CRANIAL AND BACULAR VARIATION IN POPULATIONS OF SPINY RATS (GENUS PROECHIMYS) FROM SOUTH AMERICA

By

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INTRODUCTION

Spiny rats (genus Proechimys) are hystricomorph rodents of the family Echimyidae inhabiting most forested areas of South America above the Tropic of Capricorn, and Central America northward to Nicaragua (Moojen, 1948). Although these rats frequently live near streams, they are not entirely riparian, but may inhabit semiarid grasslands (Hershkovitz, 1948) or dry forests (Allen, 1904).

The wide range of morphological variation observed in these rats has made specific determination difficult. Thomas (1927, 1928a, 1928b), Hershkovitz (1948), and Moojen (1948) commented on their variability and the taxonomic problems caused by it in specific assignment. Thomas (1928a, p. 262) remarked that "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."

The present study is an effort to measure some elements of variation in Proechimys, and thereby provide an aid toward future taxonomic work in the genus. Initially, the most useful measurements were selected by a study of nongeographic variation. The primary aims, however, were to assess geographic variation in cranial dimensions and to attempt to correlate these data with the results of analyses of skull, bacular, tooth, and pelage morphology. Taxonomic assignment was only a secondary objective since some pertinent type material was not available and information on ecology was incomplete. Descriptions were

written of the morphological features common to specimens from each locality, and comparisons made with other populations. Many of the groups described are currently recognized as separate taxa, either species or subspecies. These accounts reflect differences between populations from different localities, and offer suggestions on taxonomic assignment, but are not taxonomic descriptions in the strict sense.

NOMENCLATURAL HISTORY

The genus Proechimys is in the family Echimyidae Miller and Gidley, and the subfamily Echimyinae as outlined by Ellerman (1940) and Landry (1957).

Many specific names have been applied to members of the genus Proechimys, perhaps indicating the variability that has been noted in the genus. Some of the specific names represent well-defined, valid species, and others represent species based on minor, perhaps even individual variations.

The name Proechimys was proposed by Allen (1899b) using Echimys trinitatis Allen and Chapman, as the genotype. His concept of the genus included species of Hoplomys and Mesomys, presently accorded full generic rank in the family Echimyidae. Thomas (1921) proposed the subgenus Trinomys to characterize the spiny rats of southeastern Brazil that have a distinctive mainfold arrangement in the cheek teeth. Tate (1935) presented a thorough history of the genus Proechimys, and this has been supplemented by Ellerman (1940), Hershkovitz (1948), Moojen (1948), and Cabrera (1961). Most of the discussion that follows concerns members of the subgenus Proechimys.

Moojen (1948), fide unpublished manuscript of Remington Kellogg, and Hershkovitz (1948) pointed out that Mus (=Proechimys) guyannensis E. Geoffroy, 1803, antedates Echimys (=Proechimys) cayennensis Desmarest, 1817. However, most workers prior to 1948 had used the latter name.

Ellerman (1940) proposed that the majority of the 50 named forms of Proechimys be included in four species: P. cayennensis, P. iheringi, P. albispinus, and P. (Trinomys) setosus. In his cayennensis group he allocated 29 forms as subspecies of Proechimys cayennensis and retained five forms as full species (P. vacillator, P. hendeei, P. rattinus, P. canicollis, and P. dimidiatus) within the group. Osgood (1944) reported on Proechimys from Ecuador and Peru without following Ellerman's arrangement, although he suggested that several species did not merit specific rank.

Moojen (1948), working with Brazilian forms, recognized four species in the subgenus Proechimys (P. goeldii, P. semispinosus, P. longicaudatus, and P. guyannensis). Hershkovitz (1948), primarily concerned with Colombian forms, tentatively accepted Ellerman's contention that P. guyannensis was a composite species that included the forms known as P. longicaudatus and P. goeldii. He also suggested that P. semispinosus may not be a member of the P. guyannensis group. In addition, Hershkovitz kept the forms of P. hendeei distinct from P. guyannensis and erected a fourth group based on P. quadruplicatus Hershkovitz, 1948. Moojen (1948) relied heavily on pelage characteristics and Hershkovitz (1948) on patterns of enamel folds. Cabrera (1961) listed 57 forms in the genus Proechimys, following closely the arrangement of Moojen (1948).

MATERIALS AND METHODS

MATERIALS.-- In this study, 171 specimens (including 46 bacula, 171 skulls, and 158 skins) were examined. The majority of the specimens were those collected by the Middle American Research Unit (MARU) in connection with their field investigations of hemorrhagic fever in Bolivia and adjacent areas during 1964-1966. The MARU specimens were submitted to the Mammal Identification Service (MIS) Division of Mammals, Smithsonian Institution, for identification and deposition in the mammal collections of the United States National Museum (USNM). Additional specimens in the USNM collections from Brazil (Goldman, 1911 and 1912), Colombia (Hershkovitz, 1948), Nicaragua, and Peru, were also examined.

METHODS.-- Specimens were sorted by age, sex, and locality to assess the effects of individual variation prior to studying geographic variation. Five age classes were established but only adults (classes IV and V) were statistically analyzed. Secondary sexual variation was not significant and both sexes of like age classes were combined for geographical comparisons.

Fourteen cranial and four bacular measurements were made on the largest series of specimens (from San Ignacio, Bolivia), using dial calipers accurate to 0.1 mm. These measurements are described below and illustrated in figure 1.

Nasal length: From median anterior to posterior points (exclusive of notch) on nasal bones. a to a'.

Nasal breadth: Greatest distance across nasal bones. b to b'.

Zygomatic breadth: Greatest distance across zygomatic arches. c to c'.

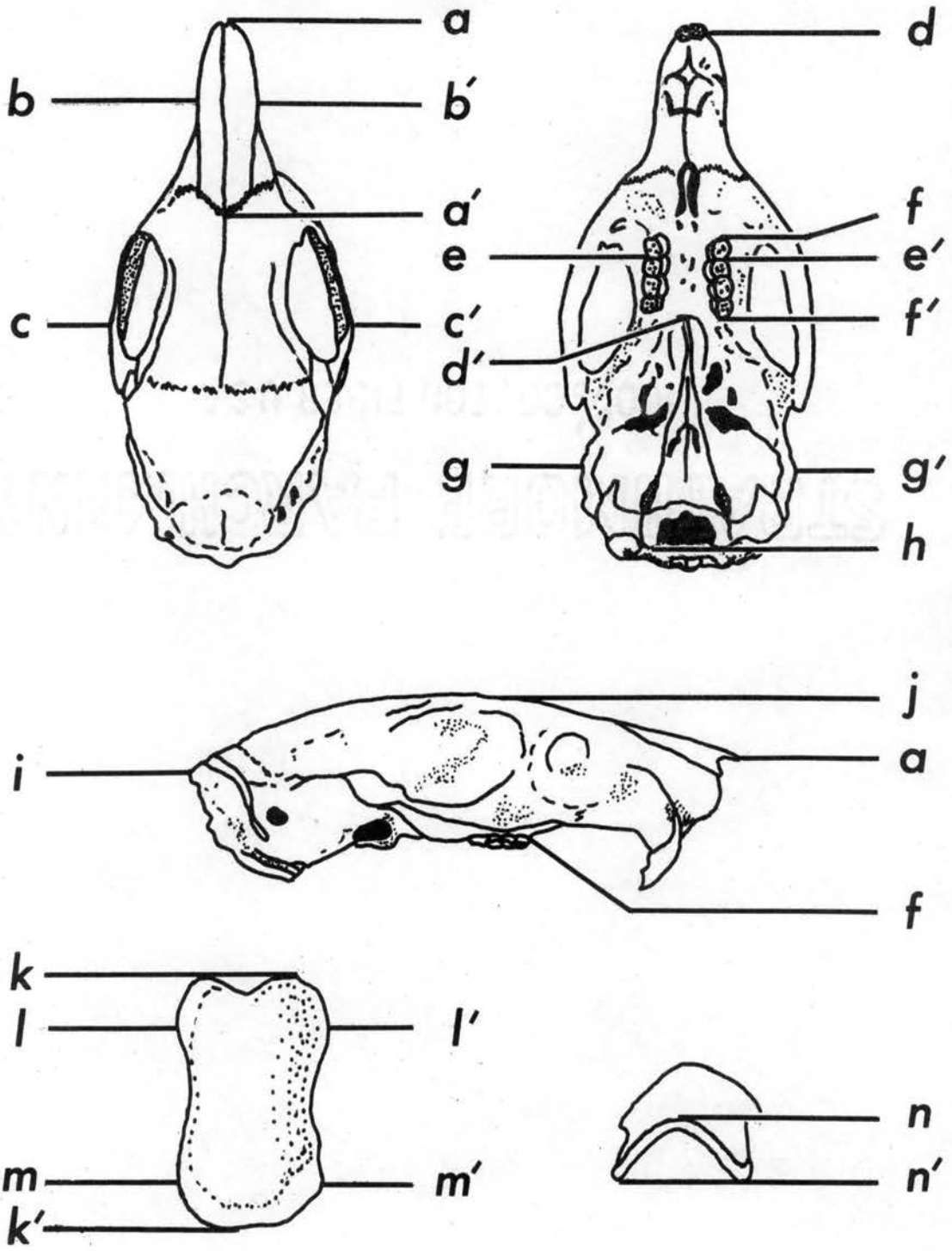


FIGURE 1. Views of skull and baculum of Proechimys showing points of reference for measurements.

Palatal length: From anteriormost point of premaxillae to anteriormost point of postpalatal notch. d to d'.

Maxillary breadth: Greatest width across maxillary bone midway between P4 and M1. e to e'.

Alveolar length, upper tooth row: Distance between anterior alveolar margin of P4 and posterior margin of M3. f to f'.

Mastoidal breadth: Greatest distance across mastoid bones. g to g'.

Condylobasal length: From anteriormost point of premaxillary bulge to posterior level of occipital condyles. d to h.

Greatest length of skull: From anteriormost point of nasal bones to posteriormost point on occipital bone. a to i.

Rostral depth: Least vertical distance from anterior alveolar border of P4. f to j.

Bacular length: Greatest length. k to k'.

Bacular width, anterior: Greatest transverse distance across ventrally projecting elements. l to l'.

Bacular width, posterior: Greatest transverse distance across base. m to m'.

Bacular depth, anterior: Greatest distance between dorsal and ventral elements. n to n'.

