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The contribution of cranial indeterminate growth to non-geographic variation in adult *Proechimys albispinus* (Is. Geoffroy) (Rodentia: Echimyidae)

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Abstract

Analysed the contribution of cranial indeterminate growth in 19 metric characters to intrapopulation variation in *Proechimys albispinus* (Is. Geoffroy). Individuals were assigned to eight age classes on the basis of tooth eruption and surface wear criteria. The variation in skull characters was partitioned into age and residual components in adult individuals of age classes 6–8. An average of 17.34 percent of the variation in skull traits is due to the age effect in the three combined age classes of adults, and the remaining 82.66 percent accounts for residual variation within age classes. Discriminant function analysis correctly classified 80 percent and 72 percent of individuals to age classes 6 and 7, respectively, whereas all individuals in age class 8 were correctly classified. The implications of these findings for the taxonomy and systematics of the genus *Proechimys* are discussed.

Introduction

The genus *Proechimys* comprises a large number of species and is taxonomically complex and poorly understood. The difficulty to identify taxonomic units in *Proechimys* has been attributed to unusual levels of intrapopulational variation in morphologic characters traditionally used in mammalian systematics (Thomas 1928). Recently, Patton and Rogers (1983) demonstrated the increase in cranial dimensions in adult individuals to be the main source of intrapopulational variation in *P. brevicauda*, since sexual size dimorphism is minimal in this species. The results of Patton and Rogers (1983) are valid for *P. brevicauda* and their generality remains to be determined. The objective of this paper is to assess the contribution of cranial indeterminate growth to intrapopulational variation in *P. albispinus* (Is. Geoffroy), as a step toward the understanding of patterns of non-geographic variation in *Proechimys* and their implications for the taxonomy of the genus.

Materials and methods

A total of 106 specimens of *P. albispinus* collected in the vicinity of Fazenda Pedra Redonda, Jequié (13°15′S, 40°05′W), state of Bahia, northeastern Brazil during 1952 and 1953, available in the mammal collection of the Museu Nacional (Rio de Janeiro) was examined in this study. Age categories were defined on the basis of tooth eruption and surface wear criteria as follows (Fig. 1):

Age 6: P4, M1, and M2 with internal fold not completely isolated, M3 worn but with internal fold not isolated;

Age 7: M1, M2, and M3 with internal fold completely isolated;

Age 8: P4 with internal and main fold completely isolated, M1 with internal fold completely worn, main fold completely isolated, M2 with internal fold completely isolated, main fold not completely isolated, M3 with internal fold completely formed and isolated, main fold not isolated.

Age classes 1, 2, 3, and 4 are juveniles and age class 5 represents adolescent individuals according to Moojen's (1948) general criteria for the genus *Proechimys*. Individuals from age classes 6–8 are adults

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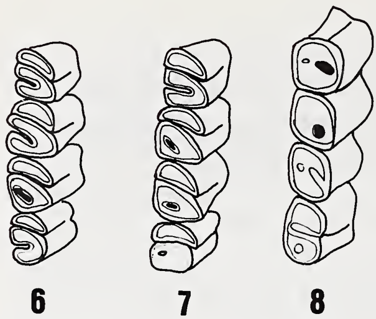

Fig. 1. Three late age classes for *Proechimys albispinus* (Is. Geoffroy) based on the pattern of surface wear of right maxillary toothrow (see text for description of age classes)

(Moojen 1948) and were selected for the analysis of the contribution of cranial indeterminate growth to within-population variation.

Nineteen cranial dimensions defined by Patton and Rogers (1983) were recorded for 63 adult individuals [age classes 6 (N = 26), 7 (N = 19), and 8 (N = 18)], as follows (Fig. 2): greatest length of skull (GSL); zygomatic breadth (ZB); palatal length B (PLB); mastoid breadth (MB); rostral breadth (RB); basilar length of Hensel (BaL); cranial depth (CD); rostral depth (RD); alveolar length of upper tooth row (MTRL); least nasal length (NL); least interorbital constriction (IOC); rostral length (RL); maxillary breadth (MaxB); diastema length (D); length of incisive foramen (IFL); length of tympanic portion of auditory bulla (BuL); post-palatal cranial length (PPL); and width of the mesopterygoid fossa (MFW).

Descriptive statistics including means and standard deviations were calculated for the 19 cranial traits for individuals in age classs 6–8. A preliminary analysis of variance indicated that only rostral length in age classs 7 and upper tooth row length in age class 8 differ significantly between the two sexes. Sexual size dimorphism is therefore virtually non-existent in *P. albispinus*, and sexes were pooled for the analysis of the added component of age variation due to indeterminate growth.

