Systematic implications of non-geographic variation in the Spiny rat genus *Proechimys* (Echimyidae)

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Abstract

Intrapopulation variation due to sex and age components is examined for 23 morphometric variables of the skin and skull for the spiny rat, *Proechimys brevicauda* Gunther. Secondary sexual variation is virtually non-existent, but age variation is extensive. Age accounts for an average of 25 percent of the total variance within variables among the age categories of reproductively active adults, with some variables exhibiting up to 50 percent age related variation. The effect of this high degree of age variation on exhibited patterns of geographic variation within *P. brevicauda* in northern Peru is examined, as is the effect of age variation on the ability to discriminate sympatric species of spiny rats in the western Amazon.

Introduction

Echimyid rodents of the genus *Proechimys* are one of the taxonomically more poorly understood groups of neotropical mammals. Only a few studies have been successful in recognizing the number of taxa sympatric at any single locality (e.g. Patton and Gardner 1972), and no study has yet been successful in following geographic character trends within a clearly definable taxon over any but the shortest of distances. Part of the reason for this situation was aptly summarized by Oldfield Thomas (1928: 262) more than 50 years ago; his often quoted statement remains true today: "The bewildering instability of the characters of these spiny rats makes it at present impossible to sort them according to locality into separate species, subspecies, or local races. . . . I confess myself defeated in any attempt at present to distinguish the local races."

The first step in the recognition of geographic units is to understand levels of within-population variability due to age, sex, or other factors for those morphometric characters standardly used in mammalian systematic studies. The "bewildering instability of characters" to which Thomas alludes is likely due, in part, to confusion between non-geographic and geographic components of character variation in the genus. Few attempts have been made in studies of *Proechimys* systematics to estimate these non-geographic components of variation, probably because of inadequate sample sizes of clearly recognizable single taxa. For example, while Martin (1970) found secondary sexual variation to be non-significant in a population of *P. "guyannensis"* from Bolivia, and calculated coefficients of variation within tooth wear categories for 18 mensural variables, he did not examine the direct effects of age per se on expressed population variability for these characters. We report here on an analysis of age and sex variation for a population of *P. brevicauda* Gunther from northern Peru and comment on systematic difficulties in the genus which arise as a result of non-geographic components of character variation.

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Materials and methods

173 specimens of *Proechimys brevicauda*, collected from the vicinity of Huampami, Rio Cenepa, Depto. Amazonas, Peru, 215 m. (Long 78.17° W, Lat. 4.47° S) during July and August 1977 and 1978, were available for analysis. Individuals were identified by the combined cranial, bacular, coloration, and plantar surface characters established earlier (Patton and Gardner 1972). [The name *P. brevicauda* Gunther is herein used for that taxon identified as *P. longicaudatus* (Rengger) by Patton and Gardner (1972). This application is based on the examination by one of us (JLP) of the lectotype (BM(NH) 69.3.31.7) chosen by Thomas (1900: 301) for Gunther's *brevicauda*.]

Four external and 19 cranial dimensions were recorded for all individuals, as follows: 1. head and body length (HBL); 2. tail length (TL); 3. hind foot length (HFL); 4. ear height (EH); 5. greatest length of skull (GSL); 6. zygomatic breadth (ZB); 7. palatal length A (taken from posterior margin of incisors to anteriormost point of post-palatal notch-PLA); 8. palatal length B (taken from anterior margin of PM^4-alveolus to anteriormost point of post-palatal notch-PLB); 9. mastoid breadth (MB); 10. rostral breadth (greatest breadth of rostrum at maxillary-premaxillary suture (RB); 11. basilar length of Hensel (BaL); 12. cranial depth (CD); 13. rostral depth (RD); 14. alveolar length of upper tooth row (MTRL); 15. natal length (NL); 16. least interorbital constriction (IOC); 17. rostral length (RL); 18. maxillary breadth (MaxB); 19. diastema length (D); 20. length of incisive foramen (IFL); 21. length of tympanic portion of auditory bulla (BuL); 22. post-palatal cranial length (PPL); and 23. width of the mesopterygoid fossa (MFW). Unless otherwise noted, measurements taken are described in Cockrum (1960); cranial dimensions are illustrated in Fig. 1. External dimensions were ta-

