Species Groups of Spiny Rats, Genus *Proechimys* (Rodentia: Echimyidae)

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ABSTRACTS

Nine species groups of the spiny rat subgenus *Proechimys,* family Echimyidae, are defined on the basis of bacular characters and qualitative features of the cranium. The latter include the structure of the incisive and mesopterygoid foramina, temporal ridge and infraorbital canal development, and counterfold pattern of the cheekteeth.

Three groups are apparently monotypic, including the *decumanus*-group of southwestern Ecuador and adjacent Peru, the *canicollis*-group of northeastern Colombia and adjacent Venezuela, and the *simonsi*-group of the western Amazon Basin from Colombia to northern Bolivia. The remaining six groups are polytypic, but the number of species in each remains unclear. The *semispinosus*-group ranges from Central America south to southwestern Ecuador in the Pacific lowlands; its only Amazonian representative is *P. oconnelli* from east-central Colombia. The *longicaudatus*-group ranges from southeastern Colombia through the western Amazon Basin into the northern Paraná Basin of Brazil and northern Paraguay. The *goeldii*-group ranges throughout the Amazon Basin from eastern Peru to eastern Brazil. The *guyannensis*-group occurs from the coastal Guianan region through the Río Negro and eastern half of the Amazon Basin in Brazil, with an isolate in Goiás and Minas Gerais states. The *cuvieri*-group has a similar distribution, but extends further up the Amazon into northern Peru, with one isolate in east-central Peru. Finally, the *trinitatus*-group is found from north-central Colombia eastward across northern Venezuela to Trinidad.

Nueve grupos de especies de la rata espinosa subgénero *Proechimys,* familia Echimyidae, son definidos primariamente en las bases de caracteres baculares que son soportados por razgos cualitativos del cráneo. El último incluye la estructura del foramen incisivo y mesopterigoideo, arista temporal y desarrollo del canal infraorbital y patrón de contraplegamiento de los dientes postcaninos.

Tres grupos son aparentemente monotípicos, incluyendo el grupo *decumanus* del suroccidente del Ecuador y adyacente Perú, el grupo *canicollis* del nororiente de Colombia y adyacente Venezuela, y el grupo *simonsi* del occidente de la cuenca amazónica desde Colombia hasta el norte de Bolivia. Los seis grupos remanentes son politípicos, pero el número de especies en cada uno permanece obscuro. El grupo *semispinosus* se extiende desde el sur de Centroamérica hasta el suroccidente ecuatoriano en las tierras bajas del Pacífico; su solo representante de la cuenca amazónica el *P. oconnelli* del centroriente colombiano. El grupo *longicaudatus* se distribuye desde el suroriente de Colombia a través del occidente de la cuenca amazónica hasta el norte de la cuenca del Paraná en Brazil y norte de Paraguay. El grupo *goeldii* se distribuye a través de la cuenca amazónica desde el Perú oriental hasta el Brazil oriental. El grupo *guyannensis* ocurre desde la región costera guayanesa a través de río Negro y la mitad oriental de la cuenca amazónica en Brazil, con un aislamiento de poblaciones en los estados de Goiás

y Minas Gerais. El grupo *cuvieri* tiene una distribución similar, pero se extiende más arriba del Amazonas en el interior del norte del Perú, con un aislamiento de poblaciones en el centroriente peruano. Finalmente, el grupo *trinitatus* es encontrado desde el centronorte de Colombia hacia el oriente a través del norte de Venezuela hasta Trinidad.

Nove grupos de espécies de ratos-de-espinho, do subgênero *Proechimys,* família Echimyidae, são definidos principalmente na base de caráteres baculares que concordam também com carácteres qualitativos do crânio. Estes incluem: a estrutura dos incisivos e do fôrame mesopterigóideo, o desenvolvimento das têmporas e do canal infraorbital, e o padrão dos molares.