Table 1. **Statistics of variation for 19 cranial characters in the three age classes of adults of *Proechimys albispinus* (Is. Geoffroy)**

See text for explanation of character abbreviations

Age classes	6		7		8				
Characters	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	P	AVC	WVC
GSL	45.13	(1.13)	46.78	(1.36)	47.69	(0.57)	0.0001	42.99	57.01
ZB	34.02	(1.05)	35.46	(1.26)	36.41	(0.89)	0.0001	39.42	60.58
PLA	15.92	(0.72)	16.83	(0.81)	17.24	(0.57)	0.0001	31.59	68.41
PLB	7.33	(0.46)	7.67	(0.59)	7.95	(0.19)	0.0052	13.37	86.63
MTRL	7.63	(0.23)	7.68	(0.46)	7.59	(0.29)	0.6547	0.00	100.00
D	11.00	(0.61)	11.75	(0.65)	11.99	(0.50)	0.0001	30.35	69.65
RL	18.32	(0.93)	19.11	(0.88)	19.87	(0.77)	0.0001	33.58	66.42
NL	15.29	(0.85)	15.94	(0.97)	15.98	(0.51)	0.0118	10.71	89.29
IOC	10.71	(0.83)	10.86	(0.45)	11.65	(0.70)	0.0040	18.84	81.16
RB	6.61	(0.73)	6.48	(0.29)	6.54	(0.43)	0.8933	0.00	100.00
CD	12.45	(0.40)	12.45	(0.41)	12.85	(0.35)	0.0134	13.27	86.73
RD	8.70	(0.47)	9.02	(0.42)	9.44	(0.31)	0.0001	32.03	67.97
MaxB	7.92	(0.55)	8.35	(0.45)	8.40	(0.23)	0.0016	14.79	85.21
ZB	23.80	(0.82)	24.45	(0.58)	24.65	(0.54)	0.0009	16.86	83.14
BuL	9.95	(0.63)	10.10	(0.50)	10.18	(0.59)	0.4709	0.00	100.00
PPL	21.61	(0.72)	22.07	(0.77)	22.23	(0.59)	0.0171	8.43	91.57
IFL	3.99	(0.40)	4.25	(0.82)	4.00	(0.58)	0.1945	0.00	100.00
MFW	3.71	(0.87)	4.51	(1.06)	5.22	(0.82)	0.0003	23.25	76.75
MB	18.66	(0.69)	19.10	(0.55)	19.12	(0.57)	0.3224	0.00	100.00
Mean variance component								14.34	82.66

Statistics given are mean ($\bar{x}$), standard deviation (SD), significance level of an analysis of variance (P), and variance components associated with among-(AVC) and within-age classes (WVC) as sources of variation.

Significant differences among the age classes were tested for each character with a univariate analysis of variance (ANOVA). The factor age class was treated as a random variable (Winer 1971), and variation in cranial characters was further partitioned into within- and among-classes components of variance. Variance components can be estimated by different methods including the least squares procedure (Sokal and Rohlf 1981). In the present study we used maximum likelihood estimates because of their statistical properties (Searle 1971; Lindgren 1976; Van Vleck and Searle 1979).

The degree of distinctiveness of each of the three adult classes was further assessed by discriminant function analysis (Morrison 1976). The factor age class was treated as a single classification variable and posterior probabilities of correct allocation to the predicted groups were calculated. The posterior probabilities of correct classification were expressed as percentages. All statistical analyses were performed with SAS-PC version 6.03 (SAS Institute 1988).