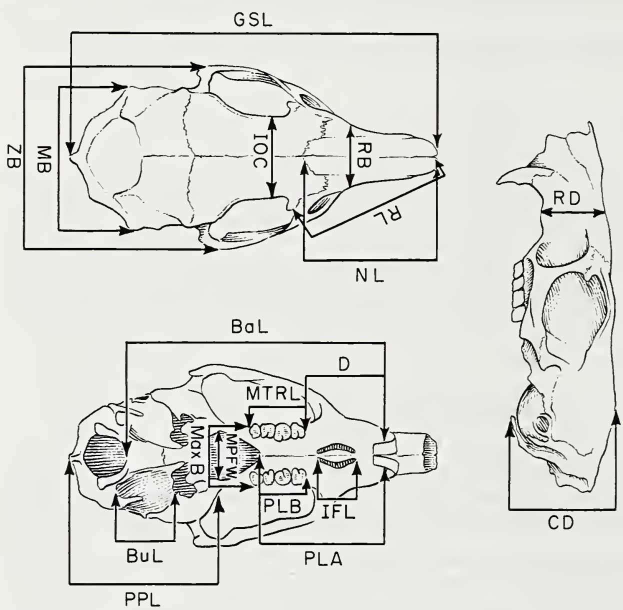

Fig. 1. Position of 19 cranial dimensions taken on skulls of *Proechimys brevicauda* Gunther (see text for explanation of dimensional abbreviations)

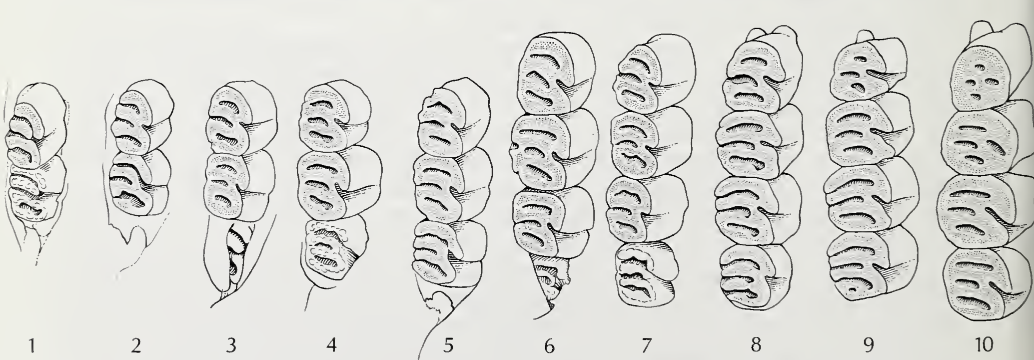

Fig. 2. Right maxillary toothrow of *Proechimys brevicauda* Gunther, illustrating wear patterns and eruption sequence for ten age categories (see text for complete description)

ken from specimen labels (all specimens measured in the field by JLP); cranial variables were taken with dial calipers graduated to 0.05 mm.

Age categories are based on tooth eruption and occlusal surface wear criteria, as follows (see Fig. 2): Age 1 – PM^4 erupted and worn, M^1 – exposed but unworn; Age 2 – M^1 worn, M^2 undeveloped; Age 3 – M^2 exposed in alveolus but unerupted; Age 4 – M^2 erupted but unworn; Age 5 – M^2 worn, M^3 undeveloped; Age 6 – M^3 exposed in alveolus but not erupted; Age 7 – M^3 erupted but unworn; Age 8 – M^3 worn, flexi on PM^4 not completely isolated; Age 9 – flexi on PM^4 and M^1 isolated; Age 10 – primary flexus on PM^4 isolated or obliterated.

The Statistical Packages for Social Sciences (SPSS: Nie et al. 1975) was used for computation of standard descriptive statistics for all variables. Straney's (1978) variance partitioning program (VARCOMP) was used to estimate sex, age, interaction, and error (=residual) components of variation for each variable. This method permits the determination of the proportion of total population variation due to each of these effects. Two separate variance analyses were performed; the first grouped adjacent age classes into five categories (age 1 and 2, 3 and 4, and so forth) in order to provide sufficient sample sizes for the lower age classes, and the second considered only variation within the "adult" age classes (8 through 10).

