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OCCASIONAL PAPERS OF THE MUSEUM OF  
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LOUISIANA STATE UNIVERSITY

BATON ROUGE, LOUISIANA

NOTES ON THE SYSTEMATICS OF *PROECHIMYS*  
(RODENTIA: ECHIMYIDAE), WITH EMPHASIS  
ON PERUVIAN FORMSBy JAMES L. PATTON<sup>1</sup> AND ALFRED L. GARDNER<sup>2</sup>

The confusion surrounding the systematics of Neotropical spiny rats of the genus *Proechimys* was aptly summarized by Oldfield Thomas (1928:262) in his often quoted statement, "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. Whether they represent the forms which have been called *brevicauda*, *simonsi*, *pachita*, or *bilda*, they all seem too variable to distinguish at all constantly from each other. . . . I confess myself defeated in any attempt at present to distinguish the local races." Subsequent attention to members of this genus has contributed little toward clarification of the situation pictured by Thomas. Our interest in the taxonomy of *Proechimys* stems from attempts to identify specimens collected by us in eastern Perú and deposited in the collections of the Louisiana State University Museum of Zoology (LSUMZ) and the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). This preliminary analysis has been facilitated by chromosomal data gathered in the four Peruvian localities represented by our material. The chromosomal information indicated four different forms from eastern Perú, all of which were taken on the "same trap line" at one locality. Additional information

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gathered through the examination of the structure of the baculum and glans, as well as skin and skull morphology, including plantar surface features of the hind feet, supports the separation of our material on karyotypic grounds. We have incorporated information from eastern Costa Rican populations for which we also have chromosomal preparations.

Basing our decisions on descriptions in the literature, we have tentatively applied names to the forms we have distinguished. Their correct allocation, however, awaits the gathering and analysis of many more data from other populations that hopefully in all cases possible will include karyotypic information, which, in our experience, has greatly facilitated the morphological separation of forms.

#### MATERIALS AND METHODS

Seventy-one specimens (from which we have also examined 22 bacula, 8 glands, and 54 karyotypes) form the basis of this report. Most of the specimens were collected by us under the auspices of the Louisiana State University Museum of Zoology and the Museum of Vertebrate Zoology, University of California, Berkeley, during the period from 1966 to 1971.

Age class determinations were based on tooth eruption sequence and degree of wear on occlusal surfaces as classified by Martin (1970:5). Tooth nomenclature and counterfold determinations follow Hershkovitz (1948:133). Chromosome material was prepared in the field using the *in vivo* colchicine, hypotonic citrate technique (Patton, 1967). Dried phalli were cleared and stained according to the method used by Hooper (1959). Many of the bacula were extracted and, unfortunately, in these specimens the glans was destroyed. The cranial and bacular measurements are in millimeters and are taken as defined by Martin (1970:5-6) except the length of rostrum (Hooper, 1952:10) and interorbital constriction (least interorbital breadth). Measurements of tail length, length of hind foot, and height of ear from notch are those recorded on the specimen labels. The lengths of head and body were computed from label information. Measurements are given only for adults with fully erupted molars. These animals correspond to Moojen's (1948:332) adult and senile categories and to Martin's (1970:5) age classes IV and V. Capitalized color terms used in the descriptions are those of Ridgway (1912).

For ease in comparison of karyotypes, the autosomal complement of each form has been divided into the following four categories: (A) large meta- and submetacentrics; (B) medium-sized to small meta- and submetacentrics; (C) large to small subtelocentrics; and (D) medium-sized to small acrocentrics. Definitions for fundamental number (FN) and chromosomal types follow Patton (1967). These categorical divisions are nonarbitrary for the chromosomal material at hand. Museum numbers, or series of numbers, marked by asterisks in the lists of specimens examined denote animals whose chromosomes have been analyzed.

#### LOCALITIES

Four localities in eastern Perú (see Map, Figure 1) and a single locality in Costa Rica are represented. Forest formations in Perú are based upon Tosi's (1960) interpretation of the Holdridge plant formation and life zone system.

Tingo María (09° 18' S, 76° 00' W), Río Huallaga, 650 meters, Departamento de Huánuco, Perú. A large community on the upper Río Huallaga. Bosque muy Humido Subtropical (Subtropical Wet Forest): extensively cleared for agriculture.

Santa Elena (near 09° 06' S, 75° 50' W), ca. 1,000 meters, ca. 35 km NE Tingo María, Departamento de Huánuco, Perú. A coffee plantation on the lower slopes of the Cordillera Azul. Bosque muy Humido Subtropical (Subtropical Wet Forest): mixture of mature and second growth forest locally cleared for agriculture.

Yarinacocha (08° 21' S, 74° 34' W), 150 meters, Departamento de Loreto, Perú. The Summer Institute of Linguistics community on Lake Yarinacocha near Pucallpa. Bosque Seco Tropical (Tropical Dry Forest): extensively cleared for agriculture.

Balta (10° 08' S, 71° 13' W), Río Curanja, ca. 300 meters, Departamento de Loreto, Perú. A small Cashinahua Indian village on the Río Curanja, a tributary of the Río Alto Purús. Bosque Seco Tropical (Tropical Dry Forest): undisturbed forest except for scattered small gardens.

Cariari (10° 22' N, 83° 31' W), Río Tortuguero, ca. 100 meters, Provincia de Limón, Costa Rica. An Instituto de Tierras y Colonización (ITCO) colony north of Guápiles. Tropical Wet Forest (following Slud, 1964): mixture of undisturbed forest and second growth; however, rapidly being cleared for agriculture.

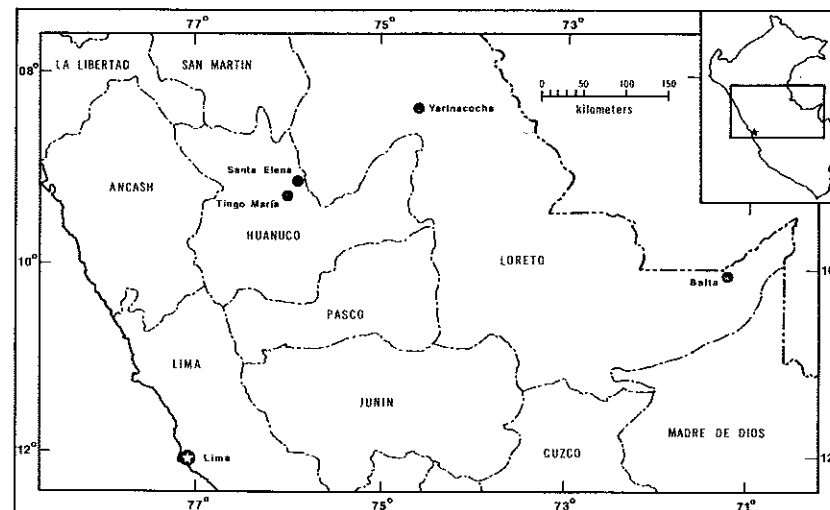


FIGURE 1. Map of central Perú showing the four localities represented by specimens of *Proechimys* herein reported on.

## SPECIES ACCOUNTS

*PROECHIMYS BREVICAUDA* (Günther)

**External features.**—Large, robust spiny rats with medium-sized ears, large hind feet, and relatively short tails. Color of dorsum from Hazel to Russet, finely and more or less evenly interspersed with small amounts of black and paler on sides of head and body (color between Sayal Brown and Pinkish Cinnamon); venter, chin, and margins of upper lips white, or chin dusky brown; large white patch at base of vibrissae in Balta specimen (absent in Yarinacocha representatives); inner surface of hind legs below knee dull grayish brown, color darker distally and completely encircling the tarsus; outer half of hind feet grayish brown, inner half from tarsal joint to ends of first two toes white; lower forelegs and forefeet white medially, grayish brown laterally (in Balta specimen brown restricted to proximal ends of metacarpals, forefeet otherwise white); tail dark brown above and whitish, irregularly shaded with gray, below. Plantar surface of hind feet with six tubercles; lateral metatarsal tubercle (fifth postdigital tubercle, *sensu* Hershkovitz, 1960:524-525) well-developed, but short; distance between medial metatarsal tubercle (mmt) and first postdigital tubercle less than width of mmt; medial and lateral metatarsal tubercles and first and fourth postdigital tubercles forming the close-set corners of a square; hallux long, extending to middle of second postdigital tubercle; distance between heel and first postdigital tubercle approximately equal to distance between first postdigital tubercle and end of third digit (Figure 2, a).