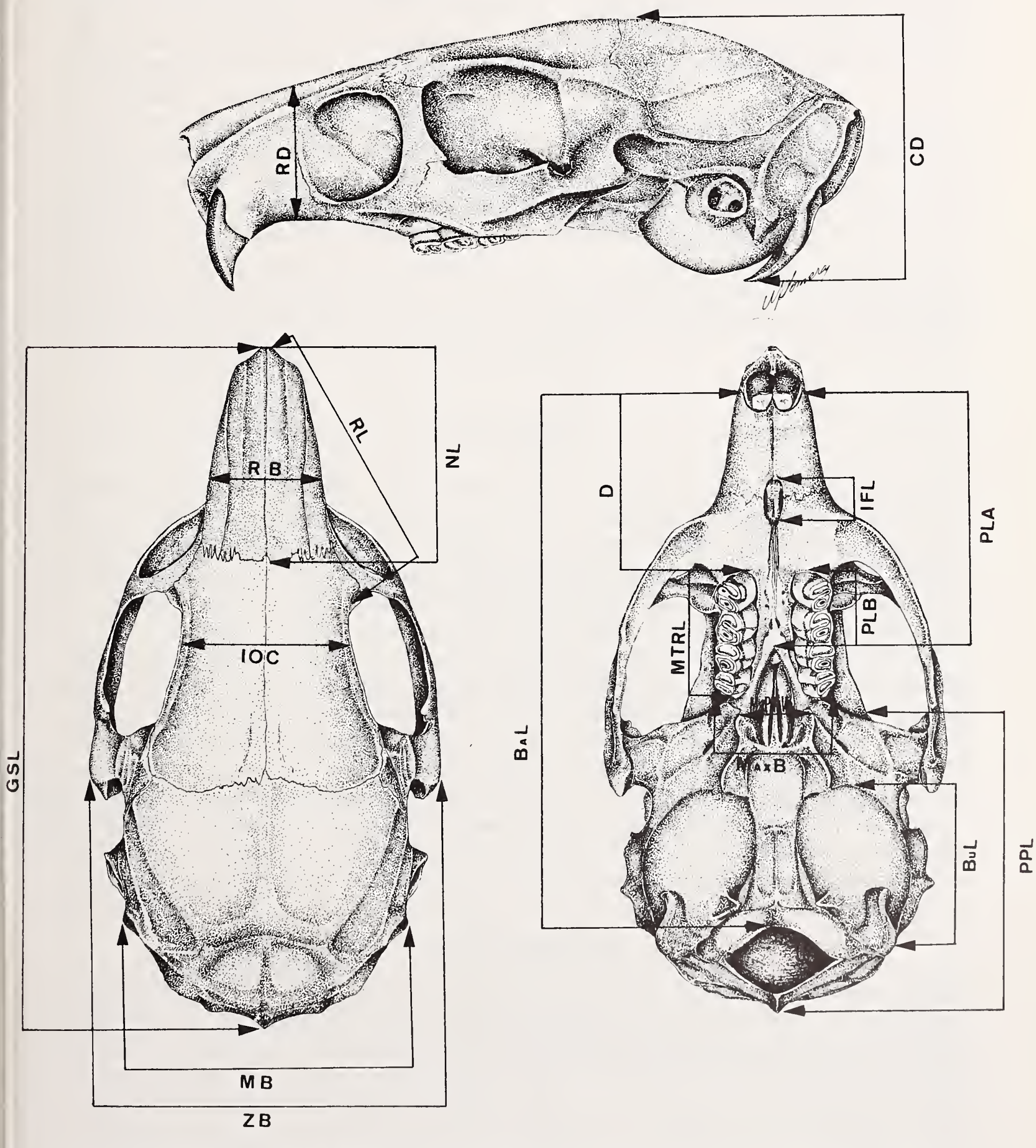

Fig. 2. Nineteen measurements taken from the skulls of *Proechimys albispinus* (Is. Geoffroy), (see text for explanation of measurement abbreviations)

Results

Most character means increase in the three age classes as expected, reflecting the fact that individuals continue to grow after they have become adults (Table 1). Univariate ANOVAs showed that all characters except mastoid breadth, length of upper tooth row, diastema, bulla length, and width of the mesopterygoid fossa differ significantly among age classes (Table 1).

An average of 17.34 percent (range, 0.00–42.99 percent) of the variation in cranial traits can be assigned to an increase in cranial dimensions due to indeterminate growth in adult individuals (Table 1). In about a third of the characters more than 30 percent of the variation in cranial dimensions can be accounted for by indeterminate growth in the adult age classes. The remaining 82.66 percent (range, 53.72–100 percent) of the variation is due to residual variability within age classes (Table 1). Discriminant functions correctly allocated 80 and 72 percent of the individuals in age classes 6 and 7 to their predicted groups, whereas all individuals of age class 8 were correctly classified to their age group (Table 2).

Table 2. **Posterior probability of correct allocation of adult individuals of *Proechimys albispinus* (Is. Geoffroy) of age classes 6–8 to their predicted age classes**

Probabilities of correct classification are expressed as percentage

Predicted age classes		6	7	8
Actual age classes	6	80.00	16.67	3.33
	7	16.00	72.00	12.00
	8	0.00	0.00	100.00

Discussion

The analysis of geographic patterns of variation is an important step for the understanding of mechanisms involved in the process of differentiation within a species (Patton and Smith 1989). It is nevertheless important to assess properly the magnitude of within-population variability before evaluating the extent of geographic variation (Thorpe 1983). Variation within populations can usually be ascribed to ontogenetic, sexual, random, and environmental factors (Straney 1978; Chesser 1983; Schmidly et al. 1988).