Results and discussion

Tooth wear categories and chronological age

Inherent difficulties with all ageing techniques based on tooth wear categories are that the classes established may not be concordant with chronological age, may be affected by diet, health, and habitat, and do not represent parametric variables. The relationship of the 10 age classes defined here to those used by other workers on *Proechimys* (e.g., Moojen 1948; Martin 1970; Fleming 1971), along with estimates of their correspondence to chronological age, are given in Table 1.

Table 1

Relationship of tooth eruption/wear age categories for *Proechimys brevicauda* Gunther to age categories used by other workers on the genus, and to probable chronological age

Following Fleming (1971) and Maliniak and Eisenberg (1971)

	Tooth eruption/Wear classes			
this study	Moojen (1948)	Martin (1970)	Fleming (1971)	estimated chronological age
1			–	
2	juvenile	I	–	
3			–	
4		II	J2	
5				
6	adolescent	III	J3	< 6 months
7			0	
8	adult	IV	1	
9			2–3	18 months
10	senile	V	4–6	

For *P. brevicauda,* completion of the subadult molt into adult pelage is accomplished by Age Class 6. Females showed first evidence of breeding (i.e., pregnancies) at Age Class 5, when still in partial juvenile pelage, and at a chronological age of from 3 to 5 months (see Maliniak and Eisenberg 1971). By Age Class 7, 57 percent of all females were either pregnant or parous (N=7), and by Age Class 8, 95 percent (N=37) had reproduced at least once. Reproductive activity among males was not evidenced until Age Class 7. 33 percent (N=6) of these males had enlarged testes, swollen seminal vessicles, and motile sperm in the epididymis. In contrast, 85 percent of Age Class 8 males (N=31) were reproductively competent by these criteria. Clearly, therefore, while female *P. brevicauda* may begin breeding at a slightly earlier age than males, both sexes reach an equivalent degree of reproductive maturity at the same tooth wear age class. The greatest shift in the proportion of mature individuals per age grouping occurs between age classes 7 and 8; this corresponds to the division used by other workers to distinguish adolescent or juvenile from adult specimens (see Table 1), and will be used as a similar dividing line here.

Characters and components of variation

Descriptive statistics for the 23 variables examined (mean, standard deviation, and coefficient of variation) are given in Table 2. The proportion of variance attributable to sex, age, and error over the 23 variables examined is given in Table 3. Obviously, age accounts for the majority of character variance when all age categories are considered (mean, 80 percent). Significantly, however, even when the analysis is restricted to the three "adult" age classes (ages 8–10), the proportion of variance due to age is still substantial (mean over all characters is 24.5 percent, range from 0.0 to 50.9 percent, Table 3). In over one-half of the characters (12 of 23) age accounts for more than 25 percent of the variance exhibited in the adult age classes. In both analyses, secondary sexual variation makes no contribution to the variance in the characters, and the interaction between sex and age is thus minimal to non-existent.

These data are similar to those provided by Martin (1970: 7; analysed in Straney 1978: 5) for *Proechimys "guyannensis"* from San Ignacio, Bolivia, where the average contribution to total variance for three characters (ZB, RD, and MaxB) of sex, age, and error was 0.0, 74.8, and 21.0 percent, respectively. For *P. brevicauda,* the average contribution to variation in these same three characters is 0.0, 81.1, and 18.7 percent (Table 3). Thus, while Straney (1978: 5) commented that the pattern of variance partitioning, particularly with regard to a very large age component among adult specimens, for *Proechimys* was unusual among the rodent taxa he examined, this pattern appears rather characteristic for the genus as a whole. Why this might be so remains to be determined, but the rather large within-population age component to adult variation does have potential consequences for systematic studies in the group.

Significance of age variation to systematics of *Proechimys*

A substantial age component in most mensural characters of *Proechimys,* even among individuals clearly adult by growth or reproductive criteria, makes many of the characters standardly employed in systematic analyses of small mammals of questionable value in this genus. In order to examine the potential significance of this problem for *Proechimys* systematics, two additional analyses were performed. The first examined the extent of within-population character variation due to age relative to that between populations over a limited geographic area of a single species. The second analysis assessed the actual importance of within-species age variation to the between-species discrimination of individual specimens.

For the first of these two analyses, Straney's (1978) VARCOMP program was used to examine variance components due to age and geography for four samples of *P. brevicauda* from northern Peru. While most of the variation was residual (62.4%; range 44.7–83.6), that proportion due to differences between the two ages 8 and 9 alone (10.2%; range 8.1–15.5) was nearly as great as the between-locality geographic component (18.5%; range 9.7–23.2). The extent of age variation for several characters (e.g., GSL, PLB, and BaL) was as great as the geographic differences exhibited by the same characters. The examination of equivalent specific age classes in geographic variation analyses for *Proechimys* species thus appears to be quite important.