Coefficients of variation (V) were calculated according to the method of Haldane (1955) for all cranial, bacular, and external measurements of specimens from San Ignacio (Table 1). Measurements having large V-values were not used as indicators of geographic variation. Broken skull parts prevented use of some measurements with low V-values. The measurements used were condylobasal, palatal, nasal, and alveolar

TABLE 1. Coefficients of Variation (V) for Bacular, Cranial, and External Measurements in a Sample (N) of Proechimys guyannensis from San Ignacio, Bolivia.

Measurement	Males, Age-Class IV		Males, Age-Class V	
	N	V	N	V
Rostral depth	13	1.32	8	3.38
Zygomatic breadth	12	2.76	8	1.41
Mastoidal breadth	12	2.85	8	2.72
Alveolar length	13	3.03	8	4.75
Palatal length	9	3.49	7	3.42
Greatest length of skull	8	3.53	5	2.88
Maxillary breadth	13	3.69	8	3.91
Condylobasal length	9	3.78	5	3.72
Hind foot length	13	4.85	8	3.59
Bacular width, anterior	8	5.02	4	13.32
Nasal length	13	6.34	8	5.39
Nasal width	13	6.47	8	1.74
Total length	11	6.60	6	4.30
Tail length	11	7.12	6	4.98
Bacular width, posterior	6	7.80	6	7.28
Bacular length	7	8.15	6	10.66
Ear length	13	11.10	8	8.16
Bacular depth, anterior	8	11.30	6	21.36

lengths; zygomatic, mastoidal, and maxillary breadths; and rostral depth.

The arithmetic mean ($\bar{X}$), standard deviation (SD) and standard error (SE) were calculated for all populations of adequate sample size according to Simpson, et al. (1960). Sample sizes were increased by pooling specimens from areas within 30 km. of each major locality. Student's *t*-tests were performed on two measurements (condylobasal length, zygomatic breadth) to test differences between some localities. Bar graphs, similar to those of Hubbs and Hubbs (1953), were constructed for all cranial measurements to demonstrate geographic variation among 11 populations. No statistical analyses were made of dental or pelage characteristics, and small sample sizes prevented statistical treatment of bacula.

Dried phalli were removed where possible from the skins of all specimens and the bacula processed according to the method of Friley (1947), although the bacula were not mounted on insect points.

Tooth nomenclature follows that of Hershkovitz (1948) and Moojen (1948), in part. Lowercase (p,m) and capital (P,M) letters designate lower and upper cheek teeth, respectively. All formulae given in the locality accounts and all references to counterfolds refer to the number of outer folds in the upper and the number of inner folds in the lower cheek teeth (*e.g.* 3/3-3/2-3/2-3/2; in figure 2, d and i). Pelage terminology follows Moojen (1948). Aristiforms, comparable to guard hairs in other mammal groups, are long, broad, flattened hairs, that are frequently spinous. Setiforms (=overhairs) are narrower than aristiforms and are less spinous. Villiforms (=underfur) and vibrissiforms (=vibrissae), the other types of hair present, are similar to those in

other mammal groups. Capitalized color terms (Ridgeway, 1912) are used in descriptions of pelage in the population accounts.

Localities on the map (figure 2), numbered consecutively from north to south, indicate the major collecting sites of specimens that were subjected to statistical analyses. Population accounts, including those both from plotted and unplotted locations, are treated in the same sequence. Morphological variants within some populations have been arbitrarily designated A, B, C, D, or E to aid in description, comparison, and discussion.

In the specimens-examined section the localities are arranged from north to south within a country. The gazetteer arrangement is alphabetical by country and locality.

NONGEOGRAPHIC VARIATION

In order to understand geographic variation, specimens from San Ignacio, Bolivia, were sorted into various combinations of age classes and sexes to measure nongeographic variation (variation within a population).

AGE VARIATION.-- Several authors have reported that age variation may be taxonomically important in Proechimys and other genera. Pictet (1841) suggested that Echimys (=Trinomys) setosus and E.(=Trinomys) myosurus were age variants of E.(=Proechimys) cayennensis. Tate (1939) reported that many species of Proechimys may simply be age variants, without specific distinctness, if sufficient samples of different age groups were available. Allen (1894), in examining large series of Neotoma micropus, suggested that age differences may incorrectly be correlated with subspecific or specific differences. Dice (1932)

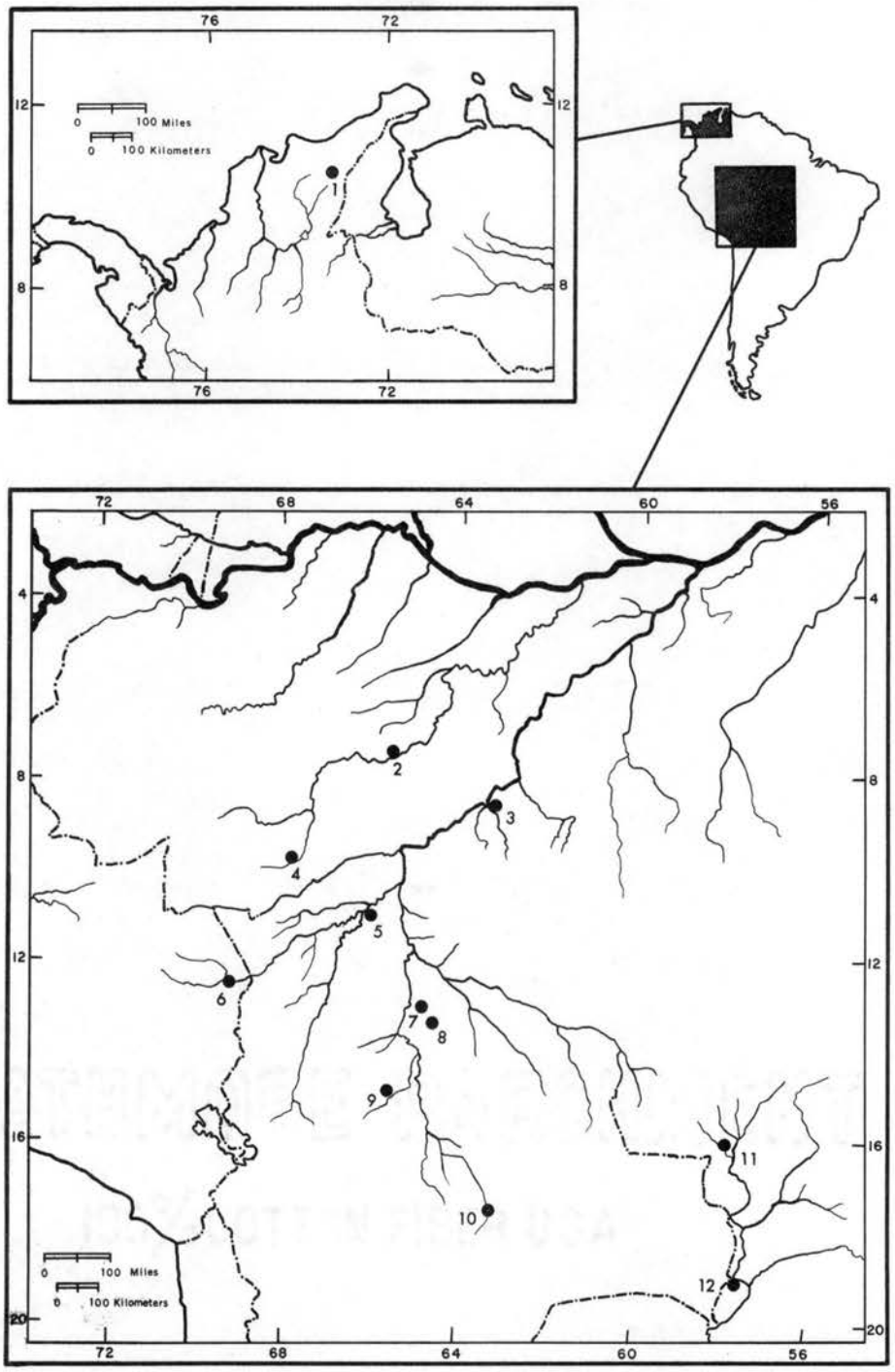


FIGURE 2. Map showing principal collecting localities (refer to gazetteer and specimens-examined section for detailed locality data): (1) Villanueva (2) Hyutanaham (3) Porto Velho (4) Río Branco (5) Riberalta (6) Puerto Maldonado (7) San Joaquín (8) Cafetal (9) San Ignacio (10) Warnes (11) Limão Balsa (12) Corumbá.

recognized this factor in Peromyscus and suggested that only individuals of similar age groups be compared in studies of geographic variation.

Degree of tooth wear is frequently utilized to establish "age" categories for comparisons of populations. Handley (1959, p. 4) reported that "tooth wear appears to be a reliable criterion of age," in Hoplomys. Moojen (1948) recognized four age classes in Proechimys, based on pelage characteristics and degree of tooth wear. Similarly, five age classes were established in this study, based primarily on tooth wear. An inherent difficulty of this aging technique is that tooth wear may not correlate with chronological age, and may be affected by diet, health, and habitat of the mammal. However, for statistical comparisons of populations, the technique proved useful.

Changes in the occlusal pattern of the teeth are illustrated in figure 3, and discussed below:

Class I (figure 3, a and f): Only P4-p4 and M1-m1 are at occlusal level and show signs of island formation from wear on the counterfolds. The middle island has not formed in p4 and P4. This class corresponds to the juvenile age recognized by Moojen (1948).

Class II (figure 3, b and g): All enamel islands appear in P4, p4, and M1. M2 and m2 appear at occlusal level, but no islands have formed. The first sign of an incipient anterior island in m1 appears in this class.

Class III (figure 3, c and h): The enamel islands in P4 and M1 are similar to those of class II, but show a reduction in size through wear; M2 is similar to M1. In m1 and m2 small incipient anterior islands form; M3 and m3 may show slight wear, although they are usually still below occlusal level where wear occurs.

Age classes II and III encompass Moojen's adolescent category.

Class IV (figure 3, d and i): The islands in P4 and p4 are reduced in size; the incipient islands of m1 and m2 merge with the middle island to form Y's, and after much wear are lost. M3 and m3 are at occlusal level, although island formation may not be completed in m3. This class includes most of Moojen's adult category.

Class V (figure 3, e and j): Many of the islands of P4 and p4 greatly reduced in size or lost entirely. The islands of M1 and m1 frequently divide into additional smaller islands, those of M2 and m2 reduced in size, and those of M3 and m3 show complete formation. Only the oldest individuals of this class would correspond to Moojen's senile category.

