ROBERT E. MARTIN

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ABSTRACT

Martin, Robert E. Cranial and Bacular Variation in Populations of Spiny Rats of the Genus *Proechimys* (Rodentia: Echimyidae) from South America. *Smithsonian Contributions to Zoology,* 35:1–19. 1970.—Specimens of *Proechimys* from 12 localities in Bolivia, Brazil, Colombia, and Peru, were studied to assess the degree of variation in bacular, cranial, and dental morphology, and pelage. Coefficients of variation and Student's *t* values were computed for selected cranial measurements to evaluate intra- and interpopulation variation. Studies on tooth wear demonstrated considerable variation in dental occlusal pattern and suggested that taxonomic assignment based entirely on dental morphology may be misleading. Descriptions and illustrations of bacula from most localities indicate that these bones are highly variable in overall dimensions, but have common structural features at a particular locality. Most specimens are tentatively referred to *Proechimys guyannensis,* although *P. canicollis, P. quadruplicatus,* and *P. steerei* were also represented. *Proechimys guyannensis* is regarded as a highly variable species. It is suggested that subspecific delimitation may not adequately express the variation observable in this species.

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Introduction

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

The wide range of morphological variation observed in these rats has made species determination difficult. This has caused problems in the taxonomy of the genus (see Thomas, 1927, 1928a, 1928b; Hershkovitz, 1948; and Moojen, 1948). 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 variation within a population. The primary aims were to: (1) assess interpopulation variation in cranial dimensions; and (2) attempt to correlate these data with the results of analyses of cranial, bacular, dental, and pelage morphology. Taxonomic assignment was only a secondary objective. Descriptions were written of the morphological features common to specimens from each locality, and comparisons made with other populations. The accounts reflect differences between populations from different localities, and offer suggestions on taxonomic assignment, but are not taxonomic descriptions in the strict sense. All specimens examined are deposited in the mammal collection of the National Museum of Natural History.

I wish to express my sincere appreciation to the individuals who aided in the completion of this report. Dr. Gary L. Ranck, formerly Curator of the Mammal Identification Service, Smithsonian Institution, directed the study and offered helpful advice and criticism. Dr. Henry W. Setzer, Associate Curator, Division of Mammals, Smithsonian Institution, aided in the statistical treatment of the data. Dr. Ronald H. Pine, Curator, Mammal Identification Service, reviewed the manuscript and sent specimens for additional study. Dr. Charles O. Handley, Jr., Curator-in-Charge, and Dr. David H. Johnson, Research Curator, Division of Mammals, gave useful advice. Dr. George E. Watson, Chairman, and other personnel of the Department of Vertebrate Zoology, Smithsonian Institution, provided helpful comments on the manuscript. Dr. Merle L.

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Kuns and associates of the Middle America Research Unit collected most of the specimens analyzed.

At Oklahoma State University, Dr. Bryan P. Glass, Professor of Zoology, served as major advisor and critically read the manuscript. Dr. Herbert L. Bruneau, Associate Professor of Zoology, and Dr. William A. Drew, Associate Professor of Entomology, served on the graduate advisory committee and read the manuscript. Dr. George A. Moore, Professor Emeritus of Zoology, gave advice and critically read the manuscript. At Texas Tech University Dr. Robert L. Packard, Professor of Biology, and Mr. Tony R. Mollhagen, provided helpful advice on the manuscript.

Mr. Paul Ryan took the photographs that aided in the preparation of Figure 3. My wife, Patricia, helped by recording data and preparing most of the illustrations. Mrs. Frank Roberts and Mrs. Daniel Carabine typed final stages of the manuscript.

This report is based on a research project conducted in 1967 while the author was a summer research assistant in the Division of Mammals, Smithsonian Institution, Washington, D.C. Financial aid during this period was provided by a stipend from the Office of Education and Training, Smithsonian Institution. The paper that resulted from that study was submitted to the Graduate College of Oklahoma State University in partial fulfillment of the requirements for the degree of Master of Science in Zoology.

Phylogeny and Nomenclature

The genus *Proechimys* was referred to the family Echimyidae by Miller and Gidley (1918), and to the subfamily Echimyinae by Ellerman (1940) and Landry (1957). Patterson and Pascual (1968) recognized five subfamilies in their synopsis of the Echimyidae: Adelphomyinae, extinct forms only; Echimyinae and Dactylomyinae, Recent forms only; Heteropsomyinae and Myocastorinae, extinct and Recent forms. Under Patterson and Pascual's arrangement *Proechimys* is included in the Heteropsomyinae.

The earliest known representatives of the Echimyidae are *Deseadomys arambourgi* and *D. loomisi*, both of the Deseadean (lower Oligocene) of Argentina (Wood and Patterson, 1959). Wood and Patterson (1959) stated that the *Adelphomys* group (including *Deseadomys*) seemed to represent a separate line that did not give rise to any Recent echimyids. According to Patterson and Pascual (1968) this assemblage, including *Paradelphomys* and *Xylechimys*, represents the subfamily Adelphomyinae.

The earliest fossil forms of *Proechimys* are of late Pleistocene or Recent age and thus shed no light on the early history of the genus. Moojen (1948) suggested that evolutionary development in *Proechimys* has been directed toward species with increased numbers of counterfolds in the cheek teeth. For evidence, Moojen mentioned the low counterfold numbers in the cheek teeth of fossil *Proechimys* from Lagoa Santa, Brazil, and like numbers in the teeth of species in the subgenus *Trinomys*. An increased number of counterfolds along with greater species diversity is present in the subgenus *Proechimys*, and may be an indication that the multicounterfold line of spiny rats is more "successful" in an evolutionary sense. Convincing evidence, however, is definitely lacking on this point.