To examine the potential impact of age variation to species level taxonomic comparisons

Table 2

Summary of variation across age classes of *Proechimys brevicauda* Gunther for 23 mensural variables, including the mean – standard deviation and coefficient of variation for both males (above) and females (below)

See text for explanation of variable abbreviations

	Age class (sample size)							
Variable	1 + 2 (9 ♂; 6 ♀)	3 + 4 (8 ♂; 7 ♀)	5 + 6 (13 ♂; 18 ♀)	7 + 8 (37 ♂; 44 ♀)	9 + 10 (11 ♂; 20 ♀)	8 (31 ♂; 37 ♀)	9 (10 ♂; 11 ♀)	10 (1 ♂; 9 ♀)
HBL	145.7–3.72	158.8–5.49	180.6–8.23	231.5–4.48	253.4–4.42	233.0–5.02	253.7–4.93	251.0
	7.66	8.47	15.11	10.95	5.51	11.39	5.83	–
	141.7–9.75	146.7–1.93	192.3–2.79	222.2–2.54	247.6–2.82	226.5–2.44	240.6–3.55	252.4–3.97
	16.86	32.15	6.15	6.76	5.10	5.70	4.17	4.72
TL	86.2–3.35	99.7–5.74	123.8–2.74	155.5–2.62	163.3–2.65	158.4–2.33	163.3–2.96	163.0
	11.65	14.10	7.33	9.51	5.13	7.78	5.44	–
	85.3–6.61	97.0–6.17	122.0–2.38	141.7–1.86	149.6–2.62	144.7–1.90	148.3–3.69	151.8–3.67
	18.96	15.58	8.04	7.75	6.31	6.94	7.04	5.40
HFL	37.4–0.85	39.8–0.94	44.9–1.02	51.9–0.37	53.0–0.33	52.3–0.38	53.1–0.35	52.0
	6.82	6.69	8.24	4.29	2.07	4.08	2.07	–
	36.0–1.93	39.4–1.13	44.7–0.59	48.9–0.43	49.9–0.48	49.6–0.30	49.2–0.64	50.7–0.65
	13.15	7.59	5.59	5.75	4.28	3.59	4.34	3.82
EH	17.8–0.60	19.3–0.31	21.3–0.50	22.5–0.17	23.2–0.33	22.7–0.18	23.3–0.34	22.0
	10.05	4.61	8.44	4.63	4.65	4.24	4.55	–
	18.0–0.73	18.1–0.46	20.7–0.23	22.1–0.16	22.7–0.29	22.2–0.18	22.5–0.34	22.9–0.51
	9.94	6.70	4.62	4.78	5.74	4.88	.00	6.71
GSL	39.66–1.06	42.31–0.89	47.89–0.68	57.21–0.69	60.62–0.88	57.77–0.69	60.04–0.82	63.50
	7.70	5.94	4.74	5.78	3.57	5.35	3.05	–
	39.97–1.10	42.34–1.29	48.46–0.66	55.18–0.54	58.05–0.46	55.89–0.49	57.33–0.47	58.67–0.69
	6.75	8.04	5.06	4.91	2.84	4.03	2.01	3.13
ZB	20.87–0.44	21.93–0.48	24.07–0.24	26.90–0.22	27.50–0.15	27.22–0.22	27.56–0.16	27.00
	6.33	5.82	3.47	4.80	1.76	4.28	1.73	–
	20.40–1.20	21.73–0.45	24.25–0.25	26.44–0.16	27.82–0.24	26.89–3.08	27.45–0.26	28.23–0.38
	14.39	5.49	4.31	4.03	3.73	3.08	3.03	4.01
PLA	13.18–0.29	14.53–0.32	16.89–0.29	19.92–0.15	22.55–0.16	20.92–0.18	22.05–0.22	24.00
	6.49	6.22	6.10	7.42	5.54	6.67	3.17	–
	13.05–0.33	14.49–0.30	17.05–0.25	19.19–0.13	21.67–0.12	20.05–0.18	21.38–0.28	21.99–0.17
	8.43	7.01	6.03	6.91	4.76	5.39	4.40	2.26
PLB	5.12–0.09	5.78–0.12	6.39–0.16	7.90–0.09	8.52–0.18	7.95–0.11	8.40–0.15	9.70
	6.49	6.22	6.10	7.42	5.54	6.67	3.17	–
	5.05–0.22	5.70–0.21	6.66–0.10	7.52–0.09	8.37–0.13	7.59–0.10	8.37–0.21	9.37–0.15
	10.83	9.66	6.25	7.81	6.88	7.89	8.10	5.51
MB	16.66–0.26	17.25–0.26	18.59–0.22	21.07–0.23	21.66–0.14	21.27–0.27	21.65–0.15	21.80
	4.34	4.23	4.23	6.68	2.10	6.82	2.20	–
	16.45–0.58	17.42–0.40	18.82–0.17	20.40–0.12	21.36–0.17	20.57–0.11	20.97–0.14	21.82–0.28
	8.58	6.14	3.72	3.88	3.61	3.21	2.24	3.81
RB	7.40–0.10	7.51–0.18	8.42–0.09	9.40–0.09	9.61–0.10	9.52–0.09	9.53–0.07	10.40
	3.94	5.67	3.73	6.00	3.47	5.29	2.27	–
	6.87–0.32	7.30–0.18	8.31–0.09	9.31–0.09	10.04–0.10	9.47–0.07	9.82–0.12	10.31–0.12
	11.57	6.00	4.40	6.20	4.41	4.44	3.99	3.41
BaL	26.99–0.64	30.70–1.44	33.15–0.43	40.10–0.41	43.34–0.49	40.65–0.42	43.13–0.49	45.20
	6.72	13.29	4.69	6.02	3.54	5.58	3.42	–
	26.25–1.62	29.34–0.99	33.96–0.37	38.60–0.30	41.73–0.28	39.12–0.10	41.13–0.29	42.39–0.40
	15.08	8.97	4.51	5.04	2.90	4.05	2.23	2.80