Variation in skull characters in *Proechimys* seems to be mostly due to indeterminate growth in adult individuals, since sexual size dimorphism is apparently very low in this genus (Martin 1970; Straney 1978; Patton and Rogers 1983; this study). The mean value of 17.34 percent found for variation in cranial dimensions in *P. albispinus* due to the age effect of combined age classes 6–8, is smaller than the value of 27.76 percent obtained by Patton and Rogers (1983) for *P. brevicauda*. We believe the amount of cranial variation due to age in the two species can be compared, since our combined age class 6–8 is roughly similar to age classes 8–10 used by Patton and Rogers (1983). It should be noted, however, that age classes based on tooth wear criteria may not be strictly a function of time (= chronological age), but may reflect differences in diet, soil type, habitat, and health. These factors alone or in combination could conceivably account for differences in the variance of cranial traits assignable to age classes in different populations or species. *P. albispinus* also differs from *P. brevicauda* in the amount of variation in skull traits that can be attributed to the age effect. Comparison of our data with those for *P. brevicauda* (Table 3 of Patton and Rogers 1983) shows that, for example, the component of variance due to age in greatest skull length is 28.4 percent in *P. brevicauda* and 42.99 percent in *P. albispinus*. The lack of correspondence in the direction of variation in cranial traits due to age is confirmed by non-significant correlations between estimates of variance components due to age for *P. albispinus* and *P. brevicauda* (Kendall's $\tau = -0.054$; Spearman's $r = -0.101$: $P > 0.05$).

Our results thus indicate that variation in skull traits due to age effects in *P. albispinus* is not as pronounced as in *P. brevicauda*, and the characters showing the largest amount of variation due to age are not the same in the two species. Nevertheless, despite the fact that most variation in cranial traits in *P. albispinus* is residual (average of 82.66 percent), the potential of age variation to confound the analysis of geographic variation and taxonomic studies at the species level does exist, and is demonstrated by the moderate to high percentages of correct allocation to age categories provided by the discriminant function analysis. By way of example, it can be supposed that in a study of geographic variation one uses a sample of individuals of age class 6 from one locality, and a sample of individuals of age class 8 individuals from another locality. Regardless of the existence of cranial differences due to locality effects, the two populations would be almost completely discriminated solely because of variation in cranial dimensions due to age differences in the two samples.

The results of Patton and Rogers (1983) plus the findings of our study seem to indicate that relatively high levels of intrapopulational variation in skull dimensions due to indeterminate growth may be characteristic to the genus *Proechimys*. The substantial age component of variation in skull traits in adult individuals of *P. brevicauda* led Patton (Patton and Rogers 1984; Patton 1987) to suggest that many characters routinely used in small mammal systematics, as well as the multivariate morphometric methods usually employed, may be of questionable value in the study of the taxonomy and systematics of the genus *Proechimys*. Patton and Rogers (1983) further suggested that equivalent age classes should be used in studies of geographic variation.

The cautionary approach of Patton and Rogers (1983) is well taken, since the existence of high levels of intrapopulational variation may pose a serious problem whenever variation in geographic space is to be assessed (Thorpe 1983). It is possible that the standard morphometric traits and multivariate procedures can be of use if the intrapopulational component of variation can be properly quantified and statistically removed. To this end, the statistical procedure of size-independent canonical discriminant analysis (Strauss 1985) may be the appropriate tool to partition out the effect of age in metric dimensions in studies of geographic variation and specific differences in *Proechimys*, in spite of the existence of high levels of intrapopulational variation. Size-independent canonical discriminant analysis basically consists of removing the effect of within-group size variation by regressing each character separately on the first pooled within-group principal component (a multivariate estimate of size), and then employing canonical discriminant analysis with the residuals obtained from the regressions to analyse variation among populations (Strauss 1985).

The technique of size-independent canonical discriminant analysis has been applied with success to studies of geographic variation in *P. dimidiatus* (Pessôa and Reis 1990; Reis et al. 1990) and *P. iheringi* (Pessôa and Reis 1991), where relatively complex patterns of differentiation have been identified. We believe that the application of this procedure will prove very helpful in the study of the taxonomy and systematics of the genus *Proechimys*.