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 taxonomic history of the genus *Proechimys*, later 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) and Hershkovitz (1948) pointed out that *Mus* (= *Proechimys*) *guyannensis* É Geoffroy St. Hilaire, 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*, with 29 subspecies; *P. albispinus*, 2 subspecies; *P. iheringi* and *P.* (*Trinomys*) *setosus*, monotypic. He also retained five other forms as full species within the *cayennensis* group (*P. vacillator, P. hendeei, P. rattinus, P. canicollis,* and *P. dimidiatus*). Osgood (1944) reported on *Proechimys* from Ecuador and Peru without following Ellerman's arrangement, although he suggested that several named forms 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 forms found in Colombia, tentatively accepted Ellerman's contention that *P. guyannensis* was a composite species. In addition, Hershkovitz regarded *P. hendeei* as distinct from *P. guyannensis* and erected a 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).

Although no attempt is made in this study to evaluate the subfamilial affinities of *Proechimys,* it is considered to be a valid genus of the Echimyidae. It was hoped that this study of morphological variation in various populations of *Proechimys* might clarify the specific status of several nominal forms in the genus, particularly *P. canicollis, P. guyannensis, P. hendeei, P. longicaudatus, P. quadruplicatus,* and *P. steerei.*

Materials and Methods

SPECIMENS.—In this study, 165 specimens (including 42 bacula, 165 skulls, and 152 skins) were examined. Most of the specimens were those collected by the Middle America Research Unit (MARU) in connection with its field investigations of hemorrhagic fever in Bolivia and adjacent areas during 1964–1966. The MARU specimens were submitted to the Mammal Identification Service, Division of Mammals, Smithsonian Institution, for identification and deposition in the mammal collections of the National Museum of Natural History. Additional specimens from Brazil and Colombia were also examined. All specimens examined are deposited in the National Museum of Natural History (USNM).

Localities on the map (Figure 1), numbered consecutively from north to south, indicate the major collecting sites of specimens. These and other localities are listed alphabetically by country in the gazetteer. "Population Accounts" refer to the numbered localities in Figure 1. 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" sections of the population accounts, the specific localities are arranged from north to south, and then west to east at similar latitudes.

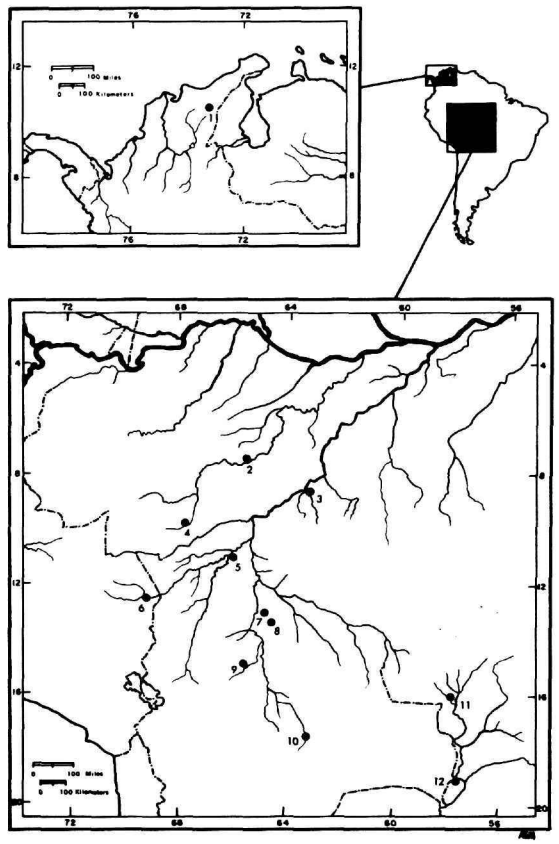

FIGURE 1.—Map showing principal collecting localities (refer to gazetteer and specimens-examined sections for detailed locality data): 1 Villanueva, 2 Hyutanaham, 3 Porto Velho, 4 Rio Branco, 5 Riberalta, 6 Puerto Maldonado, 7 San Joaquín, 8 Cafetal, 9 San Ignacio, 10 Warnes, 11 Limão Balsa, 12 Corumbá.

GAZETTEER

(Numbers in parentheses refer to localities in Figure 1)

BOLIVIA

Cafetal (8): 13°26′S, 64°35′W; SE of San Joaquín, Mamore, Beni.

Juan Latino: 17°24′S, 63°07′W; 13 km NNE Warnes, Warnes, Santa Cruz.

La Abra: 17°26′S, 63°06′W; 18 km NE Warnes, Warnes, Santa Cruz.

Riberalta (5): 10°59′S, 66°06′W; Vaca Diez, Beni.

San Ignacio (9): 14°53′S, 65°36′W; Moxos, Beni.

San Joaquín (7): 13°04′S, 64°49′W; Mamore, Beni.

Santa Rosita: 17°34′S, 63°13′W; 3 km SW Warnes, Warnes, Santa Cruz.
Warnes (10): 17°30′S, 63°10′W; Warnes, Santa Cruz.

BRAZIL

Cáceres: 16°04′S, 57°41′W; Cáceres, Mato Grosso.
Corumbá (12): 19°01′S, 57°39′W; Corumbá, Mato Grosso.
Hyutanaham[=Huitanaã, Hyutanahã](2): 07°40′S, 65°46′W; Labrea, Amazonas.
Limão Balsa (11): 16°03′S, 58°09′W; 48 km W Cáceres, Cáceres, Mato Grosso.
Porto Velho (3): 08°46′S, 63°54′W; Porto Velho, Rondônia.
Rio Branco (4): 09°58′S, 67°48′W; Rio Branco, Acre.
Santa Theresa: 19°15′S, 57°46′W; 7 km WSW Urucum, Corumbá, Mato Grosso.
Urucum: 19°09′S, 57°38′W; 22 km S Corumbá, Corumbá, Mato Grosso.