Table 2 (continued)

	Age class (sample size)							
Variable	1 + 2 (9♂; 6♀)	3 + 4 (8♂; 7♀)	5 + 6 (13♂; 18♀)	7 + 8 (37♂; 44♀)	9 + 10 (11♂; 20♀)	8 (31♂; 37♀)	9 (10♂; 11♀)	10 (1♂; 9♀)
CD	13.85–0.20	14.36–0.14	15.14–0.10	15.56–0.11	16.92–0.17	16.72–0.10	16.89–0.19	17.20
	4.16	2.83	2.48	3.86	3.15	3.28	3.29	–
	13.73–0.32	14.26–0.22	15.40–0.11	16.39–0.09	17.03–0.12	16.54–0.09	16.77–0.15	17.31–0.15
	5.67	4.13	2.82	3.71	3.17	3.21	2.91	2.67
RD	6.98–0.17	7.56–0.17	8.59–0.12	10.36–0.11	10.96–0.13	10.51–0.12	10.91–0.14	11.50
	7.09	6.44	4.95	6.70	4.04	6.19	3.92	–
	6.75–0.38	7.44–0.28	8.72–0.10	9.73–0.08	10.57–0.10	9.85–0.08	10.40–0.15	10.77–0.11
	13.89	9.96	4.61	5.39	4.41	4.69	4.87	3.12
MTRL	5.30–0.51	6.85–0.21	7.81–0.40	9.37–0.07	9.46–0.11	9.38–0.07	9.39–0.10	10.20
	16.77	6.14	13.61	4.28	3.96	4.39	3.19	–
	5.28–0.55	7.00–0.20	7.68–0.29	9.21–0.05	9.37–0.07	9.24–0.05	9.40–0.09	9.32–0.11
	20.67	9.96	11.84	3.54	3.26	3.46	3.23	3.43
NL	13.38–0.41	14.73–0.42	17.22–0.35	21.61–0.31	23.39–0.39	21.97–0.32	23.17–0.36	25.60
	8.61	8.10	7.08	8.52	5.55	8.07	4.88	–
	12.92–1.01	14.41–0.70	17.74–0.26	20.70–0.21	22.64–0.23	20.78–0.20	22.54–0.41	22.74–0.21
	19.14	12.86	5.84	6.26	4.22	5.44	5.46	2.78
IOC	9.68–0.15	10.21–0.23	10.68–0.15	11.73–0.14	12.05–0.17	11.80–0.16	12.01–0.18	12.40
	4.59	5.91	4.96	6.72	4.54	7.11	4.69	–
	9.30–0.29	10.01–0.27	10.70–0.11	11.51–0.14	12.06–0.20	11.62–0.14	12.17–0.39	11.96–0.11
	7.63	7.12	4.30	8.02	6.99	7.29	9.61	2.87
RL	14.30–0.39	15.48–0.39	18.24–0.34	22.61–0.29	24.05–0.36	22.99–0.29	23.84–0.32	26.10
	7.63	7.16	6.38	7.57	4.91	6.94	4.27	–
	13.74–0.92	15.37–0.60	18.40–0.26	21.62–0.22	23.73–0.24	21.89–0.21	23.51–0.45	23.96–0.19
	16.47	10.33	5.56	6.25	4.32	5.51	5.71	2.37
MaxB	7.00–0.08	7.03–0.15	7.60–0.12	8.23–0.12	8.50–0.12	8.32–0.08	8.48–0.13	8.70
	3.50	5.93	5.79	5.56	4.56	5.19	4.74	–
	6.67–0.10	7.11–0.09	7.51–0.07	8.05–0.06	8.61–0.08	8.13–0.05	8.46–0.08	8.78–0.11