SECONDARY SEXUAL VARIATION.-- Coefficients of variation (V) were computed for different groupings of age classes and sexes to see if secondary sexual variation was significant (Table 2). The V-values were generally smaller when sexes were grouped in a single age class and larger when age classes of like sexes were combined. In all combinations there was a significant overlap of measurements when males were compared with females. Although females were slightly smaller than males in age-class IV, they closely approximated male growth in age-class V. The smallest V-values occurred in single sex and age-class groupings, but these combinations involved small sample sizes, making statistical comparisons difficult. Sample sizes were therefore increased in the different populations by grouping sexes together within each age class.

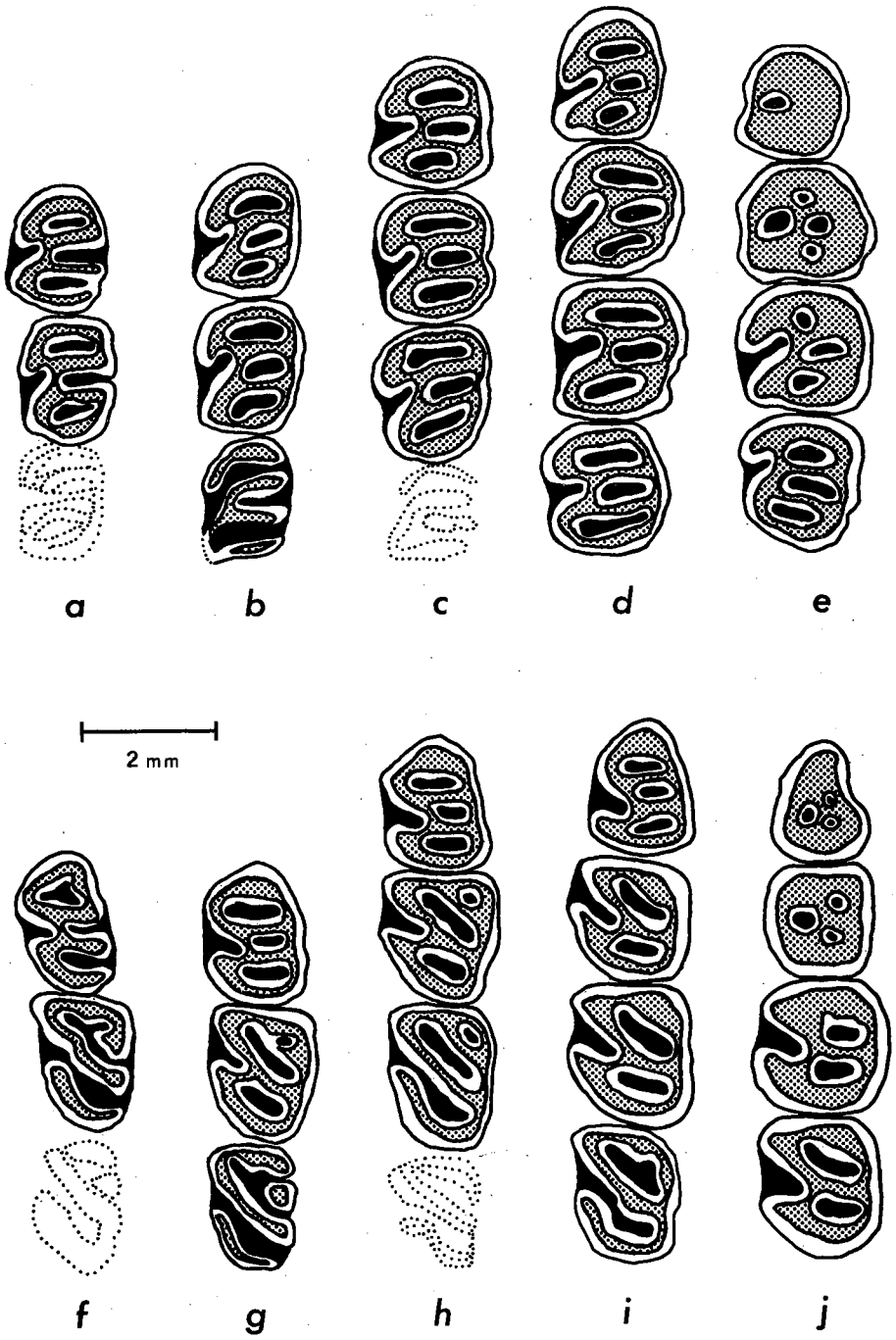


FIGURE 3. Occlusal views of left upper (a-e) and lower (f-j) cheek teeth in Proechimys guyannensis showing age classes (Roman numerals) and respective USNM catalog numbers (The uppermost tooth in each series is premolar 4. In a-e, the labial side is along the right border of the tooth row; in f-j, this side is along the left border. All specimens are males from San Ignacio, Bolivia.): (a) I, 364103; (b) II, 364104; (c) III, 364121; (d) IV, 364114; (e) V, 364129; (f) I, 364103; (g) II, 364104; (h) III, 364121; (i) IV, 364114; (j) V, 364129.

TABLE 2. Coefficients of Variation ($\underline{V}$), Means ($\bar{X}$), and Standard Deviations (SD) for Three Cranial Measurements Showing Differences in Sorting Methods. N refers to sample size.

	ZYGOMATIC BREADTH					ROSTRAL DEPTH					MAXILLARY BREADTH				
	N	$\underline{V}$	$\bar{X}$	±	1 SD	N	$\underline{V}$	$\bar{X}$	±	1 SD	N	$\underline{V}$	$\bar{X}$	±	1 SD
Age Classes, Sexes Combined	35	5.12	24.8	±	1.27	31	5.52	12.1	±	.67	32	5.96	8.2	±	.49
Males, Age Classes Combined	20	2.16	25.1	±	.54	21	4.99	12.2	±	.60	21	5.87	8.2	±	.48
Females, Age Classes Combined	15	6.98	24.3	±	1.67	11	6.33	11.9	±	.73	11	6.50	8.1	±	.52
Sexes Combined, Age-Class V	13	1.72	25.9	±	.44	13	2.75	12.7	±	.34	13	3.41	8.7	±	.29
Sexes Combined, Age-Class IV	17	4.82	24.3	±	1.15	19	3.95	11.7	±	.46	19	3.68	7.9	±	.29
Males, Age-Class V	8	1.41	25.7	±	.35	8	3.38	12.8	±	.42	8	3.91	8.7	±	.33
Females, Age-Class V	5	1.48	26.2	±	.37	5	1.18	12.6	±	.14	5	2.91	8.6	±	.24
Males, Age-Class IV	12	2.76	24.7	±	.67	13	3.37	11.9	±	.39	13	3.69	7.9	±	.29
Females, Age-Class IV	10	4.94	23.4	±	1.13	6	0.40	11.2	±	.04	6	3.26	7.7	±	.24

PHYSIOGRAPHY

Most of the specimens examined in the study were collected near streams or rivers (except those of Proechimys canicollis; see Hershkovitz, 1948) which are part of the two major drainage systems of South America. The Amazon system drains most of northern and northwestern Brazil, most of Bolivia, and portions of Peru, Ecuador, Colombia, and the Guianas. The Parana-Paraguay-Plata system drains Paraguay, Uruguay, most of Argentina, and western and southwestern Brazil. The majority of the localities (2-10, in figure 2) are located along the tributaries of the Amazon system. A region of higher elevation and drier climate separates the two drainage systems in southeastern Bolivia (Roseveare, 1948).

Extensions of the tropical rain-forest follow the tributaries of the Amazon system, and then merge with the campo of Mato Grosso, Brazil, and the Gran Chaco of southeastern Bolivia (Smith and Johnston, 1945; Roseveare, 1948).

GEOGRAPHIC VARIATION

Some geographical trends in bacular, cranial, dental, and external features were noted in comparisons of populations, although these changes were not definitely clinal in nature. Assessment of these trends was complicated by the tremendous variability of individuals within a population.

BACULUM.-- Hooper (1961), using three specimens, apparently was the first to describe the baculum of a Proechimys. No subsequent work on Proechimys bacula has been discovered in the literature. Thus, the

present study supplements and increases the available information on bacular morphology in this genus.

A total of 46 bacula were available for study, although for some localities none was found on the specimens examined, and for others the sample sizes were very small. However, those available did provide some evidence of geographic variation and illustrations were made of bacula from most localities (figure 4).

Most of the specimens from Bolivia and Corumbá, Brazil, had broad bacula, although the length was variable (figure 4; c-d and f-i). The bacula from the Puerto Maldonado population were long and slender, and with wide apical wings projecting ventrad (figure 4, a and b). The Peruvian populations had long, slender bacula (figure 4, j and k), and those from Villanueva were very narrow (figure 4, l and m). In the Riberalta population there were two types of bacula, markedly different from each other (figure 4, d and e). Clinal variation was not apparent, although bacula from the San Joaquin and Cafetal populations (figure 4, f and g) showed some mutual similarities with the long, slender bacula of the northern populations and the broad bacula of the southern populations.

CRANIAL DIMENSIONS.-- Of the eight cranial measurements analyzed (figures 5-12), geographic differences were most apparent in condylobasal (figure 5), nasal (figure 8), and palatal (figure 11) lengths, and to a lesser degree in zygomatic (figure 7) and mastoidal (figure 9) breadths and rostral depth (figure 10). Maxillary breadth (figure 6) and alveolar length (figure 12) showed little geographic variation.