COLOMBIA

Villanueva (1): 10°37′N, 72°58′W; Valledupar, Magdalena.

PERU

Puerto Maldonado (6): 12°36′S, 69°12′W; Tambopata, Madre de Dios.

Most of the specimens examined in the study were collected near streams or rivers (except those of *Proechimys canicollis* from Villanueva, Colombia, 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 Paraná-Paraguay system drains Paraguay, Uruguay, most of Argentina, and western and southwestern Brazil. Most of the localities (2–10, in Figure 1) are located along streams in 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 streams 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).

METHODS.—Specimens were sorted by age, sex, and locality to assess the degree of individual variation prior to analyzing variation between populations. Five age classes were established on the basis of tooth wear 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 population comparisons.

Specimens from one locality, San Ignacio, Bolivia, were sorted into various combinations of age classes and sexes to assess intrapopulation variation. Pictet (1841) suggested that *Echimys* (=*Trinomys*) *setosus*

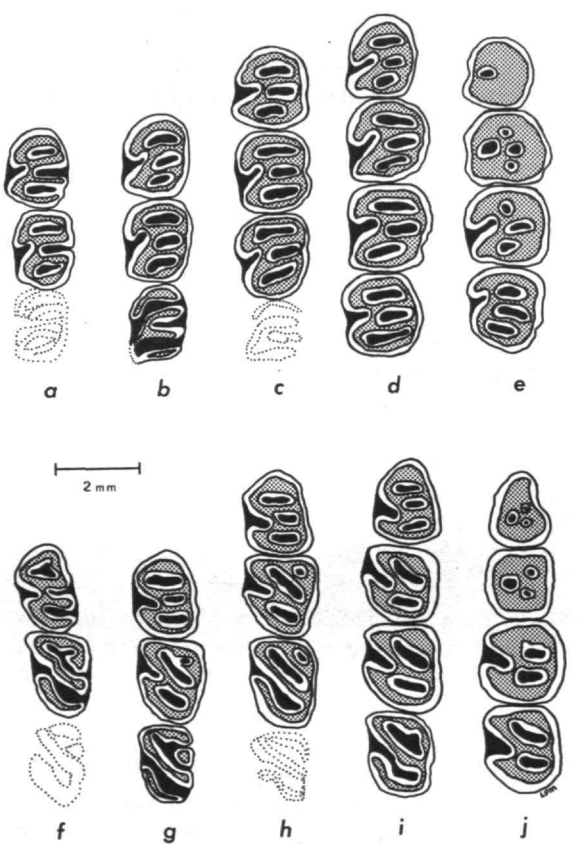

FIGURE 2.—Occlusal views of left upper (*a–e*) and lower (*f–j*) cheek teeth in *Proechimys guyannensis*. Age classes (roman numerals) and respective USNM catalog numbers: *a*, I, 364103; *b*, II, 364104; *c*, III, 364121; *d*, IV, 364114; *e*, V, 364129; *f*, I, 364103; *g*, II, 364104; *h*, III, 364121; *i*, IV, 364114; *j*, V, 364129. (The uppermost tooth in each series is premolar 4. In *a–e*, the labial side is on right border of the tooth row; in *f–j*, labial side is on left. All specimens are males from San Ignacio, Bolivia.)

and *E.* (=*Trinomys*) *myosurus* were age variants of *E.* (=*Proechimys*) *cayennensis*. Some taxa in *Proechimys* are probably based on age variants (Tate, 1939). Allen (1894), in examining large series of *Neotoma micropus*, suggested that age differences may be incorrectly interpreted as subspecific or specific differences. Dice (1932) 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. But for statistical comparisons of populations the technique proved useful.

Changes in the occlusal pattern of the teeth are illustrated in Figure 2 and discussed below:

Class I (Figure 2*a, 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 2*b, 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 2*c, 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 2*d, 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 2*e, j*): Many of the islands of P4 and p4 are greatly reduced in size or lost entirely. The islands of M1 and m1 frequently divide into additional smaller islands, those of M2 and m2 are 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.

Ten 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 3.

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′.

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

Maxillary breadth: Greatest with across maxillary bone midway between P4 and M1, e to e′.

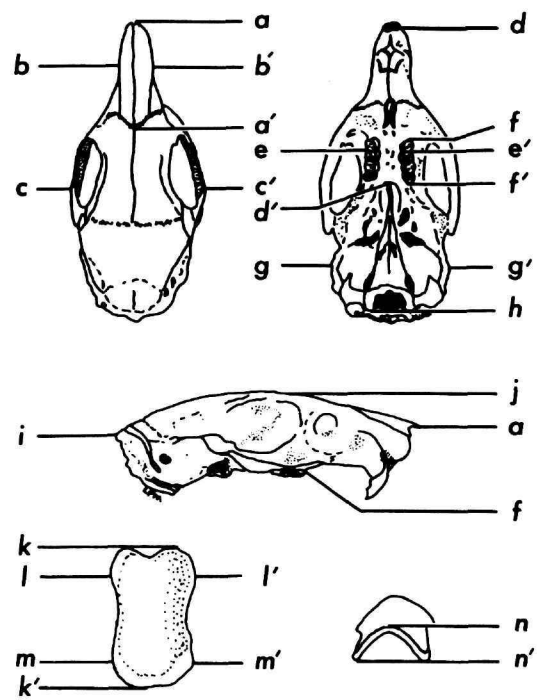

FIGURE 3.—Views of skull and baculum of *Proechimys* showing points of reference for measurements.