	3.63	3.29	4.08	4.88	3.93	3.89	3.19	3.79
D	7.98–0.22	8.60–0.23	9.84–0.16	12.12–0.16	13.03–0.16	12.30–0.17	12.95–0.16	13.80
	8.36	7.46	5.79	7.90	4.11	7.64	3.82	–
	7.70–0.56	8.80–0.33	9.99–0.11	11.61–0.12	12.68–0.11	11.81–0.11	12.46–0.16	12.97–0.09
	17.85	10.04	4.52	6.50	3.84	5.53	4.12	2.19
IFL	4.19–0.14	4.35–0.14	5.07–0.10	5.81–0.10	6.41–0.14	5.81–0.12	6.32–0.12	7.20
	9.95	9.11	7.09	10.45	6.92	11.03	5.80	–
	3.90–0.33	4.36–0.18	4.97–0.07	5.62–0.08	6.17–0.14	5.72–0.09	6.09–0.21	6.26–0.19
	20.89	10.84	5.98	9.66	10.21	9.31	11.22	9.33
BuL	8.96–0.15	9.06–0.17	9.73–0.13	10.50–0.08	10.85–0.15	10.56–0.09	10.90–0.15	10.30
	4.81	5.14	4.79	7.74	4.49	4.70	4.37	–
	8.87–0.28	9.27–0.22	9.80–0.06	10.36–0.06	10.63–0.10	10.43–0.07	10.53–0.12	10.76–0.16
	7.68	6.25	2.78	3.98	4.07	3.82	3.66	4.44
PPL	14.11–0.34	15.25–0.36	17.36–0.24	20.49–0.24	22.20–0.26	20.82–0.23	22.17–0.28	22.50
	6.83	6.75	4.57	6.81	3.63	6.01	3.82	–
	13.98–0.76	15.12–0.54	17.46–0.23	19.69–0.21	21.00–0.19	19.91–0.21	20.65–0.23	21.39–0.27
	13.29	8.74	5.36	6.84	3.97	6.45	3.47	3.80
MFW	7.54–0.22	8.27–0.23	9.32–0.20	10.89–0.15	11.96–0.18	11.11–0.15	11.93–0.20	12.20
	7.61	7.38	6.95	7.06	4.47	6.24	4.72	–
	7.38–0.52	8.30–0.36	9.29–0.18	10.74–0.17	11.43–0.20	10.90–0.14	11.06–0.25	11.80–0.24
	14.15	10.67	7.19	7.50	6.41	7.06	5.90	5.45

in *Proechimys,* two discriminant function analyses were performed on the taxa *P. brevicauda* and *P. quadruplicatus* Hershkovitz from sympatric or near sympatric localities across northern Peru. For the first run, specimens of both taxa of age classes 8 to 10 were

Table 3

Percent contribution to total variance of sex, age, and error for 23 morphometric variables from a single population sample of *Proechimys brevicauda*

See text and Fig. 1 for identification of variables. The interaction component between sex and age can be calculated by subtracting the sum of the components given from 100

