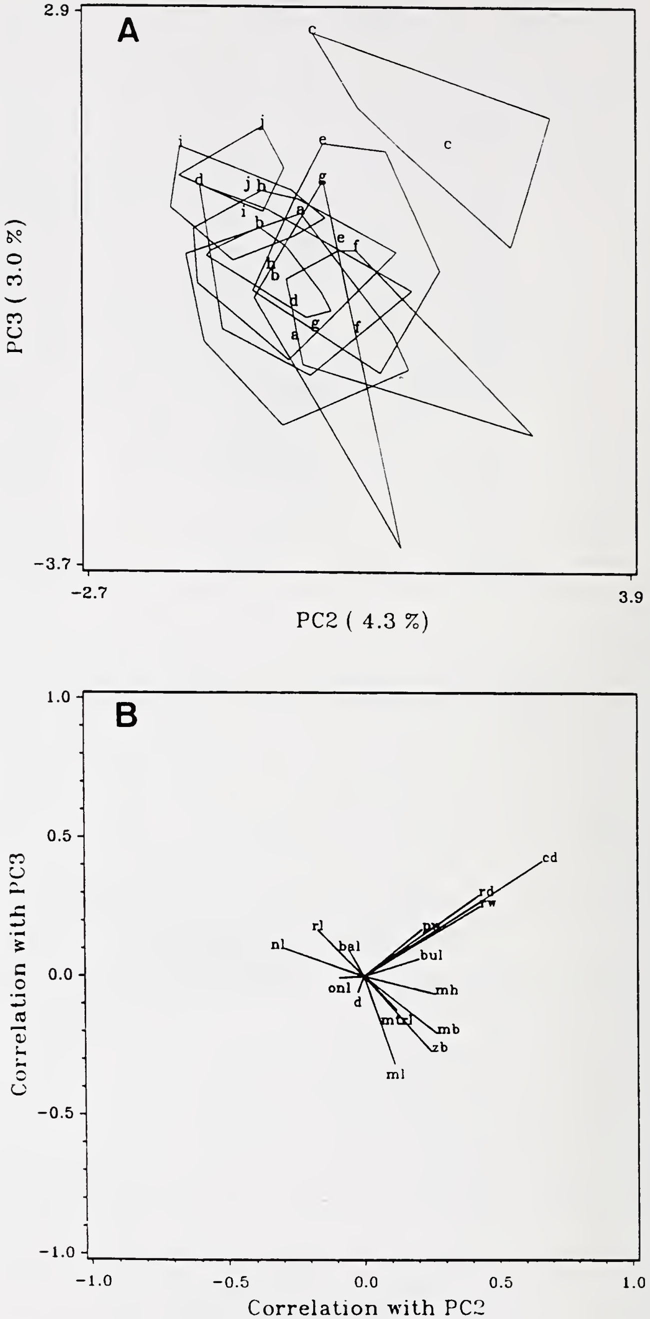

Fig. 3. Principal components analysis for ten populations of *Thrichomys apereoides.* (A) Bivariate plots of projection scores on principal components 2 and 3. Letters at the tip of polygons indicate sample locality and letters in the middle of polygons indicate sample centroids. (B) Vectors portraying the principal directions of character variation in the plane of the principal components 2 and 3