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 interpopulation variation. Broken skull parts prevented use of some measurements with low V-values. The measurements used were condylobasal, palatal, nasal, and alveolar lengths; zygomatic, mastoidal, and maxillary breadths; and rostral depth. 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 grouping, 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.

The arithmetic mean ($\bar{X}$), standard deviation (SD) and standard error (SE) were calculated for all populations of adequate sample size as defined by 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

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

TABLE 2.—Coefficients of variation (V), means ($\bar{X}$), and standard deviations (SD) for three cranial measurements showing differences in sorting methods in a sample (N) of *Proechimys guyannensis* from San Ignacio, Bolivia

Sorting Method	Zygomatic Breadth					Rostral Depth					Maxillary Breadth				
	N	V	$\bar{X}$	±	1 SD	N	V	$\bar{X}$	±	1 SD	N	V	$\bar{X}$	±	1 SD
Age classes, sexes combined	35	5.12	24.8	±	1.27	31	5.52	12.1	±	0.67	32	5.96	8.2	±	0.49
Males, age classes combined	20	2.16	25.1	±	0.54	21	4.99	12.2	±	0.60	21	5.87	8.2	±	0.48
Females, age classes combined	15	6.98	24.3	±	1.67	11	6.33	11.9	±	0.73	11	6.50	8.1	±	0.52
Sexes combined, age-class V	13	1.72	25.9	±	0.44	13	2.75	12.7	±	0.34	13	3.41	8.7	±	0.29
Sexes combined, age-class IV	17	4.82	24.3	±	1.15	19	3.95	11.7	±	0.46	19	3.68	7.9	±	0.29
Males, age-class V	8	1.41	25.7	±	0.35	8	3.38	12.8	±	0.42	8	3.91	8.7	±	0.33
Females, age-class V	5	1.48	26.2	±	0.37	5	1.18	12.6	±	0.14	5	2.91	8.6	±	0.24
Males, age-class IV	12	2.76	24.7	±	0.67	13	3.37	11.9	±	0.39	13	3.69	7.9	±	0.29
Females, age-class IV	10	4.94	23.4	±	1.13	6	0.40	11.2	±	0.04	6	3.26	7.7	±	0.24

test differences between some localities. Bar graphs, similar to those of Hubbs and Hubbs (1953), were constructed for all cranial measurements to demonstrate variation between 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 specimens and the bacula processed according to the method of Friley (1947), in part.

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*, *i*). Pelage terminology follows Moojen (1948). Aristiforms, comparable to guard hairs in other mammalian groups, are long, broad, flattened hairs that are frequently spinous. Setiforms (= overhairs) are narrower than aristiforms and less spinous. Capitalized color terms (Ridgway, 1912) are used in descriptions of pelage in the population accounts.

Population Accounts

FIGURES 1, 4

Villanueva, Colombia (1)

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 2/2-2/2-2/2-2/2-2/2 in all specimens examined.

Baculum (Figure 4*a*, *b*): 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 formina 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* in Colombia.

REMARKS.—*Proechimys canicollis* (Allen), appears distinctive in having a counterfold pattern that is not possessed by other members of the subgenus *Proechimys*. Ecological differences between this species and *Proechimys guyannensis mincae* were reported by Allen (1904, p. 440, quoted from field notes of Herbert H.

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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, specimens from Villanueva are retained as *P. canicollis*.

SPECIMENS EXAMINED.—Total 16, from Colombia: Magdalena.—Valledupar: Villanueva, 16 (12 ♂♂: USNM 280123, 280125, 280127, 280130–131, 280136–140, 280142, 28150; 4 ♀♀: USNM 280126, 280133, 280141, 280149).

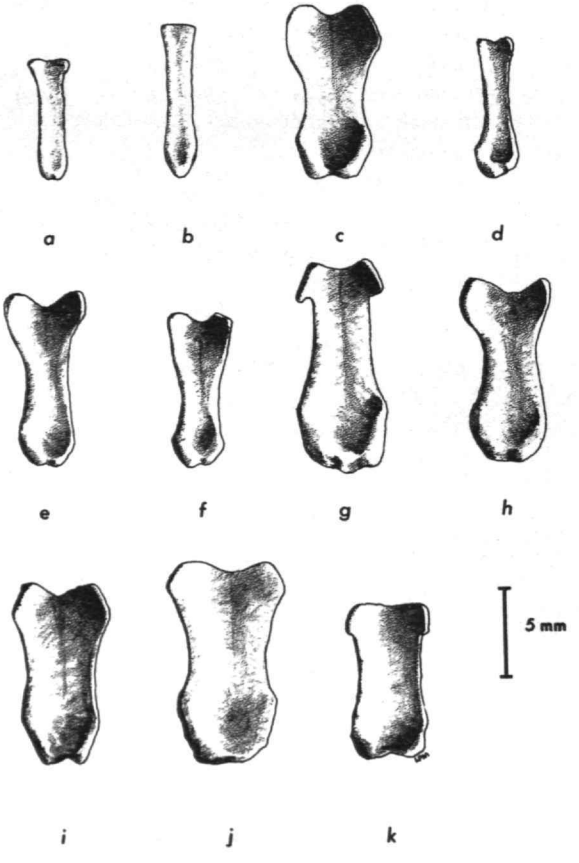


FIGURE 4.—Ventral views of *Proechimys* bacula. Taxa, localities, age classes (roman numerals), and USNM catalog numbers, listed in that order: *a, b, P. canicollis,* Villanueva, Colombia, IV, 280131 and 280125, respectively; *c, d, P. guyannensis,* Riberalta, Bolivia, IV, 363986 and 364005, respectively; *e, f, P. guyannensis,* Puerto Maldonado, Perú, IV, 364026 and 364014, respectively; *g, P. guyannensis,* San Joaquín, Bolivia, V, 363982; *h, P. guyannensis,* Cafetal, Bolivia, IV, 391403; *i, j, P. guyannensis,* San Ignacio, Bolivia, IV, 364114 and 364133, respectively; *k, P. guyannensis,* Corumbá, Brazil, IV, 364075.