Variable	ages 1–10 (combined)			ages 8–10		
	sex	age	error	sex	age	error
HBL	0.0	79.9	19.4	0.0	32.3	67.7
TL	0.0	83.1	15.5	0.0	0.0	100.0
HFL	0.0	80.7	17.6	0.0	0.5	98.6
EH	0.0	70.6	29.4	0.0	4.4	95.6
GSL	0.0	88.7	10.7	0.0	28.4	71.6
ZB	0.0	83.0	17.0	0.0	23.5	71.0
PLA	0.0	88.1	11.9	0.0	29.1	60.8
PLB	0.0	88.2	11.2	0.0	45.6	54.4
MB	0.0	82.8	16.6	0.0	33.8	59.7
MaxB	0.0	78.7	20.6	0.0	17.0	83.0
BaL	0.0	79.4	18.5	0.0	37.4	60.6
CD	0.0	86.9	12.4	0.0	50.9	49.1
RD	0.0	81.6	18.4	0.0	22.9	77.1
MTRL	0.0	85.4	13.0	0.0	39.5	60.5
NL	0.0	87.4	12.6	0.0	0.0	86.0
IOC	0.0	86.6	13.1	0.0	36.7	63.2
RL	0.0	60.0	40.0	0.0	1.6	98.4
RB	0.0	72.9	26.5	0.0	35.1	64.9
D	0.0	85.7	13.9	0.0	37.6	62.1
IFL	0.0	69.3	30.7	0.0	24.1	75.9
BuL	0.0	69.1	30.9	0.0	5.0	90.4
PPL	0.0	80.6	19.4	0.0	31.2	68.8
MFW	0.0	72.5	22.7	0.0	27.2	68.0
mean	0.0	80.0	19.2	0.0	24.5	73.4

Table 4

Percentages of individual specimens of *Proechimys brevicauda* and *P. quadruplicatus* correctly classified based on discriminant function analyses of (a) age classes 8–10 combined for both species and (b) age classes 8, 9, and 10 examined separately for both species

Actual group		Predicted group membership (%)		
		P. brevicauda	*P. quadruplicatus*	N
P. brevicauda	ages 8–10 combined	71.3	28.7	211
	age separate			
	8	99.0	1.0	103
	9	93.2	6.8	59
	10	98.0	2.0	49
P. quadruplicatus	ages 8–10 combined	23.3	76.7	128
	age separate			
	8	0.0	100.0	38
	9	3.2	96.8	63
	10	7.4	92.6	27

combined; in the second, individual comparisons across single age classes were made. Table 4 provides a summary of the proportion of specimens in each analysis correctly allocated to either species based on the a posteriori classification of individuals derived from their discriminant scores. The power to discriminate these two taxa increased by an average of some 25 percent when age classes were considered separately. In other words, age components to the variation in both species contributed to a misclassification of about one-quarter of the specimens of either species examined. Part of the reason for the difference in resolving power between the two discriminant analyses is that those variables which are most significant contributors to species discrimination (for example, PLA and MFW) are also those which have high age variation components (e.g. 39.1 and 27.2 percent, respectively, for *P. brevicauda*; see Table 3). With age related variation of such magnitude, it is no wonder that Thomas remarked on the "bewildering instability" of cranial characters in *Proechimys.*

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Zusammenfassung

Systematische Probleme nicht-geographischer Variabilität bei Stachelratten (Genus Proechimys, Echimyidae)

Untersucht wird die geschlechts- und altersbedingte Variabilität der Stachelratte *Proechimys brevicauda* Gunther anhand von 23 morphometrischen Variablen für Haut und Schädel. Meßbarer Sexualdimorphismus konnte nicht festgestellt werden, hingegen ergab sich eine große, durch das Alter bedingte Variabilität sogar im adulten Stadium. Durchschnittlich 25 % der Gesamtabweichung können für mehrere Maße festgestellt werden in den Alterskategorien reproduktionsfähiger Individuen. Im Extrem können 50 % erreicht werden. Der Effekt dieser starken altersbedingten Variabilität wird in bezug auf die geographischen Variationsmuster von *Proechimys brevicauda* im nördlichen Peru untersucht. Daraus ergeben sich Möglichkeiten, sympatrische Arten von Taschenratten im westlichen Amazonasgebiet zu erkennen.

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