Student's *t*-tests were run on seven samples of age-class IV (Table 3) and five samples of age-class V (Table 4) to see if the mean

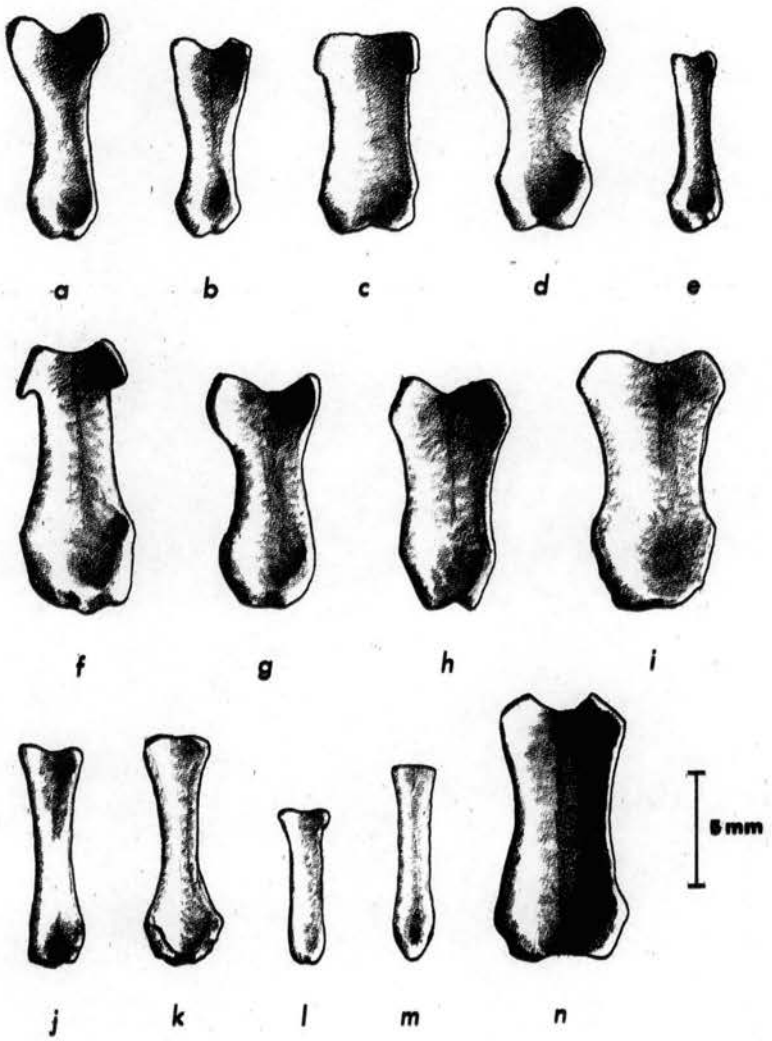
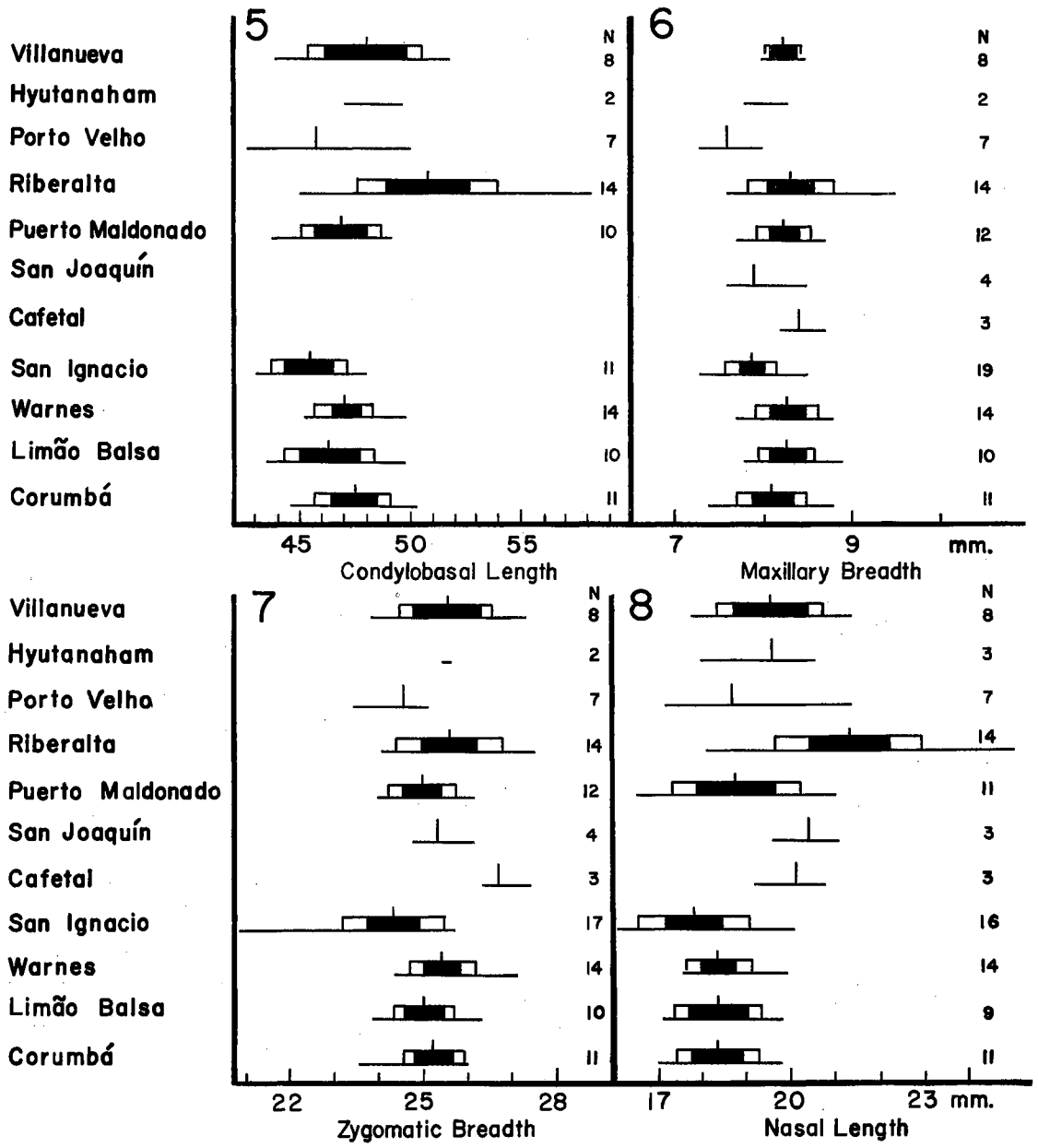
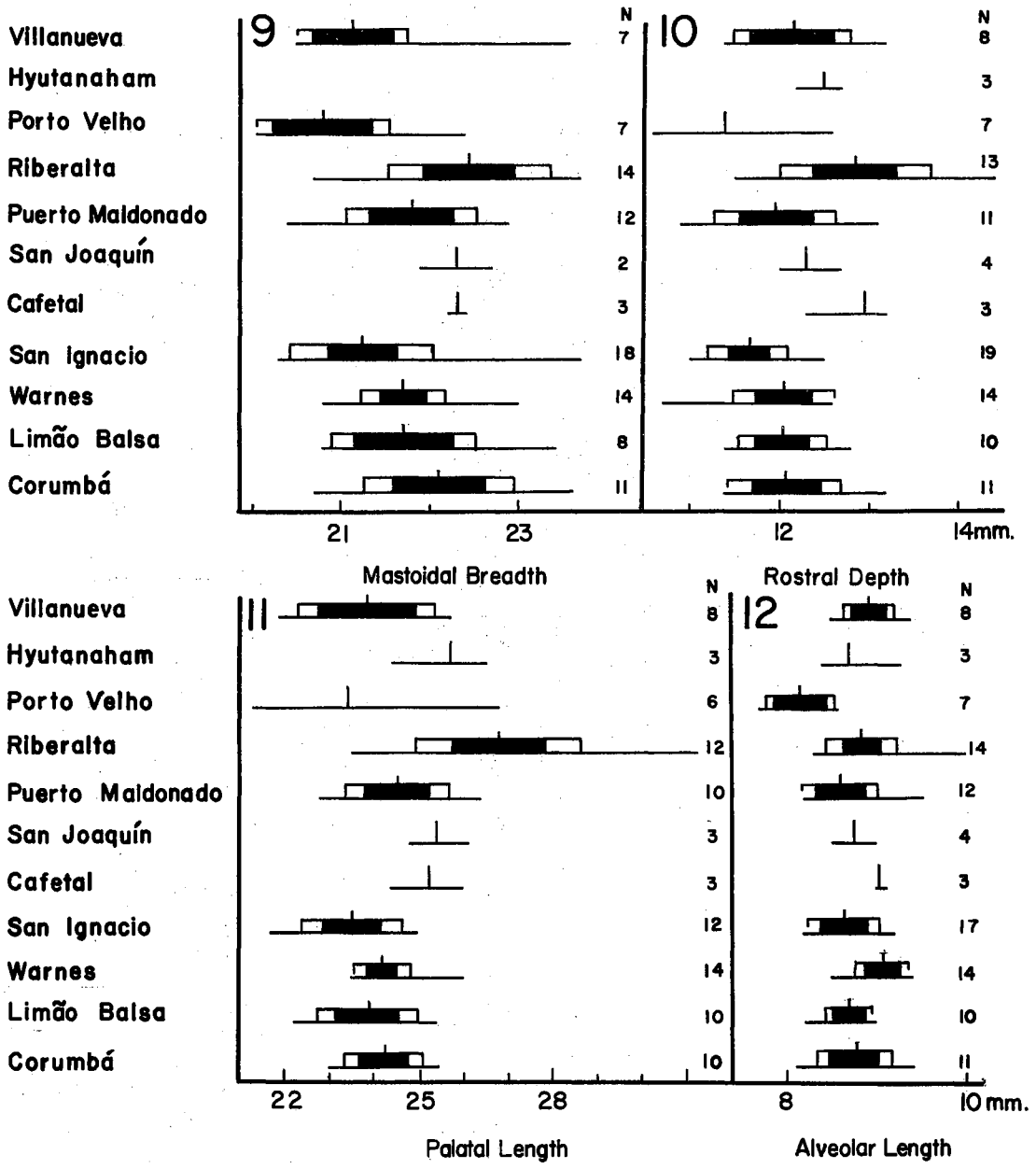


FIGURE 4. Ventral views of Proechimys bacula. Taxa, localities, age classes (Roman numerals), and USNM catalog numbers, listed in that order: (a and b) P. guyannensis, Puerto Maldonado, Peru, IV, 364026 and 364014, respectively; (c) P. guyannensis, Corumbá, Brazil, IV, 364075; (d and e) P. guyannensis, Riberalta, Bolivia, IV, 363986 and 364005, respectively; (f) P. guyannensis, San Joaquín, Bolivia, V, 363982; (g) P. guyannensis, Cafetal, Bolivia, IV, 391403; (h and i) P. guyannensis, San Ignacio, Bolivia, IV, 364114 and V, 364133, respectively; (j) P. g. poliopus, Río Tarra, Colombia, IV, 280196; (k) P. g. decumanus, Aguas Verdes, Peru, III, 303015; (l and m) P. canicollis, Villanueva, Colombia, IV, 280131 and 280125, respectively; (n) P. semispinosus, Greytown, Nicaragua, IV, 16355/23253.