Hyutanaham, Brazil (2)

DESCRIPTION.—External: "Upper parts Mars Orange on back, grading to Ochraceous-Tawny on sides . . . *Aristiforms on middorsal region:* Grayish basally, gradually blackening toward tip; total length [of aristiforms] 16–19 mm; maximum width, 0.5 mm." (Moojen, 1948, p. 338.) For additional characters of *Proechimys steerei,* 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 4*a* but longer and with more pronounced ventral groove and apical wings.

COMPARISONS.—Color of dorsum similar to specimens from Porto Velho and Rio Branco, although more reddish; aristiforms similar to those of Rio Branco population; counterfold pattern distinctive, but similar to that of specimen *C* (USNM 391008) from Riberalta; baculum similar to that of *Proechimys canicollis,* although longer and with more pronounced apical wings.

REMARKS.—*Proechimys steerei* Goldman, (type-locality, Hyutanaham, Brazil, Goldman, 1911, 1912) was considered a subspecies of *P. goeldii* by Moojen (1948). Hershkovitz (1948) included *P. steerei* in *P. guyannensis.* The counterfold pattern of the upper molars is complex and in this study has been interpreted differently than did 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 subpecific rank. It is impossible, however, 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.

SPECIMENS EXAMINED.—Total 3, from Brazil: Amazonas.—Labrea: Hyutanaham (type-locality), 3 (type, ♂, USNM 105535; topotyes: ♂, USNM 105536 ♀, USNM 105537).

Porto Velho, Brazil (3)

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 Rio Branco and Hyutanaham populations, but aristiforms much wider and color slightly paler; counterfold pattern similar to that in Rio Branco population.

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

SPECIMENS EXAMINED.—Total 9, from Brazil: Rondônia.—Porto Velho: 8 km N Porto Velho, 9 (4 ♂ ♂: USNM 364146, 390351, 390353, 390355; 5 ♀ ♀: USNM 364143–145, 390352, 390356).

Rio Branco, Brazil (4)

DESCRIPTION.—External: Aristiforms of medium width (9.5–9.7 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 tips 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 that in 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 remarks under Hyutanaham, Brazil, account). However, the Rio Branco specimens could also fall within the range of variation for *Proechimys guyannensis*, based on cranial dimensions and a conservative interpretation of the number of counterfolds.

SPECIMENS EXAMINED.—Total 3, from Brazil: Acre.—Rio Branco: 3–4 km S Rio Branco, 3 (2 ♂ ♂: USNM 364142, 364147; ♀, USNM 364148).

Riberalta, Bolivia (5)

DESCRIPTION.—External: Aristiforms of *A* (USNM 363991, 363993, 363995, 363998, 364005, 364006, 364009) and *B* (USNM 363986, 363988) specimens of medium length (18–19 mm) and width (0.5–0.6 mm); those of *C* (USNM 391008) 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 4*d*) 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 4*c*) 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; 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 4*d*). Only two specimens of *B* had bacula and no clarifying ecological information was available. It is premature to suggest that these two variants may represent sibling species and, therefore, they are referred to *Proechimys guyannensis*. Subspecific assignment is largely conjectural although 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* 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*.

Specimens examined.—Total 23, from Bolivia: Pando.—Madre de Dios: 13 km NW Riberalta, 1 (♂, USNM 364009); 5 km NW Riberalta, 3 (2 ♂ ♂: USNM 364005–006; ♀, USNM 364007); 3.5 km NW Riberalta, 3 (2 ♂ ♂: USNM 363996, 363998; ♀, 363997). Beni.—Vaca Die,: 13 km NE Riberalta, 5 (2 ♂ ♂: USNM 363999, 364002; 3 ♀ ♀: USNM 364000–001, 364003); 10 km NNE Riberalta, 1 (♀, USNM 391008); 13 km W Riberalta, 1 (♂, USNM 363991); 2.3 km W Riberalta, 1 (♀, USNM 363990); Riberalta, 8 (5 ♂ ♂: USNM 363985–986, 363988, 363993, 363995; 3 ♀ ♀: USNM 363987, 363989, 363994).

Puerto Maldonado, Peru (6)

Description.—External: Aristiforms in *D* (USNM 364012, 364014, 364026) long (18–22 mm) and of medium width (0.5–0.7 mm), those of *E* (USNM 364149, 364151, 390367) 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 frontonasal 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*e*, *f*) 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 Mato 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. But the specimens do not possess other characters of *P. hendeei* 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 Villanueva, Colombia, and northwestern Brazil.

On the present evidence, *D* and *E* seem referable to *Proechimys guyannensis*, although their subspecific affinity has not been determined.

SPECIMENS EXAMINED.—Total 24, from Peru: Madre de Dios.—Tambopata: 6 km W Puerto Maldonado, 1 (♂, USNM 364013); 4.5 km W Puerto Maldonado, 1 (♀, USNM 364030); 4 km W Puerto Maldonado, 2 (2 ♀ ♀: USNM 364150–151); Puerto Maldonado, 4 (♂, USNM 364014; 3 ♀ ♀: USNM 364015, 364149, 390366); 12 km E Puerto Maldonado, 4 (2 ♂ ♂: USNM 364031–032; 2 ♀ ♀: USNM 364033–034); 1.5 km S Puerto Maldonado, 6 (6 ♂ ♂: USNM 364019–020, 364025–028); 3 km SW Puerto Maldonado, 1 (♀, USNM 364018); 3.5 km SW Puerto Maldonado, 1 (♂, USNM 364017); 4 km SW Puerto Maldonado, 1 (♀, USNM 364021); 1.5 km SE Puerto Maldonado, 1 (♂, USNM 364024); 4 km S Puerto Maldonado, 1 (♂, USNM 364012); 15 km S Puerto Maldonado, 1 (♂, USNM 364011).