**Cranial features.**—Skull large with a narrow, elongated rostrum; supra-orbital ridges beaded, overhanging orbits, and discontinuous posteriorly across parietals to lambdoidal crests with anterior parietal portion separated from and distinctly ventral to posterior portion; incisive foramina lyre-shaped, constricted posteriorly, and extending as deep grooves onto maxillae (Figure 3, c); maxillary portion of incisive foramina septum weakly developed, attenuated, and not strongly connected to premaxillary sheath (lacking contact in 9 of 11 skulls at hand); premaxillary portion of incisive foramina septum short, usually not expanded, and with vomerine portion almost entirely enclosed in premaxillary sheath and not contributing significantly to ventral aspect of septum; lateral margins of proximal portion of para-occipital processes conspicuously indented (Figure 3, a); hamular process of pterygoids separated from auditory bullae by a distance equal to or exceeding one-half its width; mesopterygoid fossa relatively short and broad with angle

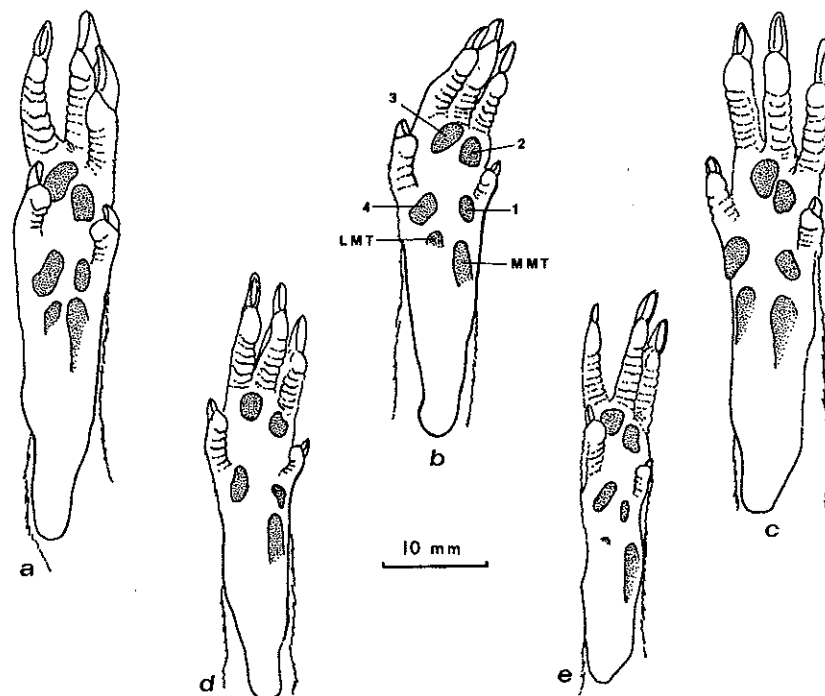


FIGURE 2. Details of the plantar surface of the right hind foot: a) *P. brevicauda*, LSUMZ 16757, Balta, Perú; b) *P. longicaudatus*, LSUMZ 14914, Balta, Perú; c) *P. semispinosus*, LSUMZ 13370, Cariari, Costa Rica; d) *P. hendeei*, LSUMZ 14915, Balta, Perú; e) *P. guyannensis*, LSUMZ 16759, Balta, Perú. MMT = medial metatarsal tubercle; LMT = lateral metatarsal tubercle; 1 to 4 = postdigital tubercles.

of indentation into posterior margin of palate averaging 35.5 degrees (30 to 45 degrees) and never extending forward beyond level of anterior one-quarter of last molars. Counterfold pattern: 3-4/4, 3-4/3, 3-5/3, 3-5/3.

**Bacula and glandes.**—No glans material has been examined from this species. The baculum, represented by four specimens (LSUMZ 14413, 14414, 14416, and 14417; see Figure 4, a to d), has a long, narrow shaft, a broadened, paddle-shaped base, and slight development of apical wings, which are separated by a wide median depression.

**Karyotype.**— $2n=24$ ;  $FN=42$  (Figure 9, e). The autosomes include a pair of moderately large metacentrics (A); seven pairs of medium-sized to small metacentrics and submetacentrics (B), of which the second pair possess ter-

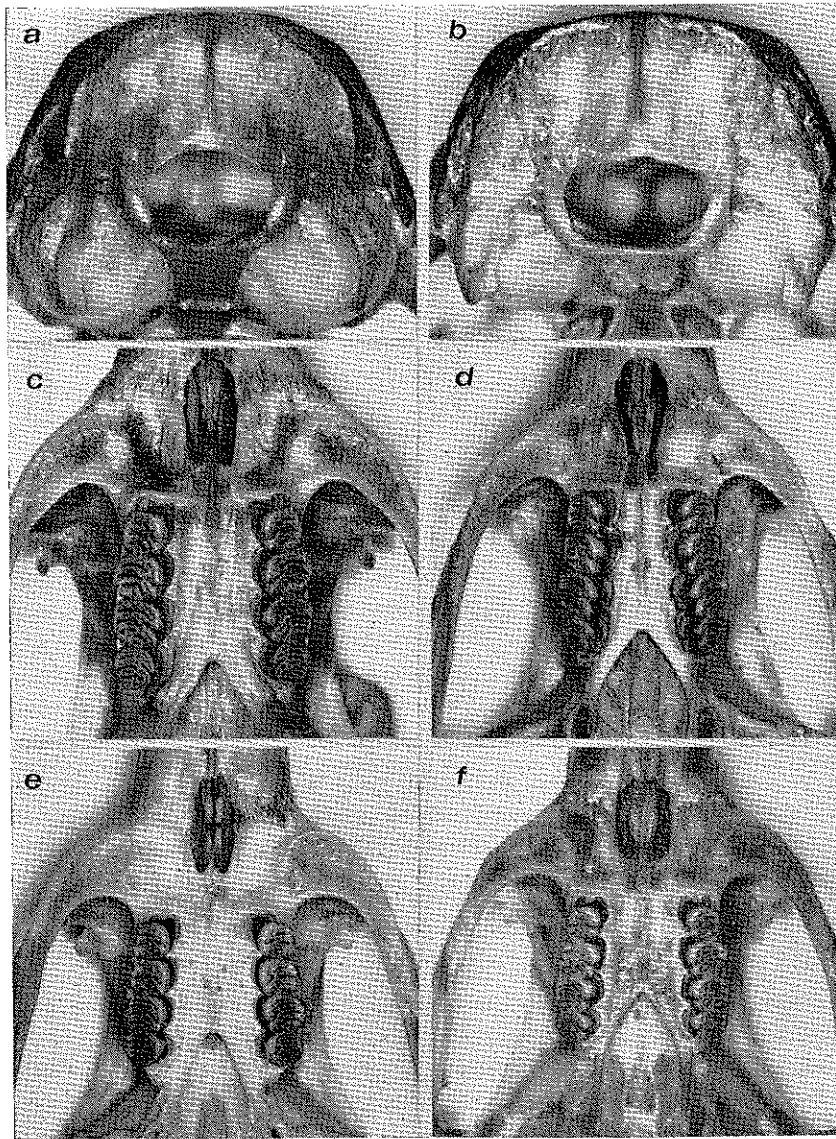


FIGURE 3. Details of the palatal and occipital structure of representative skulls of *Proechimys*: a and c) *P. brevicanda*, LSUMZ 16760; d) *P. longicaudatus*, LSUMZ 12430; b and e) *P. hendeei*, LSUMZ 14429; f) *P. guyannensis*, LSUMZ 16959.  $\times 2.5$ .

minimal satellites on the long arms; one pair each of large and medium-sized subtelocentrics (C); and a single pair of small acrocentrics (D). The X-chromosome is a moderately small acrocentric and the Y is a very small, apparently biarmed, chromosome.

*Measurements.*—The mean and range for external and cranial measurements of nine adults, unless otherwise noted: head and body, 235.0 (209-272); tail (N=6), 148.8 (109-173); hind foot, 52.1 (47-56); ear (N=8), 24.2 (22-26); greatest length of skull, 59.1 (53.4-65.6); condylobasal length, 53.0 (47.7-59.0); mastoidal breadth (N=8), 21.7 (19.6-

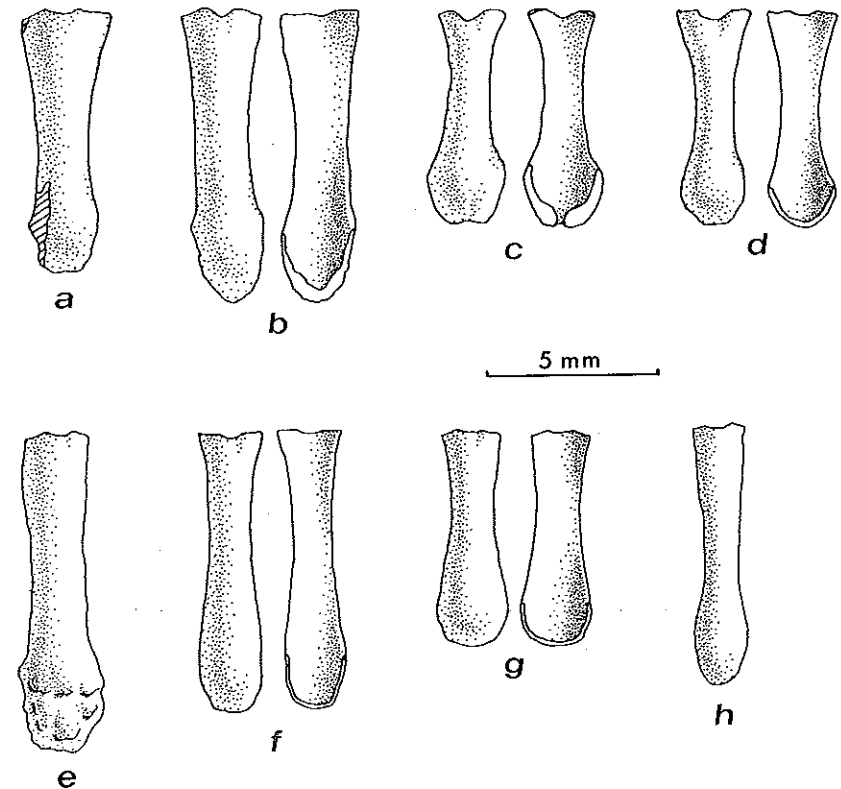


FIGURE 4. Representative bacula of *P. brevicanda* (a, LSUMZ 14413; b, LSUMZ 14417; c, LSUMZ 14414; d, LSUMZ 14416) and *P. hendeei* (e, LSUMZ 14431; f, LSUMZ 12427; g, LSUMZ 12426; h, MVZ 136654). a-d from Yarínacocha, Perú; e-h from Balta, Perú.