FIGURES 5-8. Geographic variation of four cranial dimensions in 11 samples of Proechimys, age-class IV (The sample size, N, is shown by a number at the right of each bar graph. For each sample the range is shown by a horizontal line; the mean by a vertical line; two SE on both sides of the mean by a black bar; and one SD on both sides of the mean by the black plus open bars): (5) condylobasal length (6) maxillary breadth (7) zygomatic breadth (8) nasal length.



FIGURES 9-12. Geographic variation of four cranial dimensions in 11 samples of Proechimys, age-class IV (see figures 5-8 for explanation of symbols): (9) mastoidal breadth; (10) rostral depth; (11) palatal length; (12) alveolar length.

TABLE 3. Values of Student's t and associated probability levels (P) in testing the hypothesis (H: $X_1 = X_2$) of no difference in mean measurements (condylobasal length, zygomatic breadth) between two populations, age-class IV. In each rectangle the parenthetic number represents the degrees of freedom ($N_1 + N_2 - 2$) in the test; the middle number is the t value; and the bottom numbers represent the probability of exceeding the observed value of t.

CONDYLOBASAL LENGTH

	Villanueva	Riberalta	Puerto Maldonado	San Ignacio	Warnes	Limão Balsa	Corumbá
Villanueva		(18) 2.067 0.05>P>0.02	(16) 1.100 0.3>P>0.2	(17) 2.601 0.02>P>0.01	(20) 1.187 0.3>P>0.2	(16) 1.510 0.2>P>0.2	(17) 0.529 0.7>P>0.6
Riberalta	(20) 0.102 P>0.9		(20 3.468 0.01>P>0.001	(21) 4.950 0.001>P	(24) 4.950 0.001>P	(20) 3.800 0.01>P>0.001	(21) 3.070 0.01>P>0.001
Puerto Maldonado	(18) 1.407 0.2>P>0.1	(24) 1.574 0.2>P>0.1		(19) 1.876 0.1>P>0.05	(22) 0.226 0.9>P>0.8	(18) 0.363 0.8>P>0.7	(19) 0.806 0.5>P>0.4
San Ignacio	(23) 2.523 0.02>P>0.01	(29) 3.027 0.01>P>0.001	(27) 1.698 0.2>P>0.1		(23) 2.569 0.02>P>0.01	(19) 1.130 0.3>P>0.2	(20) 2.795 0.02>P>0.01
Warnes	(20) 0.255 0.9>P>0.8	(29) 0.404 0.7>P>0.6	(24) 1.602 0.2>P>0.1	(29) 3.133 0.01>P>0.001		(22) 0.949 0.4>P>0.3	(23) 0.767 0.5>P>0.4
Limão Balsa	(19) 0.751 0.5>P>0.4	(22) 1.381 0.2>P>0.1	(20) 0.155 0.9>P>0.8	(25) 1.726 0.1>P>0.05	(22) 1.421 0.2>P>0.1		(19) 1.374 0.2>P>0.1
Corumbá	(16) 1.263 0.3>P>0.2	(23) 0.862 0.4>P>0.3	(21) 0.906 0.4>P>0.3	(26) 2.379 0.05>P 0.02	(23) 0.672 0.6>P>0.5	(19) 0.751 0.4>P>0.3	

ZYGOMATIC BREADTH

TABLE 4. Values of Student's t and associated probability levels (P) in testing the hypothesis of no difference in mean condylobasal length and zygomatic breadth measurements between two populations, age-class V. See Table 3 for explanation of values.

CONDYLOBASAL LENGTH

	Villanueva	Riberalta	Puerto Maldonado	San Ignacio	Warnes
Villanueva		(11) 0.713 0.5>P>0.4	(11) 0.028 P>0.9	(11) 0.884 0.4>P>0.3	(10) 0.564 0.6>P>0.5
Riberalta	(12) 0.649 0.6>P>0.5		(14) 0.740 0.5>P>0.4	(14) 0.859 0.5>P>0.4	(13) 0.540 0.6>P>0.5
Puerto Maldonado	(14) 0.128 P>0.9	(16) 1.036 0.4>P>0.3		(14) 1.770 0.1>P>0.05	(13) 1.430 0.2>P>0.1
San Ignacio	(17) 2.005 0.1>P>0.05	(21) 2.661 0.02>P>0.01	(19) 3.212 0.01>P>0.001		(13) 0.499 0.7>P>0.6
Warnes	(12) 0.727 0.5>P>0.4	(16) 0.871 0.4>P>0.3	(14) 1.598 0.2>P>0.1	(19) 1.659 0.2>P>0.1	

ZYGOMATIC BREADTH

differences of condylobasal length and zygomatic breadth were statistically significant in interpopulation comparisons. The Riberalta population (age-class IV) was significantly larger ($0.01 > P > 0.001$) in mean condylobasal length than the means of the Puerto Maldonado, San Ignacio, Warnes, Limão Balsa, and Corumbá populations. In zygomatic breadth (age-class IV), Riberalta versus San Ignacio was the only highly significant comparison ($0.01 > P$).

In mean zygomatic breadth (age-class V), the San Ignacio population was significantly smaller ($0.02 > P > 0.001$) than the means of the Riberalta and Puerto Maldonado populations. Riberalta versus San Ignacio was the only highly significant ($0.1 > P > 0.05$) comparison of condylobasal length (age-class V).

Similarities in mean cranial dimensions were more apparent between nearby populations than between widely separated localities. Clinal variations were not apparent, but the four southern populations (San Ignacio, Warnes, Limão Balsa, and Corumbá) were generally smaller in most cranial dimensions, although these differences were not always statistically significant.

TEETH.-- Although there were wide variations in tooth counterfold numbers within populations, some geographical trends were evident. In most populations there were three counterfolds in the upper cheek teeth, but some specimens from Greytown, Hyutanaham, and Riberalta, had indications of a fourth fold.

Variations in the number of counterfolds in the lower cheek teeth were more common. In the southern populations there were either two or three counterfolds, with a trend toward retention of two folds in m1 and m3. In east-central Bolivia the number varied from two to three, but

m1 and m3 usually had three counterfolds. In northern Bolivia, southeastern Peru, and northwestern Brazil, there were usually three counterfolds, although some premolars possessed four. Two counterfolds were the rule in the molars of specimens from Peru and Colombia.

Moojen (1948) reported that variation in counterfold number was clinal and the number of folds was reduced in response to lower humidity. The evidence from the present study indicates a reduction in the number of counterfolds in some northern and southern populations, although this situation may not be correlated with decreased humidity. Specimens from the rain-forest areas of the Río Tarra show a reduction of counterfold numbers in the lower molars, and specimens from Corumbá (campo of Mato Grosso) frequently have three counterfolds in p4, m1, and m2.

PELAGE.-- A few specimens from each locality were selected for analyses of pelage characteristics, although the resulting data were not treated statistically.

No great differences in width of aristiforms were noted in comparisons of specimens from most populations in Peru, Bolivia, and Brazil. Wide aristiforms (0.8-1.0 mm.) were found on specimens from Greytown, Porto Velho, and Aguas Verdes. In most other populations, the aristiforms were narrow (0.3-0.5 mm.) or of medium width (0.5-0.8 mm.). Aristiforms were long (18-24 mm.) in most populations but short (15-18 mm.) examples were found in some populations in northern Bolivia and northwestern Brazil.

DISCUSSION.-- In evaluating morphological variation in any group of mammals it is important to consider other biological factors (e.g. behavior, ecology, genetics) that may influence speciation. In this study, however, a biological interpretation was hampered by a lack of

detailed ecological data or personal field experience with Proechimys.

This study demonstrated that arbitrary assignment of populations to the available names did not adequately explain the variation that was observed. However, some subspecific assignments were suggested, although hopefully, not to be considered final or overshadow the evidence that the populations studied were members of a highly variable species, whose variation may not be adequately measured by the limits of the presently available subspecific names and descriptions. Perhaps the suggestion of Burt (1954), that many subspecific boundaries do not adequately define variation, is a valuable step in overcoming the tendency to retain subspecific names even when the evidence for their retention is not valid.

POPULATION ACCOUNTS

Greytown, Nicaragua

DESCRIPTION.-- External: Aristiforms long (19-24 mm.), wide (0.9-1.0 mm.); dorsum Russett to Mars Brown, venter pale; hind feet dark mediad, forefeet Tawny-Olive to Saccardo's Umber; tail unicolor, sparsely haired, Bone Brown.

Skull: Nasals long, extending well beyond posterior border of infraorbital foramen, and broader anteriad; incisive foramina tapering anteriad and posteriad, bulging in middle; palatal notch extending to middle of M3; supraorbital ridges prominent.

Teeth: Counterfold pattern 3(4)/4-3(?4)/3-3(?4)/3-3(?4)/3. For additional external, cranial, and dental characters, see Thomas (1896, p. 312).

Baculum (figure 4n): Massive, long and broad; basal one-third greatly thickened and rugose; apical and proximal regions expanded laterad, ventral groove deep; apical wings project ventrad, their lateral margins straight-edged; medial apical and proximal notches present.

COMPARISONS.-- Aristiforms wider and longer, coloration darker than all other populations examined; counterfold pattern complex, similar to specimens from Hyutanaham and one specimen (variant C) from Riberalta. Baculum more rugose and massive than any other specimens of Proechimys examined.

REMARKS.-- This subspecies, Proechimys semispinosus centralis (Thomas), has several distinctive features in the baculum, aristiforms, and teeth that are not possessed by specimens from the other localities examined. Ellerman (1940) considered the characters separating Proechimys semispinosus from P. guyannensis to be of minor subspecific importance, and reduced the races of the former to subspecies of the latter. Hershkovitz (1948) indicated that the name P. guyannensis may not apply to the Central American Proechimys (i.e. P. semispinosus) and Moojen (1948) retained the specific name P. semispinosus.

The question of specific distinctness for Proechimys semispinosus cannot be determined on morphological evidence alone. But evidence derived from the Greytown material suggests that P. semispinosus is distinct and not a race of P. guyannensis.

Villanueva, Colombia

DESCRIPTION.-- External: Aristiforms long (19-20 mm.) and narrow (0.4 mm.), soft, hidden by setiforms; dorsum pale, Light Ochraceous Buff

to Ochraceous Buff; venter with white inguinal and axillary patches, bordered by Smoke Gray areas; feet with numerous white hairs; tail not sharply bicolor, but lighter below. For additional descriptions, see Allen (1899a, p. 200) and Hershkovitz (1948, p. 131).