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Zusammenfassung

Der Anteil des unbegrenzten Schädelwachstums an der Variabilität von Schädeln gleicher Herkunft bei adulten Proechimys albispinus (Is. Geoffroy) (Rodentia: Echimyidae)

Igelratten (*Proechimys albispinus*) wachsen zeitlebens. In der vorliegenden Arbeit wird versucht, den Anteil der durch unterschiedliches Alter bedingten Variabilität an der Gesamtvariabilität bei adulten Tieren einer Population abzuschätzen. Dazu wurden die Tiere jeweils einer von acht Stufen des Gebißzustandes zugeordnet, die mit dem Alter korreliert sind. Der Einfluß des Alters auf 19 Schädelmaße wurde für die ältesten Klassen 6–8 geprüft. Er betrug etwa 17 % der Gesamtvariabilität innerhalb dieser Gruppe. Mit Hilfe einer Diskriminanzanalyse konnten 80 % der Tiere der Klasse 6, 72 % der Klasse 7 und 100 % der Klasse 8 richtig zugeordnet werden. Die Folgerungen für die Taxonomie werden diskutiert.

Literature

SAS Institute Inc. (1988): SAS/STAT User's Guide, Release 6.03 Edition. Cary, NC.

Chesser, R. K. (1983): Cranial variation among populations of the black-tailed prairie dog in New Mexico. Occas. Papers Mus., Texas Tech. Univ. **49**, 1–25.

Lindgren, B. W. (1976): Statistical theory. 3rd ed. New York: Macmillan.

Martin, R. E. (1970): Cranial and bacular variation in populations of spiny rats of the genus *Proechimys* (Rodentia: Echimyidae) from South America. Smithsonian Contrib. Zool. **35**, 1–19.

Moojen, J. (1948): Speciation in the Brazilian spiny rats (Genus *Proechimys*, Family Echimyidae). Univ. Kans. Publ., Mus. Nat. Hist. **1**, 301–406.

Morrison, D. F. (1976): Multivariate statistical methods. 2nd. ed. New York: McGraw-Hill.

Patton, J. L. (1987): Species groups of spiny rats genus *Proechimys* (Rodentia: Echimyidae). Fieldiana: Zoology, n.s. **39**, 305–345.

Patton, J. L.; Rogers, M. A. (1983): Systematic implications of non-geographic variation in the spiny rat genus *Proechimys* (Echimyidae). Z. Säugetierkunde **48**, 363–370.

Patton, J. L.; Smith, M. F. (1989): Population structure and the genetic and morphologic divergence among pocket gopher species (Genus *Thomomys*). In: Speciation and its Consequences. Ed. by D. Otte and J. A. Endler. Sunderland: Sinauer Ass. 284–306.

Pessôa, L. M.; Reis, S. F. dos (1990): Geographic variation in *Proechimys dimidiatus* (Günther) (Rodentia: Echimyidae). Zool. Anz. **225**, 383–390.

Pessôa, L. M.; Reis, S. F. dos (1991): Cranial infraspecific differentiation in *Proechimys iheringi* Thomas (Rodentia: Echimyidae). Z. Säugetierkunde **56**, 34–40.

Reis, S. F. dos; Pessôa, L. M.; Strauss, R. E. (1990): Application of size-free canonical discriminant analysis to studies of geographic differentiation. Brazil. J. Genetics **13**, 509–520.

Schmidly, D. J.; Bradley, R. D.; Cato, P. S. (1988): Morphometric differentiation and taxonomy of three chromosomally characterized groups of *Peromyscus boylii* from East-Central Mexico. J. Mammalogy **69**, 462–480.

Searle, S. R. (1971): Linear models. New York: Wiley.

Sokal, R. R.; Rohlf, F. J. (1985): Biometry. 2nd. ed. San Francisco: Freeman.

Straney, D. O. (1978): Variance partitioning and nongeographic variation. J. Mammalogy **59**, 1–11.

Strauss, R. E. (1985): Static allometry and variation in body form in the South American catfish genus *Corydoras* (Callychthyidae). Syst. Zool. **34**, 381–396.

Thomas, O. (1928): The Godman-Thomas expedition to Peru. VII. The mammals of the Rio Ucayali. Ann. Mag. Nat. Hist. ser. 7. **6**, 294–302.

Thorpe, R. S. (1983): A review of numerical methods for recognising and analysing racial differentiation. In: Numerical Taxonomy. Ed. by J. Felsenstein. Berlin: Springer Verlag. 404–423.

Vleck, L. D. van; Searle, S. R. (1979): Variance components and animal breeding. New York: McGraw-Hill.

Winer, B. J. (1971): Principles in experimental design. 2nd. ed. New York: McGraw-Hill.

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