San Joaquín, Bolivia (7)

DESCRIPTION.—External: Aristiforms long (28–34 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 basiocipital 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 4*g*): 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.—According to Moojen (1948), *Proechimys l. longicaudatus* (Rengger) and *P. longicaudatus leucomystax* Ribeiro, from western Mato Grosso, Brazil, have 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 evidence indicates a considerable overlap in characters between these two populations and those from Puerto Maldonado, Riberalta, San Ignacio, Warnes, Limão Balsa, Corumbá. Specimens from San Joaquín and Cafetal were assigned to *Proechimys guyannensis*, suggesting that the San Ignacio, Warnes, Limão Balsa, and Corumbá specimens may also be referable to *P. guyannensis*.

SPECIMENS EXAMINED.—Total 4, from Bolivia: Beni.—Mamore: San Joaquín, 1 (♂, USNM 364929); 3.2 km SE San Joaquín, 3 (3 ♀ ♀: 363981–983).

Cafetal, Bolivia (8)

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 4*h*): Long and broad, convex dorsally and 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 under San Joaquín (p. 11).

REMARKS.—These specimens are probably referable to *Proechimys guyannensis*. See under San Joaquín for reasons (p. 11).

SPECIMENS EXAMINED.—Total 3, from Bolivia: Beni.—Mamore: Cafetal, 3 (♂, USNM 391403; 2♀ ♀: USNM 391402, 391406).

San Ignacio, Bolivia (9)

DESCRIPTION.—External: Aristiforms long (17–20 mm) and 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 teeth of lower jaw (Figure 2).

Baculum (Figure 4*i, j*): Short and broad, convex dorsally, with basal and apical regions expanded laterad; median proximal notch present (Figure 4*i*) or absent (Figure 4*j*); 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 artistiforms 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). This conclusion, however, cannot be firmly substantiated by reference to the original description of *P.g. securus.*

SPECIMENS EXAMINED.—Total 32, from Bolivia: Beni.—Moxos: 3.6 km NNE San Ignacio, 3 (3 ♂ ♂: USNM 364101, 364105, 364108); road to San Ignacio Airport, 3 (♂, USNM 364114; 2 ♀ ♀: USNM 364113, 364115); San Ignacio, 21 (12 ♂ ♂: USNM 364091–092, 364095–096, 364106, 364118, 364123, 364131, 364133, 364135–136, 364138; 9 ♀ ♀: USNM 364098, 364124–125, 364132, 364134, 364137, 364139–141); 1 km SW San Ignacio, 5 (5 ♂ ♂: USNM 364116–117, 364126–127, 364129).

Warnes, Bolivia (10)

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; supraorbial 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 specimens from Corumbá, paler than San Ignacio specimens, darker than individuals of 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, in the Amazon drainage system. Limão Balsa and Corumbá are located near tributaries of the Río Paraguay, in the Paraná-Paraguay drainage system. In southeastern Boliva 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 signficant dispersal barrier to *Proechimys*.

The pelage of the Warnes specimens is similar to that described for *Proechimys l. longicaudatus* by Moojen (1948). It is equally probable, however, that these specimens may represent a pale population of *Proechimys guyannensis*.

SPECIMENS EXAMINED.—Total 22, from Bolivia: Santa Cruz.—Warnes: Juan Latino, 1 (♀, USNM 364051); La Abra, 1 (♀, USNM 364073); 1 km NNW Warnes, 6 (3 ♂♂: USNM 364065, 364067–068; 3 ♀♀: USNM 364062, 364064, 364070); 1.3 km NE Warnes, 5 (2 ♂♂: USNM 364071–072; 3 ♀♀: USNM 364059–061); Warnes, 1 (♀, USNM 391009); Santa Rosita, 8 (5 ♂♂: USNM 364048, 364050, 364053–054, 364056; 3 ♀♀: USNM 364062, 364064, 364070).

Limão Balsa, Brazil (11)

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 was situated medially in the frontonasal suture of most specimens (more than half); incisive foramina long, rounded anteriad, the lateral margins tapering sharply posteraid 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.

REMARKS.—In external, cranial, and dental characters, the specimens from Limão Balsa are similar to those from Corumbá and Warnes. The Limão Balsa and Corumbá specimens also show similarities in several features (see remarks for San Joaquín, Bolivia, p. 11) with the description of specimens assigned by Moojen (1948) to *P. longicaudatus* (Rengger). It is possible, therefore, that the variation observed in *Proechimys guyannensis* (see previous accounts) may include the range of variation known for *P. longicaudatus*. Moojen (1948, p. 315) mentioned that *P. guyannensis* and *P. longicaudatus* were sympatric at Utiariti, Brazil, which supported his case for retaining these forms as separate species. The range of variation I observed in specimens from Limão Balsa and Corumbá could include the morphological differences that Moojen observed in his Utiariti specimens. Thus, I have tentatively assigned the specimens from Limão Balsa and Corumbá to *Proechimys guyannensis*.

SPECIMENS EXAMINED.—Total 13, from Brazil: Mato Grosso.—Cáceres: Limão Balsa, 13 (7 ♂♂: USNM 364037–039, 364042, 364044, 390371, 390374; 6 ♀♀: USNM 364036, 364040–041, 364043, 390369, 390372).