Três grupos são aparentemente monotípicos, incluindo o grupo *decumanus* do sudoeste do Equador, o grupo *canicollis* do nordeste da Colombia e das áreas adjacentes na Venezuela, e o grupo *simonsi* da Bacia Amazônica ocidental, desde a Colombia até o norte da Bolívia. Os seis grupos restantes são politípicos, mas o número de espécies em cada continua incerto. O grupo *semispinosus* estende-se da America Central ao sudoeste do Equador, nas planícies do Pacífico. Seu único representante na Bacia Amazônica é *P. oconnelli,* do Centro-leste da Colombia. O grupo *longicaudatus* estende-se do sudeste da Colombia, através da Amazonia ocidental, até o norte da Bacia do Paraná no Brasil e no norte do Paraguai. O grupo *goeldii* ocorre na Bacia Amazônica, do leste do Peru ao leste do Brasil. O grupo *guyannensis* ocorre da costa guianense, até o Rio Negro e à região oriental da Bacia Amazônica no Brasil, com uma espécie isolada nos estados de Goiás e de Minas Gerais. A distribuição do grupo *cuvieri* é parecida, mas este ocorre também até o norte do Perú, com uma espécie isolada no centro-leste do País. Por final, o grupo *trinitatus* é encontrado do centro-norte da Colombia, através da Venezuela, até Trinidade.

Introduction

Spiny rats of the genus *Proechimys* represent one of the most diverse groups of Neotropical rodents; with the possible exception of tuco-tucos, *Ctenomys,* the number of taxa of spiny rats is unmatched by any other caviomorph (Woods, 1984). The genus extends throughout lowland forests from Nicaragua to northern Paraguay and the coastal regions of Brazil. Despite this diversity and large geographic range, however, the group is taxonomically one of the most poorly understood among all of the Neotropical mammals. Only a few studies have succeeded in recognizing the number of taxa sympatric at any single locality (e.g., Moojen, 1948; Patton & Gardner, 1972), and no study has been able to follow geographic character trends within a clearly defined taxon over any but the shortest distances. Diagnosis of species and hence definition of natural units in *Proechimys* have been severely hampered by the often extreme level of variability within and between populations for most morphological characters that have been examined (Moojen, 1948; Hershkovitz, 1948; Patton & Gardner, 1972). Even karyotypes, which have proven useful in differentiating sympatric taxa of spiny rats (Patton & Gardner, 1972), are often highly variable geographically (Reig & Useche, 1976; Reig et al., 1980; Gardner & Emmons, 1984).

In this report I will challenge some of these precepts of character instability (see Thomas, 1928, p. 262) by using the structure of the baculum and specific characters of the cranium to define major taxonomic groups of spiny rats. Taxa can be diagnosed, despite both within- and between-population variation, and the patterns of character variation over geography are coherent, permitting a consistent view of these taxa throughout their range. Some of the more traditional characters that have been used to make taxonomic decisions in spiny rats (e.g., counterfold patterns on the cheekteeth) are not chaotic in their variation patterns, but are quite helpful in defining units.

This paper will consider only members of the subgenus *Proechimys,* excluding entirely the group of species found along the Atlantic highlands of Brazil that compose the subgenus *Trinomys.*