23.2); length of nasals, 23.5 (20.4-27.1); zygomatic breadth, 27.3 (25.0-29.0); palatal length, 27.9 (24.9-31.1); maxillary toothrow, 9.2 (8.2-9.8); interorbital constriction, 12.4 (11.3-13.8); length of rostrum, 24.0 (21.1-28.1).

Measurements of baculum (N=4): length, 7.7 (6.5-9.8); distal width, 2.2 (1.9-2.6); proximal width, 2.1 (1.9-2.2).

*Comparisons.*—The following combination of characters serves to distinguish this species from the other forms described herein: large size, relatively short tail averaging 69.0 (62.6 to 82.4) per cent of head and body length, reddish brown color of dorsum finely and more or less evenly interspersed with small amounts of black, conspicuous dusky brown inner surface of hind legs below knees with dark color completely encircling tarsus, unique arrangement of plantar tubercles (see Figure 2), relatively long and attenuated maxillary portion of incisive foramina septum usually not fused to premaxillary portion with vomerine portion of septum inconspicuous to absent in ventral aspect, conspicuously indented lateral margins of paraoccipital processes, and shallow anterior angle of mesopterygoid fossa. Skin and skull features apparently unique to this species include: reddish brown color of dorsum finely and more or less evenly interspersed with small amounts of black; combination of large body size with comparatively short tail; dusky brown color of inner surfaces of hind legs below knees with tarsal joint completely ringed with dark brown; close-set arrangement of medial and lateral metatarsal tubercles with first and fourth postdigital tubercles as points of a square or rectangle; and paraoccipital processes with deeply indented lateral margins.

Superficially, this species is similar to the sympatric *P. hendeei* in that both are large reddish brown rats with pale hind feet. They can be easily distinguished, however, by features additional to those previously mentioned as unique to *P. brevicauda*—the number of plantar tubercles (six in *brevicauda* as opposed to five in *hendeei*) and the relative width and indentation of the mesopterygoid fossa (wide and shallow in *brevicauda*, narrow and deep in *hendeei*).

The karyotypically unique *P. brevicauda* is characterized by a diploid number of 24, a single pair of group A metacentrics, and the lack of a small pair of subtelocentric group C chromosomes with satellites. The karyotype is, however, very close to that reported by Reig *et al.* (1970) for animals they identified as *P. cherriei* from La Esmeralda, Upper Orinoco River, Estado de Amazonas, Venezuela. The two forms differ by a single centric

fusion and in the different sizes of the Y-chromosome. The Venezuelan *P. cherriei* has 26 chromosomes and isomorphic sex chromosomes.

The structure of the glans penis is not known. The narrow, elongate baculum is unlike any in the other forms we have examined except the animals we are calling *P. hendeei* from Balta. The same bacular type has been described for spiny rats identified as *Proechimys* sp. (Hooper, 1961), *P. guyannensis* Type III (Didier, 1962), and *P. canicollis* (Didier, 1962; Martin, 1970) from Colombia; for *P. steerei* from Brazil and *P. guyannensis* from Brazil and Bolivia (Martin, 1970); and for *P. guyannensis brevicauda* (Didier, 1962) from Perú.

*Remarks.*—The choice of the name *Proechimys brevicauda* for these spiny rats seems to be the least confusing of the alternatives available to us at this time. This is the only species we have thus far collected in the vicinity of Yarinacocha, and *Proechimys* from this area have been referred to rather consistently under the species-group name *brevicauda* (Sanborn, 1949; Moonen, 1948; Didier, 1962). *Proechimys brevicauda* was also collected with *P. longicaudatus*, *P. hendeei*, and *P. guyannensis* at Balta.

One male had scrotal testes measuring 21 by 41 millimeters on 8 August 1968, whereas three males had non-scrotal testes on 8 June 1966, and 7 and 8 August 1968, respectively. A postlactating female was collected on 4 August 1968.

*Specimens examined.*—PERÚ. Departamento de Loreto: Balta, Río Curanja, 300 m, 1 female (LSUMZ 16757\*); Yarinacocha, 150 m, 4 males, 6 females (LSUMZ 12416, 12439, 12440, 14412\*-17\*, 16760\*).

#### *PROECHIMYS LONGICAUDATUS* (Rengger)

*External features.*—Moderate-sized, robust spiny rats with medium-sized ears and hind feet, and relatively short tails. Color of dorsum generally uniform, from Tawny to Clay Color, coarsely streaked with black (upper parts distinctly dull, slightly darker mid-dorsally with a tendency to be grayish along sides of head and body); venter, including chin, narrow stripe along margins of upper lips, and in specimens from Balta, a very small spot at base of vibrissae, white; dark color of lower hind legs not completely encircling tarsal joint; forefeet and hind feet covered with an even mixture of whitish and pale-tipped brown hairs (except in animals from the vicinity of Tingo María whose lower legs and hind feet differ

as follows: white of underparts becoming Pinkish Cinnamon along the narrow pale stripe on inner surface of lower legs and upper surface of hind feet, outer surface of tarsal joint dark brown, band across distal end of metatarsals dusky brown, and toes except whitish digital bristles pale proximally and dusky brown distally); tail dark brown above, paler below. Hind feet with six plantar tubercles; lateral metatarsal tubercle well-developed, but short when compared to medial metatarsal tubercle (mmt); distance between mmt and first postdigital tubercle greater than width of mmt; hallux long, nearly reaching middle of second postdigital tubercle; distance between heel and first postdigital tubercle equal to or exceeding distance between first postdigital tubercle and tip of third digit (Figure 2, *b*).

**Cranial features.**—Skull medium-sized with a relatively short, blunt rostrum; supraorbital ridge elevated, usually beaded above orbits, and discontinuous posteriorly across parietals to lambdoidal crests with posterior portion (when present) dorsal to anterior portion; incisive foramina lyre-shaped, strongly constricted posteriorly, and continuing as deep grooves onto palate (Figure 3, *d*); maxillary portion of incisive foramina septum short, narrow and blade-like, and always in contact with vomerine and premaxillary portion of septum; vomerine portion of septum conspicuous and forming up to one-third of septal length; premaxillary portion of septum expanded laterally with margins of sheath usually rounded anteriorly and dorsoventrally compressed posteriorly; lateral margins of paraoccipital processes not indented; hamular process of pterygoids separated from auditory bullae by a distance less than one-half its width; mesopterygoid fossa relatively short and broad, angle of indentation into posterior margin of palate averaging 42.6 degrees (35 to 45 degrees) and never extending forward beyond level of anterior one-quarter of third molar in 19 skulls examined. Counterfold pattern: 3/3-4, 3/3, 3-4/3, 3-4/2-4.

**Bacula and glandes.**—The baculum, represented by ten specimens from three localities (Balta: LSUMZ 12430-32, 12437, 12438, and 12617; MVZ 136644 and 136648. Santa Elena: LSUMZ 12616. Tingo María: LSUMZ 14410), displays considerable variation in shape (Figure 5) which cannot be correlated with locality. Generally, the baculum is elongate and broad with well-developed apical wings. The margins are concave and the proximal and distal ends are usually about equal in width. In some specimens, the proximal end bears a median indentation of variable depth; whereas, in