Corumbá, Brazil (12)

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 4*c*): Short and broad, convex dorsally; 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.

Remarks: As stated in the remarks for the Limão Balsa population, the Corumbá specimens are probably referable to *Proechimys guyannensis*. For additional information, see (p. 13).

Specimens Examined.—Total 13, from Brazil: Mato Grosso.—Corumbá: Corumbá, 1 ♂ (USNM 364075); 10 km NE Urucum, 5 (2 ♂♂, 3 ♀♀: USNM 364089, 390368; 3 ♀♀: USNM 364086–087, 364090); Urucum, 2 (2 ♀♀: USNM 364077–078); Santa Theresa, 5 (2 ♂♂, 3 ♀♀: USNM 364079, 364081; 3 ♀♀: USNM 364080, 364084–085).

Interpopulation Variation

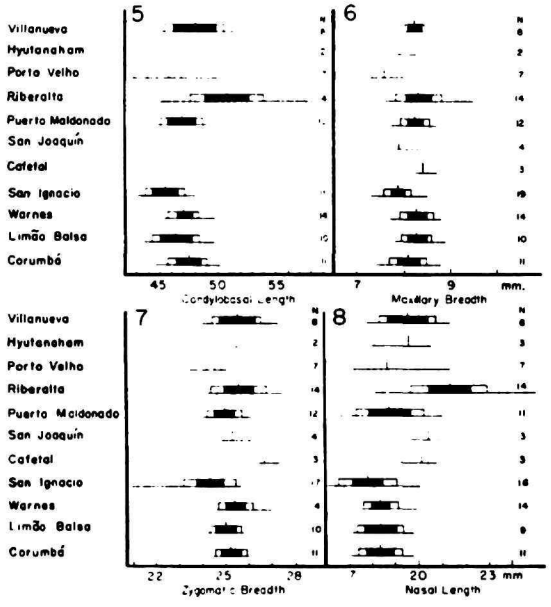
Some trends in bacular, cranial, dental, and external features were noted in comparisons of populations, although these changes were not definitely clinal in nature. Assessment of these trends was complicated by the variability of individuals within a population. The following comments on comparisons of morphological features between populations gives some indication of the nature of variability in spiny rats.

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 the available information on bacular morphology in this genus.

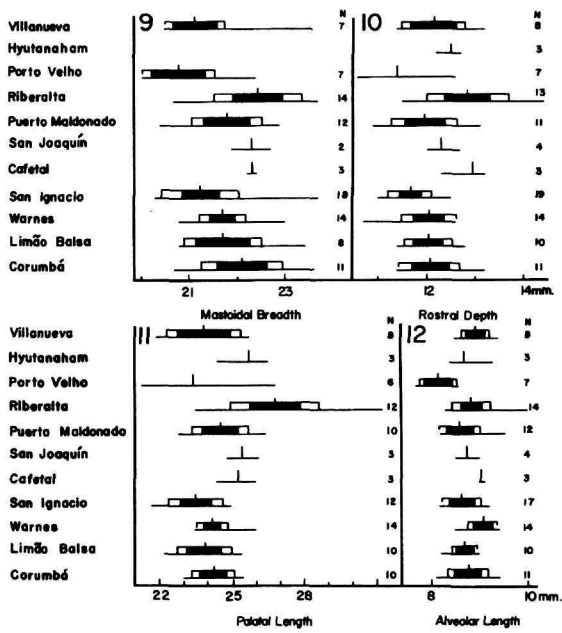
A total of 42 bacula were available for study, although for some localities none was found on the specimens examined, and for others the sample sizes were very small. Those available, however, did provide some evidence of interpopulation variation. Illustrations (Figure 4) were made of bacula from most localities.

Most of the specimens from Bolivia and Corumbá, Brazil, had broad bacula, although the length was variable (Figure 4*c*, *g*, *k*). The bacula from the Puerto Maldonado, Peru, population were long and slender, and with wide apical wings projecting ventrad (Figure 4*e*, *f*). Bacula from Villanueva, Colombia were very narrow (Figure 4*a*, *b*). In the Riberalta, Bolivia, population there were two types of bacula, (see p. 10), markedly different from each other (Figure 4*c*, *d*). Clinal variation was not apparent, although bacula from the San Joaquín and Cafetal, Bolivia, populations (Figure 4*g*, *h*) 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), interpopulation 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



Figures 5–8. Variation in four cranial dimensions between 11 populations of *Proechimys*, age-class IV: 5 condylobasal length, 6 maxillary breadth, 7 zygomatic breadth, 8 nasal length. 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.



FIGURES 9–12.—Variation in four cranial dimensions between 11 populations 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.

mastoidal (Figure 9) breadths and rostral depth (Figure 10). Maxillary breadth (Figure 6) and alveolar length (Figure 12) showed little interpopulation 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 differences of condylobasal length and zygomatic breadth were statistically significant in interpopulation comparisons. The difference was considered significant when a test of two population means resulted in a low probability value (e.g., $P<0.05$). 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 means 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 means 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 trends were evident. In most populations there were three counterfolds in the upper cheek teeth, but some specimens from Hyutanaham and Riberalta had indications of a fourth fold.

Variations in the number of counterfolds in the

TABLE 3.—Values of Student's *t* and associated probability levels (*P*) in testing the hypothesis (H: $\overline{X}_1=\overline{X}_2$) of no difference in mean condylobasal length and zygomatic breadth between two populations, age-class IV.*

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

*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*. The difference was considered significant when a test of two population means resulted in a low probability value (e.g. $P<0.05$).

TABLE 4.—Value of Student's *t* and associated probability levels (*P*) in testing the hypothesis of no difference in mean condylobasal length and zygomatic breadth 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

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 Villanueva, Colombia.