Species Groups of *Proechimys*

In the section below I provide the basic species groups of spiny rats, subgenus *Proechimys,* listing
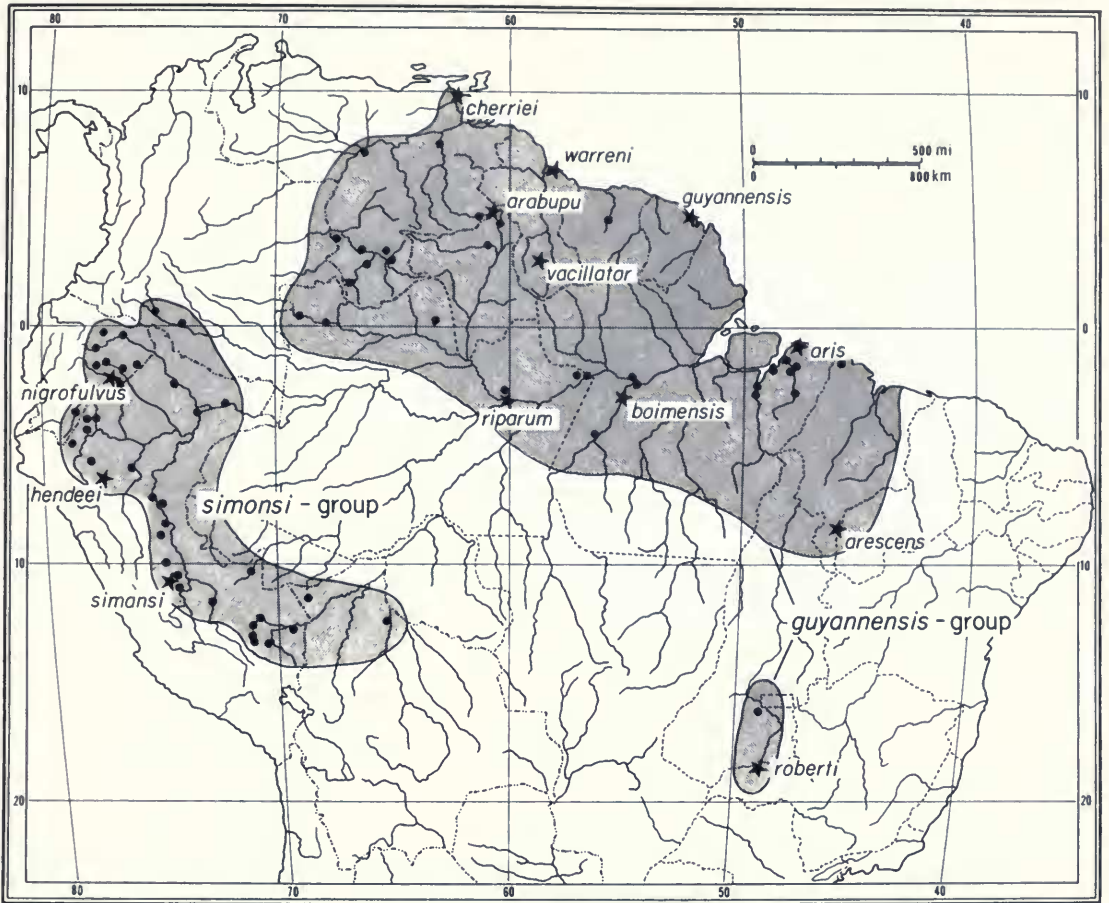
Fig. 1. Geographic distribution of taxa of the *simonsi*- and *guyannensis*-groups. Type localities for each included taxon are indicated by stars; dots represent other localities listed in the Appendix.

those named forms I consider as component parts. In recognizing these groups and their membership I make no conclusions here as to the specific, sub-specific, or other status of these names. Because of the plethora of names available and the con-fusion with which each has been applied to the genus over the past century, this synopsis is pro-vided first to allow for coherent discussion; the documentation upon which these decisions are based follows.

I recognize nine species groups within the sub-genus *Proechimys*. Five of these are widespread, while the remaining ones are more restricted in their ranges. Maps of the distribution of each group, with localities of included holotypes, are presented in Figures 1–4 (see Specimens Examined for lists of localities). Unless otherwise stated, allocation of any given holotype to a specific species-group is based on my examination of that specimen. The

groups are defined by a combination of palatal (particularly incisive foramina and mesopterygoid fossa) characters, counterfold patterns of the cheekteeth, temporal ridge development, infraor-bital notch development, and bacular characters (see below). In each case, the group name is taken from the oldest assignable name for that unit.