Skull: Nasals long, extending considerably beyond premaxillary-frontal suture; incisive foramina short and wide, expanded anteriad; palatal notch extending to middle, or slightly anterior to, M3; hamular process of pterygoid narrow, constricted at base; posterior zygomatic process involving squamosal and portion of parietal; temporal ridge short.

Teeth: Counterfold pattern 2/2-2/2-2/2-2/2 in all specimens examined.

Baculum (figure 4, l-m): Long and slender, slightly convex dorsad; basal and apical regions wider than middle portion; base thickened, with concave depression ventrad; apical region may possess wings directed ventrolaterad; width much greater than depth, especially in middle.

COMPARISONS.-- Pelage finer and grayer, and incisive foramina broader and shorter than in all other populations; baculum similar to that in Hyutanaham and Porto Velho populations. See Hershkovitz (1948, pp. 131-132) for comparisons with Proechimys guyannensis mincae.

REMARKS.-- Dentally this species, Proechimys canicollis (Allen), appears to be distinctive, having a counterfold pattern that is not possessed by other members of the subgenus Proechimys. Ecological differences between this species and Proechimys guyanensis mincae were reported by Allen (1904, p. 440, quoted from field notes of Herbert H. Smith) for the localities where the two species were found together. Hershkovitz (1948) considered P. canicollis to be annectant between

P. guyannensis and the subgenus Trinomys. On the present evidence P. canicollis seems to merit specific rank.

Río Tarra, Colombia

DESCRIPTION.-- External: Aristiforms long (19-20 mm.) and narrow (0.5 mm.); dorsum Ochraceous Tawny mixed with many dark hairs; venter white to Drab; feet dark, with a few white hairs; tail unicolor, dark. For additional characters, see Hershkovitz (1948, p. 135).

Skull: Nasals long, extending well beyond premaxillary-frontal suture; incisive foramina long and narrow, slightly bulging in middle; palatal notch extending to anterior border of M3; hamular process of pterygoid broad, widest distally; posterior zygomatic process involving squamosal and small portion of parietal; temporal ridge extending onto one-half of parietal.

Teeth: Counterfold pattern 3/3-3/2-3/2-3/2 in all specimens examined.

Baculum (figure 4j): Long and slender, convex dorsad; basal and apical regions wider than middle portion; base thickened, with slight depression near proximal end; middle portion flattened, thin; apical region with concave depression, bordered by two wings directed latero-ventrad; depth less than width throughout.

COMPARISONS.-- Darker than all other populations, with the exception of Proechimys semispinosus centralis from Greytown; palatal foramina not expanded anteriad as in P. canicollis; baculum similar to A (figure 4e) from Riberalta, but longer and less rugose basally. For additional comparisons, see Hershkovitz (1948, p. 135).

REMARKS.-- Hershkovitz (1948) referred specimens from this population to Proechimys guyannensis poliopus Osgood, and indicated that P. g. ochraceus and P. g. oconnelli were related to it, based on the presence of two counterfolds in the lower molars. However, specimens from San Ignacio and Aguas Verdes also have two counterfolds in the lower molars, although this may not be significant of a relationship between such geographically disjunct populations (Mayr, et al., 1953).

Aguas Verdes, Peru

DESCRIPTION.-- External: Aristiforms confined to center of dorsum, long (22-23 mm.) and wide (1.0 mm.); dorsum light Ochraceous-Tawny, mixed with a few black hairs; venter and feet white, tail sharply bicolor, white below, dark above.

Skull: Nasals long, broader anteriad; incisive foramina much longer than broad, but not narrow; hamular process of pterygoid thin at base, broadened distad; posterior zygomatic process present; temporal ridge prominent, extending across parietal.

Teeth: Counterfold pattern 3/?-3/2-3/2-?3/?2.

Baculum (figure 4k): Long, convex dorsad, markedly narrower in middle; lateral margins of basal area thickened and rugose, surrounding a prominent ventral depression; ventral groove extends anteriad from basal depression; apical region with slight ventral depression; apical wings expanded lateroventrad.

COMPARISONS.-- Pelage similar to Proechimys canicollis, but darker and aristiforms much wider; dental pattern similar to P. guyannensis mincae and the San Ignacio population; baculum distinctive, although similar in shape to P. g. poliopus.

REMARKS.-- Although the label indicates Aguas Verdes, Peru, the characters of the specimens agree closely with the description of Proechimys decumanus (Thomas) from Chongon, Guayas, Ecuador (Thomas, 1899, p. 282). Available maps do not show an Aguas Verdes in Peru, although there is an Agua Verde, in Guayas Province, Ecuador. The possibility that the latter locality is the same as Aquas Verdes should be considered until clarifying evidence is available.

Ellerman (1940) relegated Proechimys decumanus to a race of P. guyannensis, although Osgood (1944) suggested, reservedly, that the species might be distinct. If the specimens from Aguas Verdes are referable to P. decumanus, these data support Ellerman's contention that P. decumanus is a race of P. guyannensis.

Hyutanaham, Brazil

DESCRIPTION.-- External: "Upper parts Mars Orange on back, grading to Ochraceous-Tawny on sides...Aristiforms on mid dorsal region: Grayish basally, gradually blackening toward tip; total length, 16-19 mm; maximum width, 0.5 mm." (Moojen, 1948, p. 338). For additional characters, see Goldman (1911, pp. 238-239).

Skull: Nasals broader anteriad, tapering posteriad; incisive foramina short, narrow, slightly expanded in middle; palatal notch extending to middle of M3 or slightly posteriad; posterior zygomatic process confined mostly to squamosal; temporal ridge short, weak.

Teeth: Counterfold pattern variable, 3/4-3(?4)/3(?4)-3(?4)/3(?4)-3(?4)/3(?4), with wear on the molars a fourth island may appear.

Baculum: Long (7.7 mm.) and narrow (1.9 mm. at anterior end), with ventral groove and convex dorsum; basal and apical regions wider than

middle; widest anteriad, wings project ventrad. Similar to figure 5A but longer and with more pronounced ventral groove and apical wings.

COMPARISONS.-- Color of dorsum similar to specimens from Porto Velho and Río Branco, although more reddish; aristiforms similar to those of Río Branco population; counterfold pattern distinctive, but similar to that of specimen (C) from Riberalta; baculum similar to that of Proechimys canicollis, although longer and with more pronounced apical wings.

REMARKS.-- This species, Proechimys steerei Goldman, was considered a subspecies of P. goeldii by Moojen (1948), although Hershkovitz (1948) included the species as a member of the composite P. guyannensis. The counterfold pattern of the upper molars is complex and in this study has been interpreted differently than Moojen (1948) and Hershkovitz (1948). There are probably three counterfolds which could separate into four distinct islands through wear.

In general appearance, Proechimys steerei is a distinctive form and may be worthy of at least subspecific rank. However, it is impossible to judge the merits of including P. steerei as a race of P. guyannensis or P. goeldii, without further study of the relationships of these forms in the Amazonian region.

Porto Velho, Brazil

DESCRIPTION.-- External: Aristiforms wide (0.8-1.0 mm.) and short (15-17 mm.); dorsum Ochraceous-Tawny mixed with many black hairs; venter white, sharply demarcated from sides; feet Pinkish Buff to Cinnamon-Buff, interspersed with white hairs; tail sharply bicolor.

Skull: Nasals long (extending beyond infraorbital foramen, USNM 364146) or short (extending to infraorbital foramen, in 364145); incisive foramina broader anteriad, tapering sharply posteriad; palatal notch extending to middle of M3 (USNM 364146) or midway between M2 and M3 (USNM 364145); hamular process of pterygoid constricted at base, expanded in middle, and forming a sharp point distad; posterior zygomatic process involving squamosal and portion of parietal; temporal ridge evident, but not forming a prominent line. Zygoma sharply tapering anteriad (USNM 364145) or approximately parallel to long axis of skull (USNM 364146).

Teeth: Counterfold pattern 3/3(4)-3/3-3/3-3/3.

Baculum: None available for study.

COMPARISONS.-- Similar in many external features to the Río Branco and Hyutanaham populations, but aristiforms much wider and color slightly paler; counterfold pattern similar to that in Río Branco population.

REMARKS.-- Specimens from this locality are provisionally included in Proechimys guyannensis, although in coloration they are similar to P. steerei and P. guyannensis. The cranial differences between USNM 364145 and 364146 probably represent individual differences within the population.

Río Branco, Brazil

DESCRIPTION.-- External: Aristiforms of medium width (0.5-0.7 mm.) and length (18-19 mm.); dorsum Cinnamon Brown to Ochraceous-Tawny, grading to Buckthorn Brown on sides; venter white, tail bicolor; forefeet Prout's Brown, hindfeet Buckthorn Brown.

Skull: Nasals extending to level of infraorbital foramen, not broadened anteriad; hamular processes of pterygoid similar to those of

Porto Velho specimens, but tip less pointed; posterior zygomatic process involving squamosal and part of parietal; temporal ridge not evident.

Teeth: Counterfold pattern 3/4(3)-3/3-3/3-?/?.

Baculum: Long and slender, convex dorsad; basal and distal regions slightly expanded laterad; slight median groove along ventral surface; similar to specimen from Hyutanaham, but smaller.

COMPARISONS.-- Similar to specimens from Porto Velho, although somewhat darker; aristiforms similar to those from Hyutanaham.

REMARKS.-- Only age-class III specimens were available for study, which makes comparisons with older specimens of questionable value.

Specimens from this locality are very similar in external appearance and dental pattern to those from Hyutanaham. The dental similarities are more evident if the specimens from Hyutanaham truly have only three counterfolds in the upper molars (see p. 30). However, the Río Branco specimens could also represent a range of variation in Proechimys guyannensis, based on cranial dimension and a conservative interpretation of the number of counterfolds.

Riberalta, Bolivia

DESCRIPTION.-- External: Aristiforms of A and B specimens of medium length (18-19 mm.), and width (0.5-0.6 mm.); those of C short (16-17 mm.) and narrow (0.3 mm.); dorsum of A and B Ochraceous-Tawny, grading to Buckthorn Brown on sides; dorsum of C Cinnamon-Brown to Ochraceous-Tawny, with many black hairs; feet of A Buffy Brown, those of B white, and those of C white and Mummy Brown.