Moojen (1948) reported that variation in counterfold number was clinal and the number of folds were 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, but no attempt was made to make a correlation with climatic factors.

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 Porto Velho. 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.

Conclusions

This study on cranial and bacular variation in *Proechimys* has led to several conclusions which should be of use in future studies of this genus.

Eight of ten cranial measurements (condylobasal length; nasal length; palatal length; zygomatic breadth; mastoidal breadth; rostral depth; maxillary breadth; and alveolar length) were found to be statistically significant in showing differences between populations. The four bacular measurements, however, were not statistically significant.

Dental wear poses problems in determination of taxa owing to changing occlusal patterns at different age levels. Taxonomic assignment can be misleading if dental patterning is the only criterion used.

Similarities in cranial dimenisons are more apparent between adjacent than widely separated populations even though no consistent pattern could be demonstrated.

Bacula of specimens from any given locality are usually quite similar in structure although overall dimensions vary.

Most specimens examined are considered to be *Proechimys guyannensis*. Specimens from Villanueva, Colombia are *Proechimys canicollis*; a single specimen from Riberalta, Bolivia, represents *Proechimys quadruplicatus;* and specimens from Hyutanaham, Brazil, are referred to *Proechimys steerei,* but as additional knowledge is gained may be found to represent *P. guyannensis.*

Several factors should be considered in further studies of *Proechimys.* Namely, the range of variation that was observed in these populations may not be adequately expressed by subspecific delimitation. In addition, the specific status of several forms, particularly *Proechimys guyannensis* and *P. longicaudatus,* remains unresolved. Thus, the role of isolating mechanisms, particularly ecological and behavioral, deserves

more careful consideration. Studies, both observational and experimental, that consider these factors will contribute greatly to our understanding of speciation in *Proechimys*.

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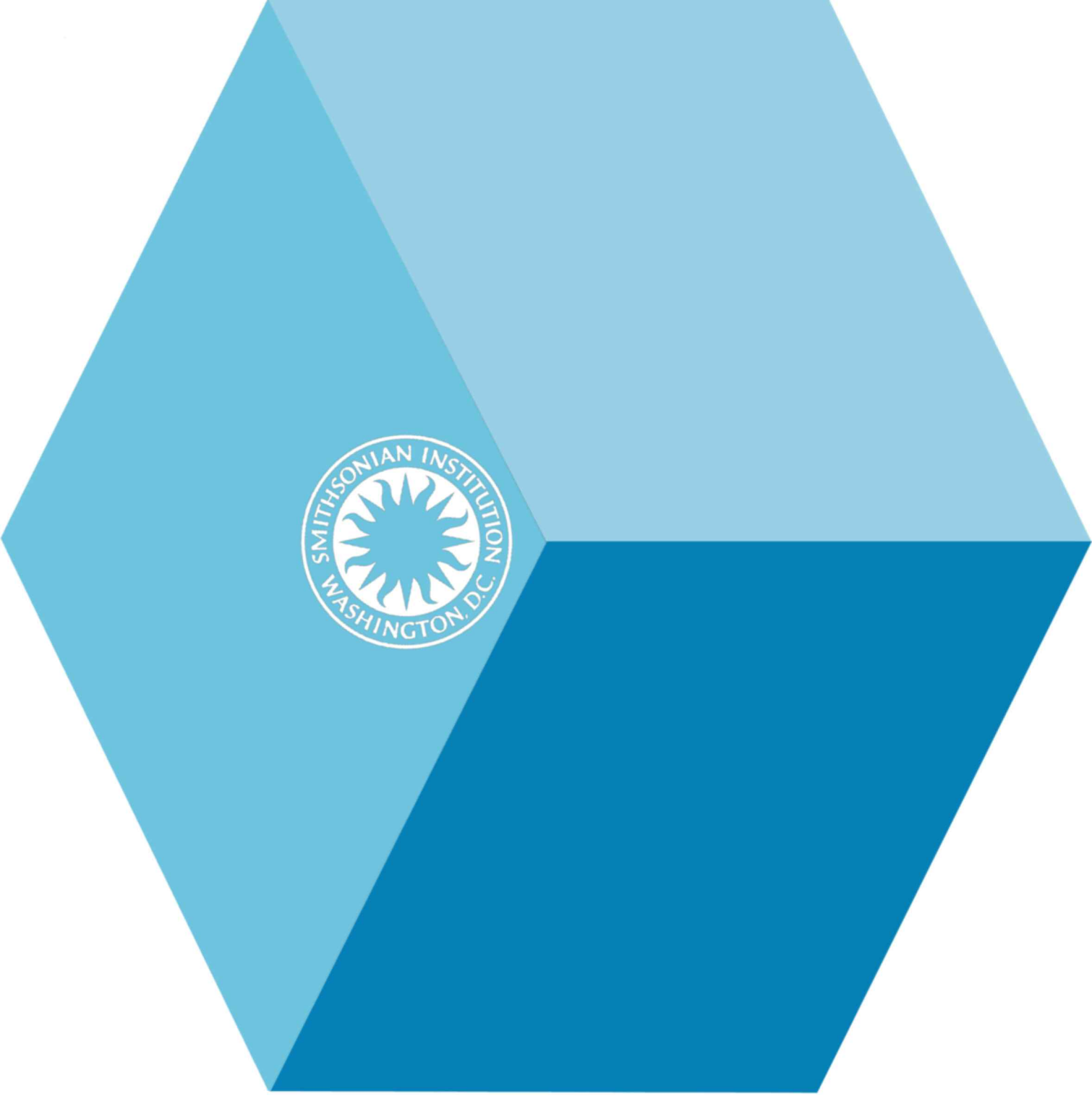
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