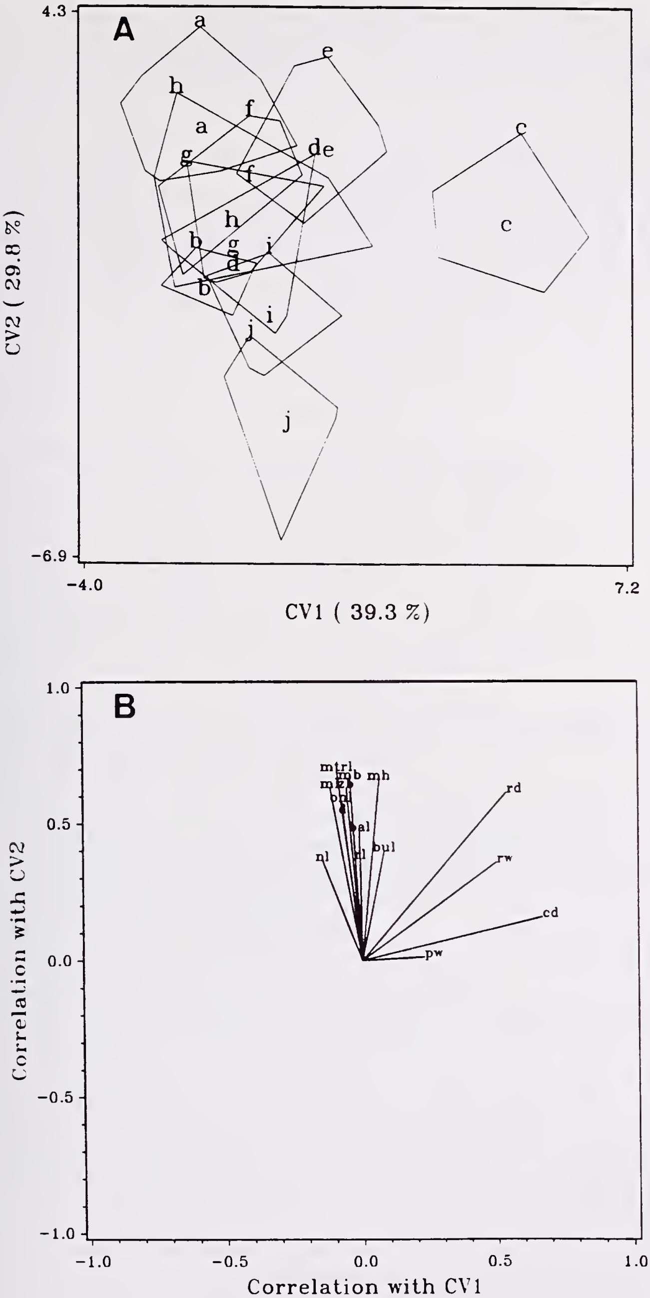

Fig. 4. Canonical discriminant analysis for ten populations of *Thrichomys apereoides*. (A) Bivariate plots of projection scores on canonical variates 1 and 2. Letters at the tip of polygons indicate sample locality and letters at the middle of polygons indicate sample centroids. (B) Vectors portraying the principal directions of character variation in the plane of the first two canonical variates

bel, Santana do Ipanema, Feira de Santana, and Palmeiras. Variation in this group is structured in a cline of decreasing cranial dimensions from northern to southern localities. The second group is represented by a single population from Bodocó, which was allocated to *T. a. laurentius*, and does not fall on the cline of decreasing cranial dimensions.

The morphologic evidence presented here for the patterns of variation in *T. apereoides* can be interpreted according to current views on the structure of subspecific variation. Barrowclough (1982) and Thorpe (1987) have stressed that evidence for the recognition of subspecies should not be based on continuous clinal variation, but that populations should occupy discrete regions in character space. The nature of cranial differences among populations of *T. apereoides* is also relevant to the definition of infraspecific differentiation. The two components of form, i.e., size and shape have been attached different weights in taxonomy and systematics, with the latter component (shape) being held as a better predictor of genetic variation and relatedness and phylogeny (Gould and Johnston 1972; Thorpe 1983; Rohlf and Bookstein 1987). Recently, Patton and Brylsky (1987) demonstrated that size is phenotypically plastic in populations of the pocket gopher *Thomomys bottae*, and shifts in cranial size are a response to environmental (nutritional) quality. On the other hand, cranial shape variation was found to be correlated with genic differences in recognized subspecies of *T. bottae*. Smith and Patton (1988) elaborated further on the relation between cranial size and shape and ecologic and historical (phylogenetic) components of differentiation, and suggested that independent evolutionary units (= subspecies, sensu Smith and Patton, 1988) should be recognized for geographic units showing concordant patterns of cranial shape and genetic variation.

Based on current view of the structure of subspecific variation (cf. Barrowclough 1982; Patton and Brylski 1987; Thorpe 1987; Patton and Smith, 1989, 1990), the craniometric data suggest the existence of two geographic units based on cranial shape: one represented by the population from Bodocó and the other including populations from Itapagé, Campos Sales, Triunfo, Caruaru, Floresta, Princesa Izabel, Santana do Ipanema, Feira de Santana, and Palmeiras. This result is not consistent with Moojen's (1952) subspecific arrangement of *T. apereoides* in northeastern Brazil and raises two points. First, *T. a. laurentius*, which according to Moojen (1952) ranges in distribution from the state of Ceará to the state of Pernambuco, may not be monophyletic but rather be composed of two geographic units. Second, the populations from Feira de Santana and Palmeiras in the state of Bahia which were allocated to *T. a. inermis*, were shown in fact to be continuously connected with other populations assigned to *T. a. laurentius*. Our samples from the state of Bahia are not from Jacobina, the type locality of *T. a. inermis*, and thus definition of the status of this subspecies can only be established when material from this locality becomes available. Additional sampling will also be necessary to determine the geographic extent of the cranial morphology represented by the population from Bodocó. A finer geographic sampling of the cranial morphology coupled with surveys of genic and chromosomal variation will be needed to better understand the structure of variation and evolution in *T. apereoides*.

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Zusammenfassung

Kraniometrische Variation und Unterartgliederung bei Thrichomys apereoides in Nordost-Brasilien (Rodentia: Echimyidae)

Das Verbreitungsgebiet der Stachelratte *Thrichomys apereoides* reicht von Nordost- über Zentral-Brasilien bis nach Paraguay. Fünf Unterarten werden gegenwärtig anerkannt, auch wenn diese Formen nicht deutlich charakterisiert sind und ihre Diagnosen meist auf Färbungsmerkmalen basieren. Für die vorliegende Studie wurden Schädel von 243 Exemplaren vermessen und die Werte einer multivariaten statistischen Analyse unterzogen. Die Resultate stimmen nicht mit der gegenwärtigen Unterartgliederung überein. Populationen, die traditionell als *T. a. laurentius* und *T. a. inermis* bestimmt wurden, bilden in bezug auf ihre Schädelmaße ein Kontinuum, unterscheiden sich andererseits aber in der Schädelform von einer Population aus Bodocó im Bundesstaat Pernambuco. Innerhalb *T. apereoides* gibt es offenbar zwei gut unterscheidbare Populationen, deren systematischer Status diskutiert wird.

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