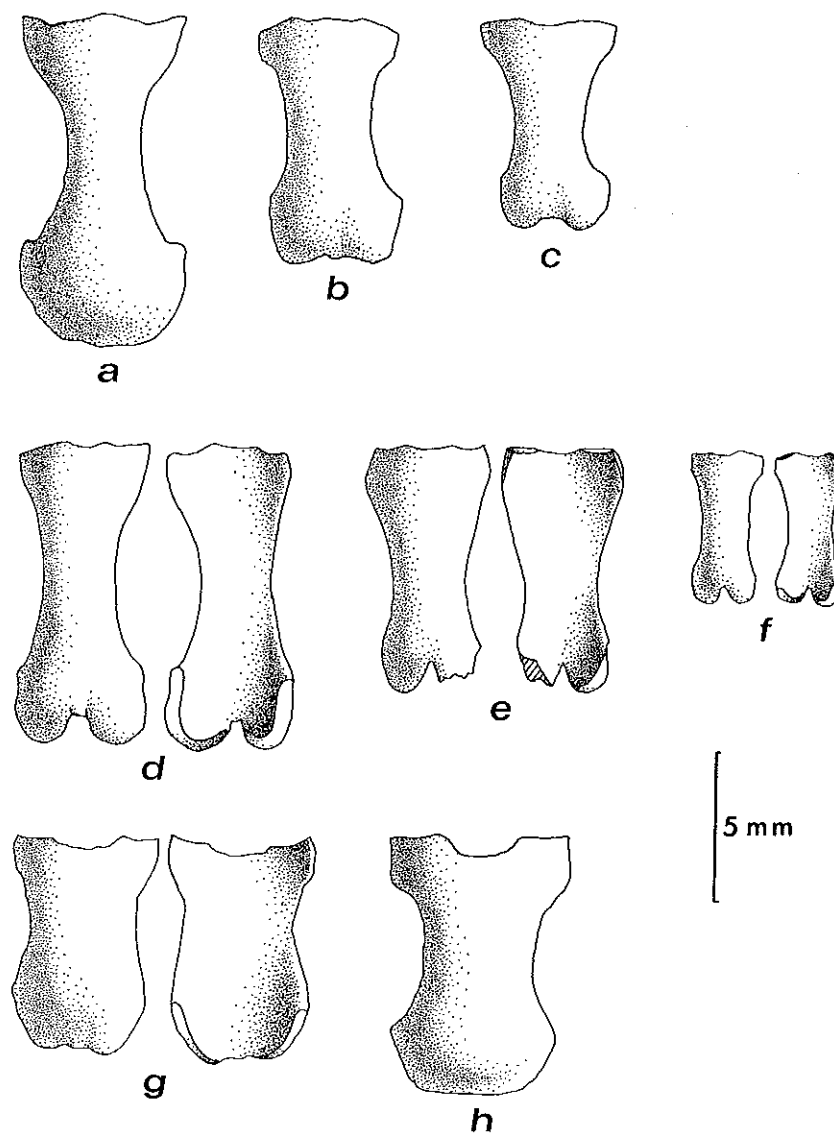


FIGURE 5. Representative bacula of *P. longicaudatus* (*a*, LSUMZ 12438; *b*, MVZ 136644; *c*, LSUMZ 12437; *d*, LSUMZ 12431; *e*, LSUMZ 12432; *f*, LSUMZ 12617; *g*, LSUMZ 14410; *h*, LSUMZ 12616. *a-f* from Balta, Perú; *g* from Tingo María, Perú; and *b* from Santa Elena, Perú.

others this indentation is absent. The shaft is arched dorsally from base to tip and transversely concave ventrally along its entire length.

The glans penis (five specimens examined) is short, thick, and subcylindrical (Figure 6). The index of robustness (greatest diameter/length) is 0.63. The epidermis has sloughed off in these specimens revealing a deeply corrugated, or pleated, dermis. The corrugations extend from the base to the tip on the dorsal surface of the glans, but are restricted to the tip on the ventral surface. Slight ventrolateral swellings at about mid-length set off by deep troughs below and shallow depressions above, characterize

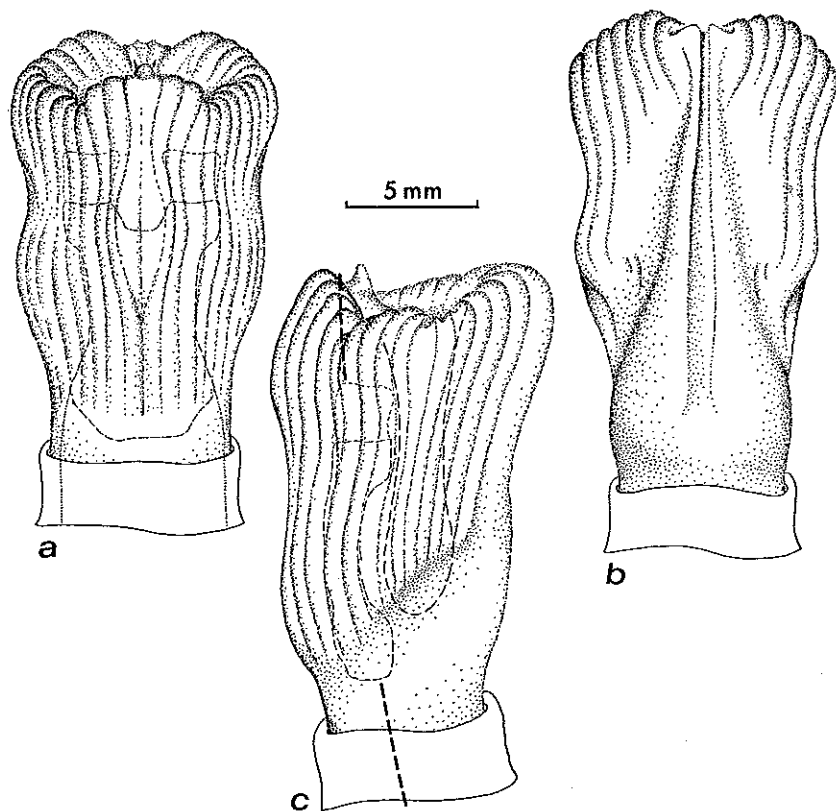


FIGURE 6. Glans penis of *Proechimys longicaudatus* as viewed: *a*, dorsally; *b*, ventrally; and *c*, laterally. LSUMZ 12616, Santa Elena, Perú. The heavy dashed line indicates the orientation of the urethra.

the general appearance of the glans. The most prominent feature of the ventral surface is an ampulla-shaped mass bordered laterally by deep troughs and bisected midventrally from near the base to the tip of the glans by a deep groove. The intromittent sac is large and deep (about three-quarters of glans length) with a comparatively thick ventral wall.

*Karyotype*.— $2n=28$ ;  $FN=50$  (Figure 9, *d*). The autosomes include a pair of moderately large submetacentrics (A); eight pairs of medium-sized to small metacentrics and submetacentrics (B); two pairs of large and one pair of small subtelocentrics (C), of which the small pair possess terminal satellites on the long arms; and a single pair of moderately small acrocentrics (D). The X-chromosome is a moderately small acrocentric and the Y is a very small acrocentric.

*Measurements*.—The mean and range for external and cranial measurements of 20 adults, unless otherwise noted: head and body ( $N=19$ ), 210.4 (189-228); tail ( $N=14$ ), 135.6 (114-155); hind foot ( $N=19$ ), 47.4 (43-50); ear ( $N=19$ ), 21.6 (19-24); greatest length of skull ( $N=19$ ), 52.3 (48.8-56.5); condylobasal length ( $N=18$ ), 46.6 (42.9-50.1); mastoid breadth ( $N=18$ ), 20.8 (19.3-22.8); length of nasals, 19.1 (17.1-23.3); zygomatic breadth, 25.2 (23.5-27.5); length of palate, 24.4 (22.1-27.7); maxillary breadth, 8.3 (7.3-9.4); alveolar length of maxillary tooth-row, 8.7 (8.0-9-6); interorbital breadth ( $N=12$ ), 11.5 (11.0-12.8); length of rostrum ( $N=12$ ), 20.7 (18.5-23.9).

Measurements of baculum ( $N=10$ ): length, 8.8 (4.7-11.6); distal width, 4.6 (1.7-5.3); proximal width, 4.2 (1.8-5.1).

*Comparisons*.—The following combination of characters serves to distinguish this species from all other forms described herein: medium-sized body, relatively short tail averaging 64.4 (58.9-72.3) per cent of head and body length, rather uniform, dull reddish to clay-brown color of dorsum coarsely streaked with black, maxillary portion of incisive foramina septum short with vomerine portion conspicuous (up to one-third of septal length) from ventral view, hamular process of pterygoids long and nearly touching auditory bullae, and mesopterygoid fossa short and broad with shallow anterior angle. The color pattern of the feet (forefeet and hind feet of Balta specimens nearly unicolored and dark or, as in specimens from vicinity of Tingo María, hind feet dark on lateral margins and across terminal portions of metatarsals), is also distinctive of our *P. longicaudatus*. Skin and skull features apparently unique to *P. longicaudatus* include drab



reddish to clay-brown color of dorsum, conspicuous vomerine contribution to septum of incisive foramen, and very broad angle of anterior border of mesopterygoid fossa.

This species is similar to the Costa Rican *P. semispinosus* in the majority of external and cranial features. The two species can be distinguished, however, by color pattern (*P. longicaudatus* is uniformly darker and duller dorsally), length of lateral metatarsal tubercle (well-developed in both species, but short in *longicaudatus* and long, almost equalling length of medial metatarsal tubercle, in *semispinosus*), development of parietal portion of supraorbital ridges (ridge continuous across parietal in *semispinosus* as opposed to discontinuous with posterior portion usually obsolete in *longicaudatus*), and development of vomerine portion of septum of incisive foramina (conspicuous in *longicaudatus* and inconspicuous or absent in *semispinosus*).