Skull: Nasals in A, B, and C long, broadened anteriad, extending posteriad to level of infraorbital foramen, or slightly behind; incisive foramina in A, B, and C slender, slightly expanded in middle; palatal notch variable in A and B, extending anteriad to rear margin of M3 or to middle of M3; palatal notch in C extending to middle of M3; posterior zygomatic process in A and B involving squamosal and expanded laterad, that in C involving squamosal, not expanded laterad; temporal ridge in A and B not pronounced, involving one-half of parietal, that in C not pronounced, involving one-fourth or less of parietal.

Teeth: Counterfold pattern in A, 3/3(4)-3/3(4)-3/3(4)-3/3(4), in B, 3/3-3/3-3/3-3/3, and in C, 3(?4)/4-3(?4)/3-3(?4)/3-?3/3.

Baculum: In A (figure 4e) long and slender, slightly convex dorsad; basal one-fourth thickened, wider than apical region; ventral groove evident, shallow in middle; apical wings project sharply ventrad. In B (figure 4d) long and broad, convex dorsad; basal one-third thickened, lateral margins surrounding a deep depression; apical wings broadly expanded ventrad, lateral margins straight-edged or rounded; shaft noticeably narrower in middle, shallow. No baculum of C was available for study.

COMPARISONS.-- External and cranial characters of A and B similar, but bacula markedly different (see above); coloration in C much darker and aristiforms shorter and narrower; cranial dimensions of A and B much larger than in all populations examined statistically; coloration in A and B darker than in San Ignacio, Warnes, Limão Balsa, and Corumbá populations, but lighter than C and specimens from Cafetal and San Joaquín.

REMARKS.-- Bacular difference is the basis for distinguishing between two morphological variants (A, B) in this population. Evidence from other rodent groups (See: Burt and Barkalow, 1942; Hershkovitz, 1962 and 1966) indicates that the differences in bacular shape and structure between A and B are greater than could be expected from one population of a single species. In general, age and size did not correlate with bacular type, and the largest specimens (A) had small bacula (figure 4e). Only two specimens of B had bacula and no clarifying ecological information was available. Thus, it is risky to suggest that these two variants may represent sympatric species. Therefore, they are referred to Proechimys guyannensis, although subspecific assignment without access to type material or a better understanding of variation in this species is largely conjectural. However, the description by Thomas (1901) for Proechimys guyannensis bolivianus agrees in some respects with the specimens. Also, Riberalta is on the Río Beni and the type locality for P. g. bolivianus is near the Río Mapiri, an upper tributary of the Río Beni.

Variant C (USNM 391008) differs markedly from A and B. In several features, C compares favorably with the description given for Proechimys quadruplicatus Hershkovitz, although the dorsal medial color band is not so evident, and the pattern of the upper molars is similar to P. "steerei" from Hyutanaham. The "fourth" fold in M1 and M2 is small and slightly posteriad to the third fold. However, the evidence strongly favors assigning this specimen to Proechimys quadruplicatus.

Puerto Maldonado, Peru

DESCRIPTION.-- External: Aristiforms in D long (18-22 mm.) and of medium width (0.5-0.7 mm.), those of E short (16 mm.) and of medium width (0.6 mm.); dorsum of D Cinnamon-Brown, grading to Buckthorn Brown on sides, that of E Ochraceous-Tawny, mixed with some black hairs, feet of D Saccardo's Umber with some white hairs, those of E white; venter white and tail bicolor in both D and E.

Skull: Nasals in D broader anteriad, extending posteriad to infraorbital foramen; nasals in E long and slender, broadly rounded posteriad, with small "internasal" bone situated mediad in the fronto-nasal suture; incisive foramina in D long and narrow, those in E shorter and broader; palatal notch variable in D, extending anteriad to rear margin of M3 or anteriad to middle of M3; palatal notch of E reaching posterior margin of M2; hamular process of pterygoid broadened and supraorbital ridge not massive in D and E; posterior zygomatic process expanded laterad in D, but not in E; temporal ridge weak, extending across parietal in D, more pronounced in E.

Teeth: Counterfold pattern in D, 3/3-3/3(2)-3/3-3/2(3), in E, 3/3-2(?3)/3-2(?3)/3-2(?3)/3.

Baculum: In D (figure 4, a and b) long, broadened anteriad, convex dorsad; apical wings involving one-third of length, directed ventrad; ventral groove present, less pronounced in basal one-third; basal region somewhat thickened, with medial notch, but lateral margins not excessively rugose; middle region much narrower. No bacula of E were available for study.

COMPARISONS.-- Variants D and E darker than all Bolivian and Matto Grosso populations examined; aristiforms similar to those of Bolivian

and Mato Grosso populations; posterior zygomatic process in D more widely expanded laterad than in E; palatal notch of E extending further anteriad than in D or other populations examined.

REMARKS.-- The character of the palatal notch in E is distinctive and approaches the condition found in Proechimys hendeei Thomas. However, the specimens do not possess other characters mentioned by Thomas (1926) and Hershkovitz (1948). The coloration is paler and p4 has only three counterfolds.

In D the cranial, dental, and external characters lie within the ranges observed in specimens of Proechimys guyannensis from other localities, although the bacula are distinctive. In external characters the specimens from this locality approach the conditions described for Proechimys guyannensis bolivianus. The bacula, however, are similar in length and width to those from Colombia, northwestern Brazil, and Aguas Verdes.

On the present evidence, D and E seem referable to Proechimys guyannensis, although evidence as to their subspecific identity is not conclusive.

San Joaquín, Bolivia

DESCRIPTION.-- External: Aristiforms long (23-24 mm.) and of medium width (0.7 mm.); dorsum Ochraceous-Tawny grading to Buckthorn Brown on sides, with a few black hairs; venter white, feet Buffy Brown to white; tail sharply bicolor, dark above, white below; feet white and brown.

Skull: Nasals slightly broadened anteriad, ending posteriad at level of infraorbital foramen; incisive foramina long and narrow,

slightly broader anteriad; palatal notch extending to middle of M3; hamular process of pterygoid slightly constricted at base, and expanded in middle; supraorbital ridge very prominent, posterior zygomatic process involving squamosal and part of parietal; temporal ridge extending posteriad to basioccipital crest, but not pronounced.

Teeth: Counterfold pattern 3/3-3/3(2)-3/2(3)-3(2)/2(3); the retention of an isolated anterior island in m2 and m3 accounts for some of the variability.

Baculum (figure 4f): Long and broad, convex dorsad; basal one-third thickened and rugose, with ventral depression; lateral wings project ventrad, their distal margins straight-edged; ventral groove evident throughout length, shallow in middle.

COMPARISONS.-- Coloration similar to that of Cafetal population, darker than specimens from San Ignacio, Warnes, Limão Balsa, Corumbá, and Proechimys guyannensis from Riberalta; aristiforms similar to those of Cafetal population, but longer; baculum distinctive, most similar to that of the specimen from Cafetal.

REMARKS.-- Moojen (1948) defined Proechimys l. longicaudatus (Rengger) and P. longicaudatus leucomystax Ribeiro, from western Matto Grosso, Brazil, as having a counterfold arrangement of 3/3-3/2-3/3-3/2. Some of the specimens from San Joaquín and Cafetal approach this dental arrangement. The two bacula available from the San Joaquín and Cafetal specimens are distinctive, but show similarities with those from Riberalta, San Ignacio, and Corumbá. This morphological evidence indicates a considerable overlap in characters between these two populations and those from Puerto Maldonado, Riberalta, San Ignacio, Warnes, Limão Balsa, and Corumbá. Specimens from San Joaquín and Cafetal are assigned

to Proechimys guyannensis, suggesting that the San Ignacio, Warnes, Limão Balsa, and Corumbá specimens may also be referable to P. guyannensis.

Cafetal, Bolivia

DESCRIPTION.-- External: Similar to specimens from San Joaquín, but aristiforms shorter (19-20 mm.).

Skull: Nasals broadened anteriad, extending posteriad to level of infraorbital foramen; incisive foramina narrow anteriad and posteriad; palatal notch extending anteriad to middle of M3; posterior zygomatic process involving squamosal and forming a thin shelf; temporal ridge extending across parietal, not pronounced.

Teeth: Counterfold pattern 3/3-3/3(2)-3/3-3/3.

Baculum (figure 4g): Long and broad, convex dorsad; ventral groove present; apical wings broader than basal region, and projecting ventrad; distal margins of apical wings rounded; base broader than middle, thickened on lateral edges; ventral depression and medial notch present basally.

COMPARISONS.-- Similar to specimens from San Joaquín, but incisive foramina broader anteriad. For additional comparisons, see account under San Joaquín.

REMARKS.-- These specimens are probably referable to Proechimys guyannensis. See account under San Joaquín for reasons.

San Ignacio, Bolivia

DESCRIPTION.-- External: Aristiforms long (17-20 mm.), of medium width (0.5-0.7 mm.); dorsum Buckthorn Brown mixed with a few black hairs;

venter white, not sharply demarcated from sides; hind feet brown and white.

Skull: Nasals extending posteriad to infraorbital foramen, slightly broadened anteriad; incisive foramina long and slender, slightly expanded in middle; palatal notch variable, extending anteriad to rear margin of M2 or M3; hamular process of pterygoid constricted at base, expanded in middle, and tapering to distal point; supraorbital ridge prominent; posterior zygomatic process involving squamosal and small portion of parietal; no temporal ridge extending onto parietal.

Teeth: Counterfold pattern 3/3-3/2(3)-3/2(3)-3/2(3); degree of tooth wear affects number of islands formed in lower jaw (figure 3).

Baculum (figure 4, h and i): Short and broad, convex dorsad; basal and apical regions expanded laterad; median proximal notch present (figure 4h) or absent (figure 4i); ventral groove present, but may be shallow in some specimens; basal one-third thickened and rugose, lateral margins surrounding a ventral depression.

COMPARISONS.-- Coloration lighter than in Puerto Maldonado, Cafetal, and San Joaquín, darker than in Warnes, Limão Balsa, and Corumbá populations; counterfold pattern and aristiforms similar to those of Warnes population, but overlapping with other populations; baculum similar to that of Proechimys guyannensis, (B) from Riberalta.

REMARKS.-- The San Ignacio and Warnes populations seem referable to Proechimys guyannensis, since there is considerable overlap in cranial and dental characters, and dimensions, with the other populations of P. guyannensis discussed earlier. Both of these populations are near tributaries of the Río Mamore. The specimens from San Ignacio may be referable to Proechimys guyannensis securus Thomas, whose type

locality is on the upper Río Secure, a tributary of the Río Mamore (Thomas, 1902). However, this conclusion cannot be firmly substantiated by reference to the original description of securus, and assignment of the San Ignacio specimens to this race could, at present, be suggested only on the basis of geography.