guyannensis-group

Named forms in this group include:

> guyannensis (E. Geoffroy, 1803)
> cherriei Thomas, 1899
> roberti Thomas, 1901
> vacillator Thomas, 1903
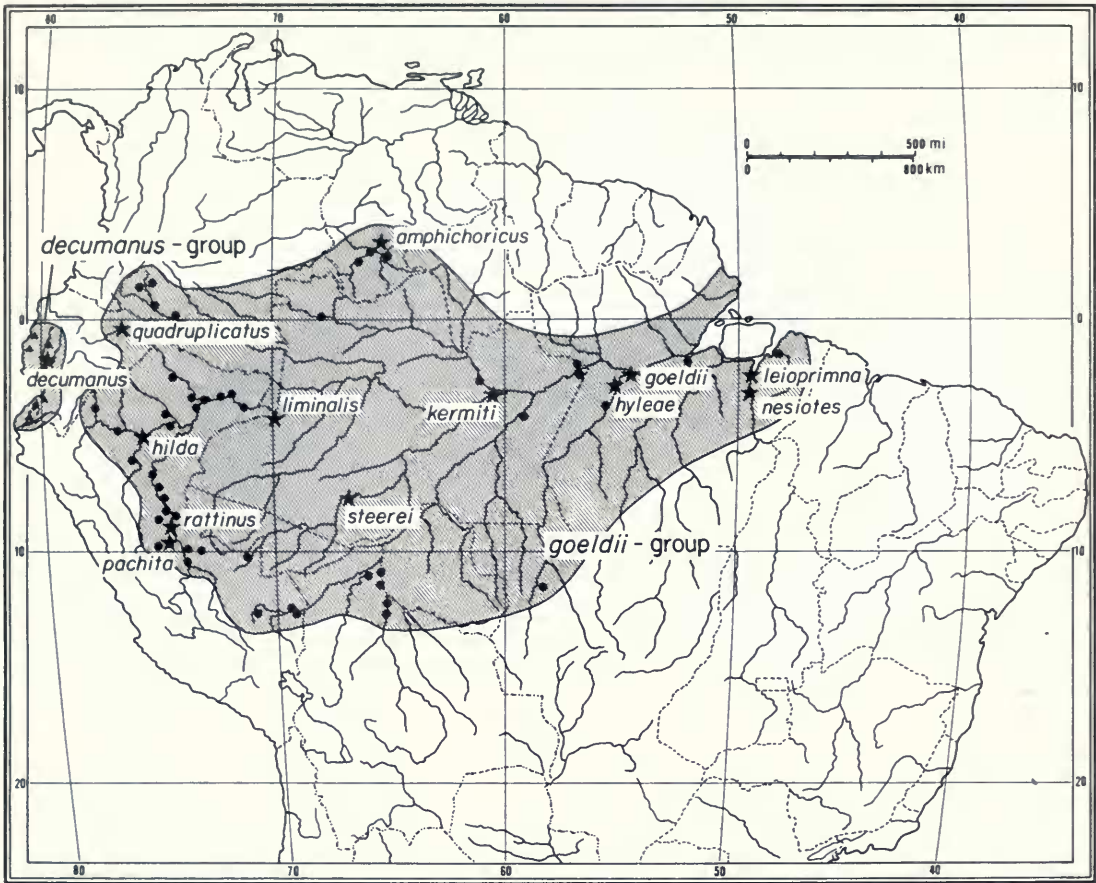> oris Thomas, 1904
> warreni Thomas, 1905

Fig. 2. Geographic distribution of taxa of the *goeldii*-group (dots) and *decumanus*-group (triangles). Type localities of taxa are indicated by stars.

boimensis Allen, 1916
arescens Osgood, 1944
riparum Moojen, 1948
arabupu Moojen, 1948

COMMENTS—On the basis of septal patterns in the bullae, Gardner and Emmons (1984) included these taxa in their *brevicauda*-group, an all-inclusive unit combining taxa that are here allocated to six separate groups. As will be apparent below, my *guyannensis*-group only shows close similarity to the taxa included in the *simonsi*-group. Members of these two groups share virtually no characters with the remaining taxa listed by Gardner and Emmons (1984) in their *brevicauda*-group.