The karyotype of *P. longicaudatus* is also very similar to that of *P. semispinosus*, from which it differs only in lacking the pair of minute metacentric chromosomes.

The glans penis is unique among those examined in its relatively thick and blunted appearance, corrugated dermis of dorsal and lateral surfaces, ampulla-shaped ventral swelling, and deep groove along ventral midline. The highly variable baculum is similar in general shape to those figured by Martin (1970) as representing *P. guyannensis* from Perú, Bolivia, and Brazil, and by Didier (1962) as his *P. guyannensis* Type II from Colombia.

*Remarks.*—At the present time it seems almost impossible to select the correct name from the many that might be applied to this species and, although we believe it to be distinct, evidence suggests close relationship with Central American populations currently recognized as *P. semispinosus*. One reason for employing the name *P. longicaudatus* for this species is to emphasize that *longicaudatus* of most authors is almost certainly composite.

*Proechimys longicaudatus* was the only spiny rat collected at Santa Elena and Tingo María; however, it was found together with *P. brevicauda*, *P. bendeei*, and *P. guyannensis* at Balta.

At Balta, a female was pregnant with three 16-millimeter fetuses on 1 August 1966, another with three 45-millimeter fetuses on 5 July 1968, a third with one 56-millimeter fetus on 6 July 1968, and a fourth with

three 56-millimeter fetuses on 15 July 1968. A female from Santa Elena contained two 23-millimeter fetuses on 12 August 1968.

*Specimens examined.*—PERÚ. *Departamento de Huánuco*: Santa Elena, 35 km NE Tingo María, Carretera Central, 1,000 m, 1 male, 1 female (LSUMZ 12616, 14411\*),; Tingo María, 1 male (LSUMZ 14410\*). *Departamento de Loreto*: Balta, Río Curanja, 300 m, 12 males, 16 females (LSUMZ 12429-34, 12436-38, 12617, 14914, 16748, 16749\*-53\*, 16755\*; MVZ 136644\*-49\*, 136651\*-53\*, 136655\*, 136656\*).

#### *PROECHIMYS SEMISPINOSUS* (Tomes)

*External features.*—Large spiny rats with medium-sized ears, large hind feet, and long tails. Color of dorsum from Auburn to Tawny, coarsely streaked with black, and clearer (less streaked) along sides of head, body, and legs; venter white; darker color of lower hind legs extending onto proximal one-third of metatarsals, otherwise hind feet covered with a mixture of light brown and whitish hairs with these feet often appearing darker on lateral margins; color of lower forelegs and forefeet dusky-brown; tail dark brown above, whitish below. Six plantar tubercles on hind feet; lateral metatarsal tubercle well-developed and long, its length approximating that of medial metatarsal tubercle (mmt); distance between mmt and first postdigital tubercle greater than width of mmt; hallux long, extending to middle of second postdigital tubercle; distance between heel and first postdigital tubercle equal to distance between first postdigital tubercle and tip of third digit (Figure 2, c).

*Cranial features.*—Skull large with a relatively short, broad rostrum; supraorbital ridges beaded, broadly overhanging orbits, and continuing posteriorly as well-developed, elevated ridges across squamosal and parietal bones to lambdoidal crest; incisive foramina lyre-shaped, strongly constricted posteriorly, and forming conspicuous grooves that extend onto anterior portion of palate; maxillary portion of septum of incisive foramina variable in development and always in contact with long, well-developed, and laterally expanded premaxillary sheath; vomer not contributing to ventral aspect of septum; lateral margins of proximal portion of paraoccipital processes not conspicuously indented; hamular process of pterygoids separated from auditory bullae by a distance equal to, or greater than, one-half the width of that process; mesopterygoid fossa relatively long and broad; angle of indentation into posterior margin of palate shallow, averaging 39.1

degrees (30 to 45 degrees) and never extending forward beyond level of anterior one-third of last molar in six skulls examined. Counterfold pattern: 3/3-4, 3-4/3, 3-4/3, 2-4/2-3.

*Bacula and glandes.*—No glans material has been examined from this species. The baculum, represented by two specimens (LSUMZ 13366 and 13368), is characterized by its massiveness—its breadth approximating one-half its length (Figure 7, *a* and *b*). The margins are deeply concave, the base is broadly expanded and thickened, and the distal portion is wide with

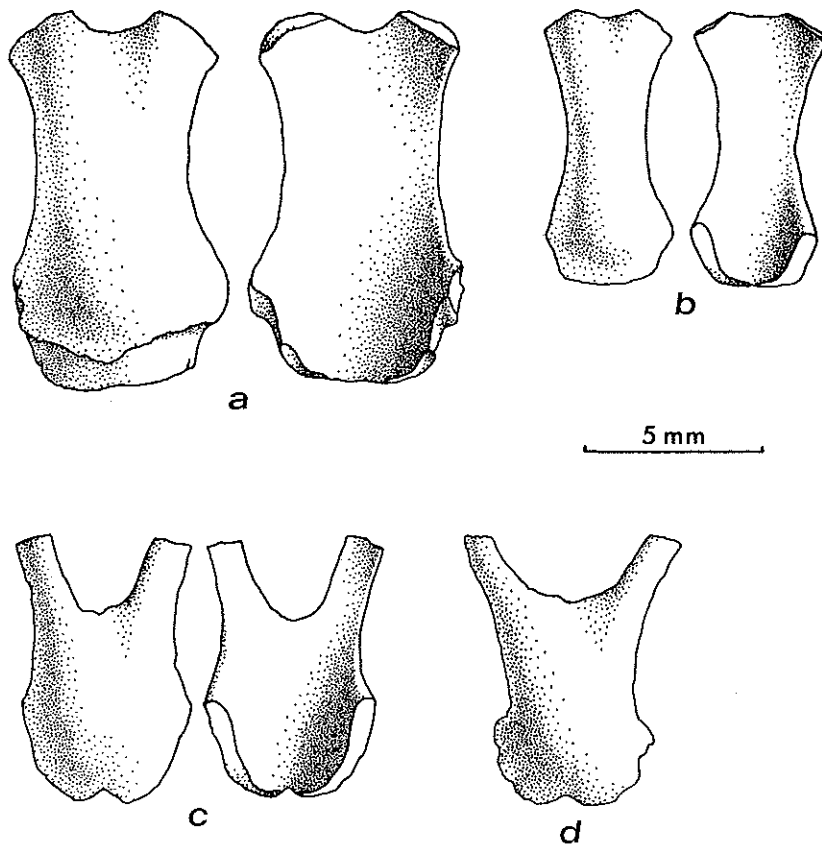


FIGURE 7. Representative bacula of *P. semispinosus* from Cariari, Costa Rica (*a*, LSUMZ 13366; *b*, LSUMZ 13368) and *P. guyannensis* from Balta, Perú (*c*, LSUMZ 12424; *d*, LSUMZ 16759).

the well-developed apical wings separated by a median depression. Proximal and distal portions are transversely convex dorsally and deeply concave ventrally.

*Karyotype.*— $2n=30$ ;  $FN=54$  (Figure 9, *c*). The autosomal complement includes one pair of large submetacentrics (A); nine pairs of medium-sized to small metacentrics and submetacentrics, including one pair of minute metacentrics (B); two pairs of large subtelocentrics and one pair of small subtelocentrics (C), the long arms of the latter with secondary constrictions; and one pair of small acrocentrics (D). The X-chromosome is a moderately small acrocentric, and the Y is a very small acrocentric.

*Measurements.*—The mean and range for external and cranial measurements of five adults, unless otherwise noted: head and body, 222 (202-275); tail ( $N=1$ ), 180; hind foot, 53.0 (48-58); ear, 23.6 (22-25); greatest length of skull, 57.3 (52.7-64.2); condylobasal length, 51.3 (48.0-57.7); mastoidal breadth, 19.9 (18.5-22.0); length of nasals, 21.6 (19.4-25.0); zygomatic breadth, 27.0 (25.9-28.9); palatal length, 27.3 (25.5-30.8); maxillary breadth, 8.6 (8.3-8.9); alveolar length of maxillary toothrow, 9.7 (9.2-10.0); interorbital constriction, 13.0 (12.3-13.4); length of rostrum, 22.7 (20.5-26.0).

Measurements of the baculum ( $N=2$ ): length, 9.4 (8.3-10.4); distal width, 4.7 (3.7-5.7); proximal width, 5.0 (3.6-6.3).

*Comparisons.*—The combination of large body, short tail averaging 65.1 (64.8-65.4) per cent of head and body length, dark reddish brown color of dorsum coarsely streaked with black, generally dark feet, enlarged lateral metatarsal tubercle, strongly beaded supraorbital crests continuing posteriorly as prominent ridges on parietals to lambdoidal crests, and broad, shallow mesopterygoid fossa serve to distinguish this species from all other forms described herein. External and cranial features apparently unique to *P. semispinosus* include: well-developed and long lateral and medial metatarsal tubercles and prominent supraorbital crests that continue posteriorly across parietals as conspicuous ridges.