Warnes, Bolivia

DESCRIPTION.-- External: Aristiforms long (18-20 mm.) and narrow (0.5-0.6 mm.); dorsum Ochraceous-Buff, mixed with a few black hairs; venter and feet white; tail bicolor.

Skull: Nasals broadly rounded anteriad, gradually tapering posteriad; incisive foramina broader anteriad than posteriad, a median shelf evident posteriad; palatal notch variable, extending to middle of M3 or to posterior one-third of M2; hamular process of pterygoid not expanded or forming a distal point; supraorbital ridge prominent; posterior zygomatic process involving squamosal and small part of parietal; temporal ridge extending across parietal.

Teeth: Counterfold pattern 3/3-3/2(3)-3/2(3)-3/3.

Baculum: None available for study.

COMPARISONS.-- Similar in coloration to Corumbá, paler than San Ignacio specimens, darker than Limão Balsa populations; aristiforms and counterfold pattern similar to those of San Ignacio population.

REMARKS.-- Specimens from this population share features in common with those from San Ignacio, Limão Balsa, and Corumbá.

Warnes is near one of the upper tributaries of the Río Mamore, which is part of the Amazon drainage system. However, Limão Balsa and Corumbá are located near tributaries of the Río Paraguay, which are

part of the Paraná-Paraguay drainage system. In southeastern Bolivia these two drainage systems are separated somewhat by the higher elevations of the Gran Chaco (Roseveare, 1948). Based on the similarities between the two Mato Grosso populations and those of San Ignacio and Warnes, it is doubtful that the Gran Chaco is a significant dispersal barrier to Proechimys.

The pelage of the Warnes specimens is similar to that defined for Proechimys l. longicaudatus by Moojen (1948). However, it is equally probable that these specimens may represent a paler population of Proechimys guyannensis.

Limão Balsa, Brazil

DESCRIPTION.-- Aristiforms long (18-21 mm.) and of medium width (0.6-0.7 mm.); pale, dorsum Ochraceous-Buff, mixed with a few black hairs; flanks and shoulders lighter than dorsum; venter and feet white; tail bicolor.

Skull: Nasals long and narrow, tapering posteriad; small, narrow, "internasal" bone situated mediad in the fronto-nasal suture of many specimens; incisive foramina long, rounded anteriad, the lateral margins tapering sharply posteriad and forming a median shelf; palatal notch extending near middle of M3; hamular process of pterygoid narrowed at base, not bulging in middle or forming a distal point; supraorbital ridge prominent; posterior zygomatic process forming a shelf; temporal ridge ill-defined.

Teeth: Counterfold pattern 3/3-3/2(3)-3/3(2)-3/2.

Baculum: None available for study.

COMPARISONS.-- With the exception of the Villanueva population, the palest of the specimens examined; aristiforms and counterfold patterns similar to those of San Ignacio, Warnes, and Corumbá populations.

REMAKRS.-- In external, cranial, and dental characters, the specimens from Limão Balsa are very similar to those from Corumbá and Warnes. The Limão Balsa and Corumbá specimens also show similarities with Moojen's (1948) definition of Proechimys l. longicaudatus, (see remarks for San Joaquín, Bolivia). As suggested earlier, these populations may represent variation in P. guyannensis, since there is a considerable overlap in morphological characters with populations from localities discussed earlier. Moojen (1948, p. 315), however, mentioned that P. guyannensis villacauda and P. longicaudatus leucomystax occur together in the same locality (Utiariti, Brazil), but did not suggest any ecological or other mechanisms which might keep these forms separate. Pending such evidence, the Limão Balsa and Corumbá populations should tentatively be considered members of a more variable, broadly defined Proechimys guyannensis.

Corumbá, Brazil

DESCRIPTION.-- External: Aristiforms long (18-22 mm.) and of medium width (0.6-0.7 mm.); dorsum Ochraceous-Tawny, grading to Ochraceous-Buff and Buckthorn Brown on sides; feet tan to white; venter white; tail bicolor.

Skull: Nasals long and slender, extending posteriad to infraorbital foramen, broadly rounded anteriad; palatal notch extending anteriad to middle of M3 or beyond; hamular process of pterygoid narrowed at base, either rounded or pointed distad; supraorbital ridge very

pronounced; posterior zygomatic process involving squamosal and small part of parietal; temporal ridge not extending across parietal.

Teeth: Counterfold pattern 3/3-3/3-3/2(3)-3/2.

Baculum (figure 4c): Short and broad, convex dorsad; basal and apical regions expanded laterad; median proximal notch and ventral groove present; basal one-third thickened and rugose; apical wings project ventrad, lateral margins straight-edged or rounded.

COMPARISONS.-- Darker than Limão Balsa specimens, but similar in other respects; bacular shape similar to that of Proechimys semispinosus centralis (figure 4n), but smaller and less rugose.

REMARKS.-- As stated in the remarks for the Limão Balsa population, the Corumbá specimens are probably referable to Proechimys guyannensis. For additional information, see the previous account.

SPECIMENS EXAMINED

NICARAGUA Río San Juan.-- Greytown, 2.

COLOMBIA Magdalena.-- Valledupar: Villanueva, 16. Norte de Santander.-- Río Tarra, 2.

PERU Aguas Verdes, 2. Madre de Dios.-- Tambopata: Puerto Maldonado (City), 4; 6 km. west Puerto Maldonado, 1; 4.5 km. west Puerto Maldonado, 1; 4 km. west Puerto Maldonado, 2; 4 km. southwest Puerto Maldonado, 1; 3.5 km. southwest Puerto Maldonado, 1; 3 km. southwest Puerto Maldonado, 1; 1.5 km. south Puerto Maldonado, 6; 15 km. south Puerto Maldonado, 1; 4 km. south Puerto Maldonado, 1; 1.5 km. southeast Puerto Maldonado, 1; 12 km. east Puerto Maldonado, 4.

BOLIVIA Pando.-- Madre de Dios: 13 km. northwest Riberalta, 1; 5 km. northwest Riberalta, 3; 3.5 km. northwest Riberalta, 3. Beni.-- Vaca Diez: Riberalta (City), 8; 13 km. west Riberalta, 1; 2.3 km. west Riberalta, 1; 10 km. north-northeast Riberalta, 1; 13 km. northeast Riberalta, 5. Mamore: San Joaquín, 1; 3.2 km. southeast San Joaquín, 3; Cafetal, 3. Moxos: San Ignacio (City), 21; road to San Ignacio Airport, 3; 3.6 km. north-northeast San Ignacio, 3; 1 km. southwest San Ignacio, 5. Santa Cruz.-- Warnes: Juan

Latino, 1; La Abra, 1; Warnes (City), 1; 1 km. north-northwest Warnes, 6; 1.3 km. northeast Warnes, 5; Santa Rosita, 8.

BRAZIL Amazonas.-- Labrea: Hyutanaham, 3. Rondonia.-- Porto Velho: 8 km. north Porto Velho, 9. Acre.-- Río Branco: 3-4 km. south Río Branco, 3. Mato Grosso.-- Cáceres: Limão Balsa, 13. Corumbá: Corumbá, 1; Urucum, 2; 10 km. northeast Urucum, 5; Santa Theresa, 5.

GAZETTEER

(Numbers in parentheses refer to localities in figure 2)

BOLIVIA

Cafetal- 13°26'S, 64°35'W
Southeast of San Joaquín, Mamore, Beni, (8).

Juan Latino- 17°24'S, 63°07'W
13 km. north-northeast Warnes, Warnes, Santa Cruz.

La Abra- 17°26'S, 63°06'W
18 km. northeast Warnes, Warnes, Santa Cruz.

Riberalta- 10°59'S, 66°06'W
Vaca Diez, Beni, (5).

San Ignacio- 14°53'S, 65°36'W
Moxos, Beni, (9).

San Joaquín- 13°04'S, 64°49'W
Mamore, Beni, (7).

Santa Rosita-17°34'S, 63°13'W
3 km. southwest Warnes, Warnes, Santa Cruz.

Warnes- 17°30'S, 63°10'W
Warnes, Santa Cruz, (10).

BRAZIL

Cáceres- 16°04'S, 57°41'W
Cáceres, Mato Grosso.

Corumbá- 19°01'S, 57°39'W
Corumbá, Mato Grosso, (12).

Hyutanaham [= Huitanaã, Hyutanahã] - 07°40'S, 65°46'W
Labrea, Amazonas, (2).

Limão Balsa- 16°03'S, 58°09'W
48 km. west Cáceres, Cáceres, Mato Grosso, (11).

Porto Velho- 08°46'S, 63°54'W
Porto Velho, Rondonia, (3).

Río Branco- 09°58'S, 67°48'W
Río Branco, Acre, (4).

Santa Theresa- 19°15'S, 57°46'W
7 km. west-southwest Urucum, Corumbá, Mato Grosso.

Urucum- 19°09'S, 57°38'W
22 km. south Corumbá, Corumbá, Mato Grosso.

COLOMBIA

Río Tarra- 08°36'N, 73°01'W
Norte de Santander.

Villanueva- 10°37'N, 72°58'W
Valledupar, Magdalena, (1).

NICARAGUA

Greytown- = San Juan del Norte - 10°56'N, 83°42'W
Río San Juan.

PERU

Aguas Verdes- location unknown, see text.

Puerto Maldonado- 12°36'S, 69°12'W.
Tambopata, Madre de Dios, (6).

CONCLUSIONS

1. Of 14 measurements made on the skull and baculum of Proechimys, eight cranial measurements (condylobasal, palatal, nasal, and alveolar lengths; zygomatic, mastoidal, and maxillary breadths; and rostral depth) were found most useful in testing the significance of geographical variation. Bacular measurements were highly variable.
2. Variation between age classes was much more significant than variation between sexes. Thus, sexes can be combined for statistical comparisons of populations.
3. Cranial measurements did not provide a reliable means of separating species or demonstrating minor interpopulation differences.
4. Variations in age and tooth wear create problems of interpretation in counting the number of counterfolds and islands in the cheek teeth. Due to this variability, species determinations cannot be made solely on the basis of dental pattern.
5. Evidence from bacular morphology, while inconclusive, did suggest the possible occurrence in one population of two sympatric species not detectable by examination of other morphological data.
6. Proechimys guyannensis is a wide-ranging, highly variable species whose variability may not best be indicated by the

assignment of local populations to subspecies in the conventional manner.

7. Ecological data are badly needed for determining the relationships of suspected sympatric species.

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