*Proechimys semispinosus* is similar to *P. longicaudatus*; however, they can be distinguished by the features outlined previously (see under *Comparisons* in the account for *P. longicaudatus*). *Proechimys semispinosus* is easily distinguished from *P. brevicauda* and *P. hendeei*, spiny rats of similar size, by the number, development, and arrangement of plantar tubercles—

five plantar tubercles in *bendeei* as opposed to six in *semispinosus* and *brevicauda*, distance between medial metatarsal tubercle and first postdigital tubercle less than width of mmt in *brevicauda* and *bendeei*, but greater in *semispinosus*. The apparent absence of the vomer in the ventral aspect of the septum of the incisive foramen is a feature *P. semispinosus* shares with the otherwise very different and much smaller *P. guyannensis*.

The karyotype of *P. semispinosus* ( $2n=30$ ) is similar to that of *longicaudatus* ( $2n=28$ ), differing only in the presence of a pair of minute metacentric chromosomes.

The baculum is similar in general morphology to that described herein for *P. brevicauda*. It is also similar to bacula described by Martin (1970) for *P. guyannensis* from Bolivia and Brazil.

*Remarks.*—The name *P. semispinosus* is the name currently assigned to Costa Rican populations of *Proechimys*, and we have no reason to question its application at this time.

*Specimens examined.*—COSTA RICA. Provincia de Limón: Cariari, 2 males, 3 females (LSUMZ 13366, 13367\*-70\*).

#### PROECHIMYS HENDEEI (Thomas)

*External features.*—Large rats with relatively long ears, large hind feet, and long tails. Color of dorsum in live or fresh animals between Burnt Sienna and Sanford's Brown, coarsely streaked with varying amounts of black (faded color of dorsum in prepared specimens near Cinnamon, and in some, as pale as Pinkish Cinnamon), clearer (less streaked with black) and slightly paler on sides of head, body, and legs; venter, chin, sides of upper lips, spot at base of vibrissae (spot sometimes confluent with upper lips and chin), and undersurfaces of forelimbs and hind limbs, white; reddish to dusky-brown color of lower legs extending across tarsal joint and over outer surface of hind feet to base of, and sometimes including, fourth digit; inner margin of hind feet and digits 1, 2, 3, as well as inner margin of digit 4, white (in some specimens hind foot appears almost entirely white, and in others distinctly bicolored with the darker outer margin separated from the plantar surface by a narrow white stripe); forefeet pale dusky-brown with varying amounts of white on inner and outer margins; tail dark brown above, white below. Five plantar tubercles; lateral metatarsal tubercle absent; medial metatarsal tubercle (mmt) well-developed

and elongate; distance between mmt and first postdigital tubercle less than width of mmt; hallux long, extending approximately to middle of second postdigital tubercle; distance between heel and first postdigital tubercle less than distance between first postdigital tubercle and tip of third digit (Figure 2, *d*).

*Cranial features.*—Skull large with relatively long, narrow rostrum; supra-orbital ridge beaded, broadly overhanging orbits in most individuals, and discontinuous across parietals, where anterior portion of crest is inferior to posterior portion; incisive foramina ovoid in outline, not strongly constricted posteriorly (Figure 3, *e*); deep post-foraminal grooves not present on anterior portion of palate; maxillary portion of septum of incisive foramina attenuated and usually not in contact with vomerine and premaxillary portion (no contact in 11 of 15 skulls examined); vomer almost entirely enclosed in premaxillary sheath and not contributing significantly to ventral aspect of septum; premaxillary portion of septum usually expanded anteriorly with rounded margins; lateral margin of proximal portion of paraoccipital process not conspicuously indented (Figure 3, *b*); hamular process of pterygoids separated from auditory bullae by a distance exceeding one-half its width; mesopterygoid fossa long and narrow, angle of indentation into posterior margin of palate acute, averaging 30 degrees (25 to 35 degrees) with indentation varying from a level near the middle of  $M^3$  forward to a level near the middle of  $M^2$  in 15 skulls examined. Counterfold pattern: 3/3-4, 3-4/3, 3-4/3, 3-4/2-3.

*Bacula and glandes.*—The glans penis of this species is essentially identical to that described and figured by Hooper (1961:2-5) for *Proechimys* sp. from Colombia. The shape of the glans is subcylindrical, elongate, and relatively slender. Index of robustness (greatest diameter/length) of the single specimen available to us from Perú and that calculated from Hooper's (1961:4) drawing are 0.35 and 0.37, respectively. The baculum, represented by four specimens (LSUMZ 12426, 12427, and 14431; MVZ 136654) is elongate and narrow with a rounded and slightly broadened base (Figure 4, *e* to *b*). The weakly expanded apical end is usually characterized by a small lateral platform on each side separated by a shallow median depression. The straight shaft is slightly convex dorsally and concave ventrally. The total length of the baculum is approximately two-thirds that of the glans, with the os penis alone slightly more than one-half the glans length.

*Karyotype.*— $2n=32$ ;  $FN=58$  (Figure 9, *b*). The autosomal complement

includes two pairs of large submetacentrics (A); eight pairs of medium-sized to small metacentrics and submetacentrics, including one pair of minute metacentrics (B); one pair of large and three pairs of small subtelocentrics (C), of which one of the latter pairs have secondary constrictions on the long arm; and one pair of medium-sized acrocentrics (D). The X-chromosome is a moderately small acrocentric and the Y is a small acrocentric.

*Measurements.*—The mean and range for external and cranial measurements of 12 adults, unless otherwise noted: head and body, 226.8 (200-263); tail (N=9), 177.4 (154-205); hind foot, 51.2 (46-57); ear, 25.4 (23-29); greatest length of skull (N=11), 57.3 (53.5-61.3); condylobasal length (N=11), 51.7 (47.6-55.5); mastoidal breadth, 21.3 (18.9-23.2); length of nasals (N=11), 21.9 (20.1-24.0); zygomatic breadth, 26.3 (24.0-27.9); palatal length (N=11), 25.6 (23.5-27.8); maxillary breadth, 8.5 (7.9-9.1); alveolar length of maxillary toothrow, 8.7 (8.2-8.9); interorbital breadth (N=10), 11.4 (10.2-12.3); length of rostrum (N=8), 23.0 (21.0-25.2).

Measurements of baculum (N=4): length, 8.2 (6.6-9.8); distal width, 1.8 (1.5-1.9); proximal width, 2.0 (1.7-2.4).

*Comparisons.*—The combination of large size, relatively long tail averaging 80.1 (67.0-94.4) per cent of head and body length, pale straw-brown dorsum coarsely streaked with black (color of dorsum definitely reddish and darker in fresh specimens), white chin and sides of mouth, nearly all white or bicolored white and brown forefeet and hind feet, five plantar tubercles (lateral metatarsal tubercle absent in all specimens examined), ovoid outline of incisive foramen, lack of deep grooves on maxillary portion of palate, and acute palatal border of narrow, elongate mesopterygoid fossa serve to distinguish this species from all other forms described herein.

Skin and skull characteristics apparently unique to *P. hendeei* include rapidly fading color of dorsum, absence of fifth plantar tubercle, relatively smooth surface of palate between cheek teeth and incisive foramen, and deeply indented acute angle of posterior margin of palate.

This species is similar in size and color (in fresh specimens) to the sympatric *P. brevicauda*. The two can readily be distinguished, however, by the number of plantar tubercles (five in *hendeei* and six in *brevicauda*), the configuration of the incisive foramina and maxillary portion of palate (foramina constricted posteriorly and deep grooves on anterior palate in *brevicauda* in contrast with ovoid outline of foramina and nearly smooth

surface of anterior palate in *hendeei*), and the anterior angle of the mesopterygoid fossa (wide in *brevicauda* and acute in *hendeei*).

Superficially, *P. hendeei* is also similar to the sympatric *P. guyannensis* in that occasionally *P. guyannensis* lacks the fifth postdigital tubercle and both species share some features of the incisive foramina, palate, and mesopterygoid fossa. But *hendeei* is a much larger animal and greatly exceeds *P. guyannensis* in nearly all dimensions.

Karyotypically, *P. hendeei* differs most from the other species examined in the number and size of the group A, C, and D elements. It is the only species we have examined with two group A chromosomes. Examples of *Proechimys* with the same karyotype have been recorded from Puerto Asis, Estado de Putumayo, Colombia (O. A. Reig, pers. comm.).

The glans penis is distinct from all other glands examined, differing in its narrow and elongated shape and in its distally directed apical mass containing the urethral opening. The glans appears to be identical to the one figured and described by Hooper (1961) for *Proechimys* sp. from Colombia. The baculum is also similar to that described herein for *P. brevicauda*.

*Remarks.*—The name *Proechimys hendeei* is provisionally applied to this species because the characters of the palatal notch, the relatively short incisive foramina, and the body proportions and size roughly agree with those of the holotype as diagnosed by Thomas (1926:162-164). As far as we can now determine, the greatest contrast between our specimens and those described under *hendeei* by Thomas (1926), Osgood (1944), and Hershkovitz (1948), is in the color—our animals being much paler.

*Proechimys hendeei* was found only at Balta, where it is sympatric with *P. brevicauda*, *P. longicaudatus*, and *P. guyannensis*.

One female from Balta contained three 10-millimeter fetuses on 12 August 1966, another from the same locality carried a single 48-millimeter fetus on 15 July 1968, and a third had three 62-millimeter fetuses on 21 June 1968.

*Specimens examined.*—PERÚ. Departamento de Loreto: Balta Río Curanja, 300 m, 8 males, 10 females (LSUMZ 12425-28, 12435, 14424, 14426\*-29\*, 14431\*, 14915, 14916, 16750\*, 16754\*, 16756\*, 16758\*; MVZ 136650\*, 136654\*).

*PROECHIMYS GUYANNENSIS* E. Geoffroy St.-Hilaire

**External features.**—Small spiny rats with disproportionately long ears, small hind feet, and disproportionately long tails. Color of dorsum between Orange-Cinnamon and Cinnamon, heavily streaked middorsally with black, becoming progressively less heavily streaked laterally on back and sides of head and body; venter, chin, margins of upper lip, and small spot at base of vibrissae, white; dark color of lower hind leg terminating as a band that completely encircles tarsus; forefeet and hind feet entirely white or forefeet white medially and dusky-brown laterally; tail dark brown above, pale brown to white below. Number of plantar tubercles five or six, lateral metatarsal tubercle weakly developed or absent, distance between medial metatarsal tubercle (mmt) and first postdigital tubercle greater than width of mmt, hallux short and not reaching second postdigital tubercle, distance between heel and first postdigital tubercle much less than distance between first postdigital tubercle and end of third digit (Figure 2, *e*).

**Cranial features.**—Skull small with a narrow and elongate rostrum; supraorbital ridge usually beaded and continuous posteriorly onto anterior portions of parietal; incisive foramina ovoid or lyre-shaped, constricted posteriorly in some individuals, and forming weak grooves extending posteriorly onto maxillary portion of palate (Figure 3, *f*); maxillary portion of incisive foramina septum dorsoventrally compressed and in contact with moderately expanded and keel-sided premaxillary sheath; vomer not visible on ventral margin of septum; lateral margin of proximal portion of para-occipital process sometimes weakly indented; hamular process of pterygoids separated from auditory bullae by a distance equal to or less than the width of that process; mesopterygoid fossa long and narrow, angle of indentation into posterior margin of palate acute, averaging 31.7 degrees (30 to 40 degrees) in six skulls examined, and variable in depth, extending forward in some to near middle of M<sup>2</sup>. Counterfold pattern: 3/3-4, 3/2-3, 3/3, 3/2.

**Bacula and glandes.**—The glans of the one specimen examined (LSUMZ 16759), is short, very stout, and considerably heavier at the tip than at the base. The index of robustness is 0.67. Externally, the glans is characterized by ventrolateral swellings located slightly distal to midlength and a pronounced keel-like midventral ridge that extends from near the base to the apex. The urethral opening is directed dorsally and is surrounded by a distinctive enlarged lip that protrudes from the dorsal rim of the glans (Figure 8). The lateral margins of the rim surrounding the intro-

mittent sac are slightly crenulated, and the midventral rim is strongly indented. The intromittent sac is wide and rather shallow (extending proximally only to near midlength of baculum). The ventral wall of the sac is extremely thick and approximates one-half of the diameter of the glans.

The baculum, represented by two specimens (LSUMZ 12424 and 16759—see Figure 7, *c* and *d*), is massive and relatively long (nearly four-fifths of glans length). The shaft is broad with a thickened and expanded base. The proximal two-thirds of the os penis is transversely convex dorsally

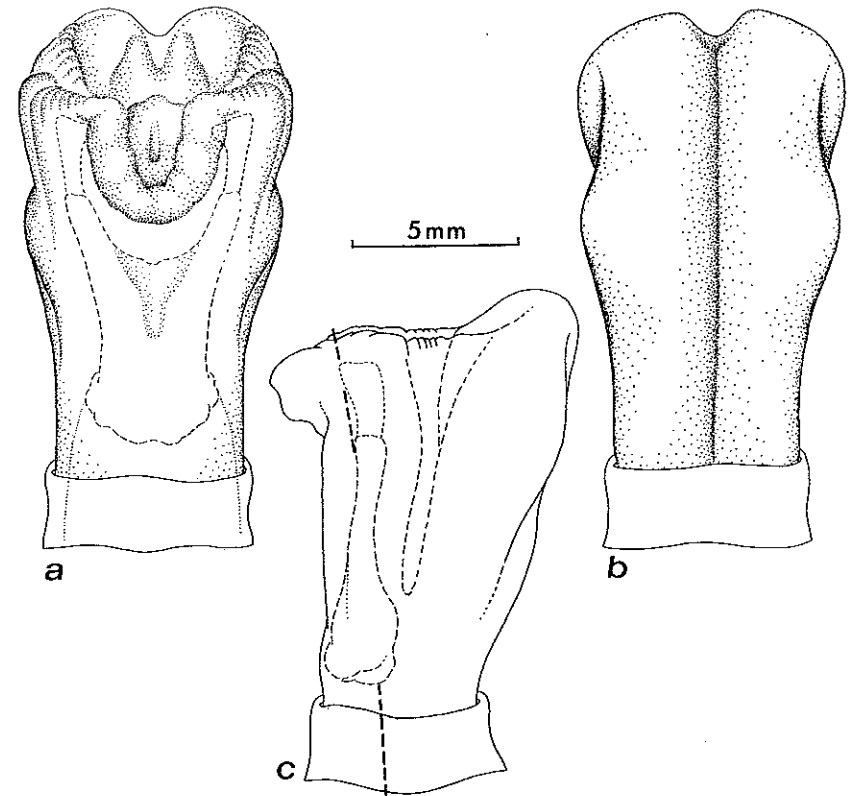


FIGURE 8. Glans penis of *Proechimys guyannensis* as viewed: *a*, dorsally; *b*, ventrally; and *c*, laterally. LSUMZ 16759, Balta, Perú. The heavy dashed line indicates the orientation of the urethra.

and deeply concave ventrally. The distal end has a pair of diverging apical extensions separated by a wide and deep median depression. Each apical bony extension or wing bears a straight cartilaginous shaft and the baculum is so situated that its distal portion nearly circumscribes the swollen, dorsally directed, urethral mound.

**Karyotype.**— $2n=40$ ;  $FN=56$  (Figure 9, a). The autosomal complement lacks group A chromosomes; includes seven pairs of medium-sized to small metacentrics and submetacentrics (B), with one pair of metacentrics minute; two pairs of moderately small subtelocentrics (C), the smallest of which bear secondary constrictions on the long arms; and three pairs of medium-sized and seven pairs of small acrocentrics (D). The X-chromosome is a moderately small acrocentric and the Y is a small acrocentric.

**Measurements.**—The mean and range for external and cranial measurements of five adults, unless otherwise noted: head and body ( $N=4$ ), 185.7 (182-193); tail ( $N=4$ ), 128.0 (124-134); hind foot ( $N=4$ ), 40.5 (38-42); ear ( $N=4$ ), 21.5 (20-23); greatest length of skull ( $N=3$ ), 47.5 (46.0-48.3); condylobasal length ( $N=3$ ), 42.6 (40.9-43.5); mastoidal breadth ( $N=3$ ), 18.4 (17.8-19.3); length of nasals, 17.2 (16.2-19.1); zygomatic breadth ( $N=3$ ), 22.9 (21.9-23.6); palatal length, 21.3 (20.2-22.9); maxillary breadth, 7.5 (7.1-8.0); alveolar length of maxillary tooth-row, 7.5 (7.3-8.0); interorbital breadth, 10.3 (9.8-10.8); length of rostrum, 18.5 (17.4-19.7).

Measurements of the baculum ( $N=2$ ): length, 7.2 (7.1-7.3); distal width, 5.3 (4.9-5.7); proximal width, 4.5 (4.1-4.8).

**Comparisons.**—The combination of small size and moderately short tail, averaging 69.3 (67.8-70.3) per cent of head and body; cinnamon brown dorsum coarsely streaked with black, especially middorsally; dark color of lower hind leg completely encircling tarsal joint; white hind feet with short hallux and weakly developed or absent lateral metatarsal plantar tubercle; absolutely, but not proportionally smaller cheek teeth; vomer absent from ventral aspect of septum of incisive foramen; weak development of palatal grooves on maxillae; narrow, deeply indented, mesopterygoid fossa, serve to distinguish this species from all other forms described herein. Skin and skull features apparently unique to *P. guyannensis*, in addition to small overall dimensions, include: hallux short, lateral metatarsal tubercle very small or absent, distance between heel and first postdigital tubercle much less than distance between first postdigital tubercle and end of third

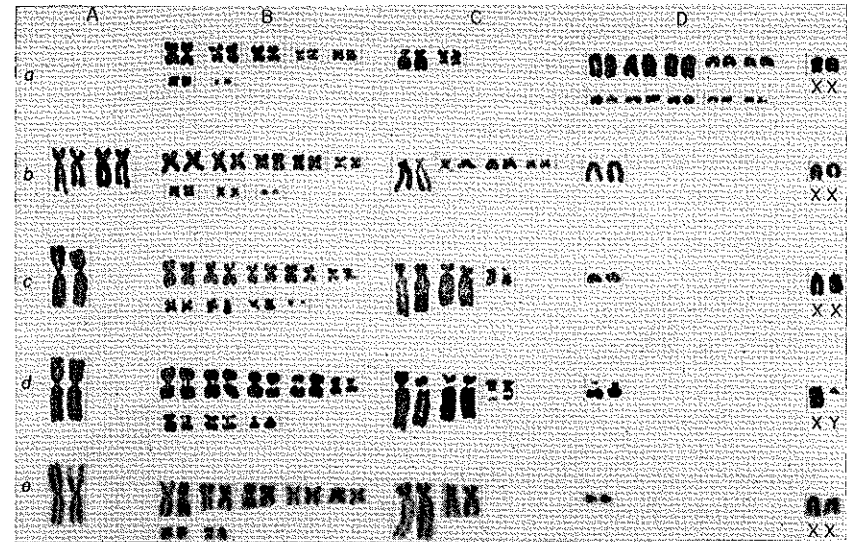


FIGURE 9. Representative karyotypes of five species of *Proechimys*: a) *P. guyannensis*,  $2n=40$ ,  $FN=56$ , Balta, Perú, LSUMZ 14425; b) *P. bendeei*,  $2n=32$ ,  $FN=58$ , Balta, Perú, LSUMZ 14426; c) *P. semispinosus*,  $2n=30$ ,  $FN=54$ , Cariari, Costa Rica, LSUMZ 13369; d) *P. longicaudatus*,  $2n=28$ ,  $FN=50$ , Tingo María, Perú, LSUMZ 14410; e) *P. brevicauda*,  $2n=24$ ,  $FN=42$ , Balta, Perú, LSUMZ 16757.

digit, comparatively small incisive foramina lacking vomerine contribution to ventral aspect of septum, and weakly developed grooves on maxillary portion of palate.

*Proechimys guyannensis* is unquestionably much smaller than any of the other species we have examined. Despite size, glandes, and karyotype differences, *P. guyannensis* is closest to the sympatric *P. bendeei* in external and cranial features. Among features shared by both species are the white hind feet and sometimes missing lateral metatarsal tubercle (*P. bendeei* occasionally has all white hind feet and always has only five plantar tubercles); the spatial relationship of the first postdigital tubercle with the heel and with the end of the third digit; the lack of the vomer in the ventral aspect of the incisive foramen septum, and the narrow and deeply indented mesopterygoid fossa. *Proechimys guyannensis* is similar to *P. brevicauda* in that both species have the tarsal joint completely ringed with the darker color of the lower leg.

The karyotype of *P. guyannensis* is unique in its high chromosome number and the lack of group A chromosomes. The glans is also unique in its stout and blunt shape, smooth surface, shallow intromittent sac, and swollen, dorsally directed, urethral mound. The baculum, while also unusual, is similar to that described and figured by Didier (1962) for his *P. guyannensis* Type I from Colombia and Guyana.

*Remarks.*—We have decided to use the name *P. guyannensis* for this form despite our conviction that *guyannensis* of most authors is composite—as was acknowledged by Ellerman (1940, for *cayennensis*) and Hershkovitz (1948). *Proechimys guyannensis* was found along with *P. breviceauda*, *P. longicaudatus*, and *P. hendeei* at Balta.

A female from Balta was pregnant with two 14-millimeter fetuses on 21 July 1968.

*Specimens examined.*—PERÚ. Departamento de Loreto: Balta, Río Curanja, 300 m, 3 males, 3 females (LSUMZ 9275, 12424, 14425\*, 14430, 14432, 16759\*).

#### DISCUSSION

Our present concern with the taxonomy of spiny rats is limited to members of the subgenus *Proechimys*. Species of the other subgenus (*Trinomys*) currently recognized in *Proechimys* are restricted in distribution to eastern Brazil (Moojen, 1948; Cabrera, 1961).

Oldfield Thomas relied upon color pattern and cranial features, particularly the development of cranial ridges, the configuration of the incisive foramina, and the length and shape of the hamular process of the pterygoids, to distinguish between the forms he recognized. Ellerman (1940), considering the majority of these features to be reflections of age and individual variation, tentatively recognized only twelve species out of the approximately 50 forms that had been named up to that time, and included ten of the species (one an *Echimys* as pointed out by Hershkovitz, 1948:129) under the subgenus *Proechimys*. Hershkovitz (1948), relying primarily upon the number of enamel folds in the cheek teeth, placed the previously named forms in the subgenus *Proechimys* in six species (*canicollis*, *iberingi*, *hendeei*, *dimidiatus*, *guyannensis*, and *ignotus*) and described a seventh, *P. quadruplicatus*. Moojen (1948) used a combination of pelage and dental features (principally the development of aristiforms and the counterfold patterns)

to characterize the five species (*guyannensis*, *longicaudatus*, *semispinosus*, *goeldii*, and *canicollis*) he recognized in the subgenus *Proechimys*. Moojen did not treat *P. quadruplicatus*; however, he did expand the subgenus *Trinomys* to include *iberingi* and *dimidiatus*. Cabrera (1961), largely following Moojen, recognized seven species (*canicollis*, *goeldii*, *guyannensis*, *hendeei*, *longicaudatus*, *quadruplicatus*, and *semispinosus*) under *Proechimys* (*sensu stricto*). Didier (1962) reported on bacula from a number of caviomorph rodents identified and sent to him by Philip Hershkovitz of the Field Museum. *Proechimys* was represented among these by bacula from five species (*guyannensis*, *quadruplicatus*, *hendeei*, *canicollis*, and *albispinus*—the last representing the subgenus *Trinomys*). Didier, attempting to coordinate his findings with Hershkovitz's identifications, reached the following conclusions: *P. guyannensis guyannensis* was represented by four distinct bacular types; the bacula of *P. breviceauda*, *P. trinitatis*, and *P. oris* were essentially alike and, while superficially similar to the Type III baculum of *P. g. guyannensis*, were different from all others in his sample; the baculum of *P. quadruplicatus*, although distinct, was somewhat similar to the shorter Type IV baculum of *P. g. guyannensis*; and the bacular types of *P. mincae*, *P. hendeei*, and *P. canicollis* were each unique. Only one of the four penises of *P. (Trinomys) albispinus* he examined contained a baculum—a minute bone imbedded in cartilage and lacking distinctive features.

Martin (1970) included descriptions and figures of the types of bacula he found in his study of the morphological variation in several population samples of *Proechimys*; however, he was unaware of Didier's important paper. Martin recognized four species (*guyannensis*, *canicollis*, *quadruplicatus*, and *steerei*) from the samples he studied and concluded that the specific status of several forms, particularly of *P. guyannensis* and *P. longicaudatus*, remained unresolved.

Separation of the morphological forms represented in our samples of *Proechimys* was initiated on the basis of the five different karyotypes we found. Subsequently, we discovered a number of color pattern peculiarities and morphological features characterizing each form that permitted the assignment of specimens not represented by chromosomal data to karyotype groups. Nonchromosomal features other than size that have proven valuable for distinguishing the forms in our relatively small and admittedly limited representation of the genus are the color patterns, the configuration of the plantar surfaces of the hind feet, the shape of the incisive foramina and the composition of their septum, the shape and depth of the mesopterygoid

fossa, the development of parietal ridges, the configuration of the paroccipital processes, and the size, shape, and surface features of the glands and bacula.

Features of the aristiforms and the counterfold patterns of the cheek teeth, two characters utilized by Hershkovitz (1948) and Moojen (1948), were not very helpful in distinguishing among our specimens. These characters might have proven useful had more species of *Proechimys* been represented in our material. Nevertheless, by applying Hershkovitz's (1948:130) key to our specimens we would assign all of our 32 *P. longicaudatus*, 5 *P. semispinosus*, and 6 *P. guyannensis* to his *P. guyannensis* along with 8 of our 11 *P. brevicauda*. Two of the three remaining *P. brevicauda* (the third is a skin only) would be assigned to his *P. quadruplicatus*, and all of our *P. hendeei* would correspond to his *P. hendeei*. On the other hand, by relying on Moojen's (1948:334) key we would make the following identifications of our specimens: all 6 *P. guyannensis*, 29 of the 32 *longicaudatus*, 10 of the 17 *P. hendeei*, and 2 of the 11 *P. brevicauda* assigned to *P. longicaudatus*; 3 *P. longicaudatus*, 4 *P. brevicauda*, and 6 *P. hendeei* assigned to *P. goeldii*; 1 *P. hendeei*, 3 *P. brevicauda*, and 3 *P. semispinosus* assigned to *P. semispinosus*; and 2 *P. semispinosus* assigned to *P. guyannensis*.

Didier's (1962) and Martin's (1970) data support our view that the majority of species of *Proechimys* are poorly diagnosed and that several, as currently understood, are composite. The finding of four superficially similar species at Balta bears out with surprising force Hershkovitz's (1948:139) cautioning remark that, when making comparisons, "Reliance cannot be placed upon 'topotypes,' or even 'paratypes,' . . . as two or more species of very similar appearing spiny rats may occur in the same locality."

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