This group is confined in its distribution to the Guianan region and southern Venezuela through the central Amazon Basin of Brazil, with an isolate (*roberti*) in Minas Gerais and Goiás states in Brazil (see map, fig. 1). It is sympatric with members of

the *cuvieri*-group in the Guianan region (see Petter, 1978) and with those of both the *cuvieri*- and *goeldii*-groups in the central Amazon Basin.

goeldii-group

Included are the following named forms:

goeldii Thomas, 1905
steerei Goldman, 1911
kermiti Allen, 1915
pachita Thomas, 1923
hilda Thomas, 1924
rattinus Thomas, 1926
quadruplicatus Hershkovitz, 1948
liminalis Moojen, 1948
amphichoricus Moojen, 1948
hyleae Moojen, 1948
nesiotes Moojen, 1948
leioprimna Moojen, 1948

COMMENTS—I have not examined the holotypes of *liminalis* Moojen or *hyleae* Moojen; their inclusion here is based on the original descriptions (Moojen, 1948).

This group is distributed throughout the Amazon Basin, from the most western margins in northern Bolivia, eastern Peru, Ecuador, and southeastern Colombia to southern Venezuela east along the central Amazon to the lower Rio Tapajós in Pará state, Brazil (see map, fig. 2). Members of this group are sympatric with those of the *guyannensis*-group and *cuvieri*-group in the central and eastern Amazon Basin, and with those of the *cuvieri*-, *longicaudatus*-, and *simonsi*-groups in the western parts of the Basin.

longicaudatus-group

Named forms in this group include:

> *longicaudatus* (Rengger, 1830)
> *brevicauda* (Gunther, 1877)
> *boliviensis* Thomas, 1901
> *securus* Thomas, 1902
> *gularis* Thomas, 1911
> *leucomystax* Ribeiro, 1914
> *elassopus* Osgood, 1944
> *villacauda* Moojen, 1948
> *ribeiroi* Moojen, 1948

COMMENTS—The taxa *leucomystax* Ribeiro, *villacauda* Moojen, and *ribeiroi* Moojen are included on the basis of descriptions given in Moojen (1948); I have not examined the holotypes.

The *longicaudatus*-group is confined to the western and southwestern parts of the Amazon Basin and northern Paraná Basin, from northern Paraguay and adjacent Brazil west and northwest through Bolivia, eastern Peru, eastern Ecuador, and southeastern Colombia (see map, fig. 3). In this region it is sympatric with members of the *goeldii*-, *cuvieri*-, and *simonsi*-groups.

simonsi-group

Included members are:

> *simonsi* Thomas, 1900
> *hendeei* Thomas, 1926
> *nigrofulvus* Osgood, 1944

COMMENTS—This is perhaps the most readily recognizable of all groups of *Proechimys*; the level of differences with sympatric taxa of the *goeldii*-, *longicaudatus*-, or *cuvieri*-groups is geographically consistent and quite sharp.

The *simonsi*-group is geographically restricted to the western margins of the Amazon Basin from northern Bolivia through eastern Peru and Ecuador to southeastern Colombia (see map, fig. 1). In this region, it ranges to higher elevations than any other species in the genus, occurring as high as 2000 m.

cuvieri-group

This group includes only the nominate form:

> *cuvieri* Petter, 1978

COMMENTS—Specimens assigned to this species are relatively few in number and are known from localities scattered from the coastal Guianan region and along the Amazon River from near its mouth to northern Peru (see map, fig. 4). In the Guianas, *cuvieri* is sympatric with *guyannensis*; in central Brazil, with *guyannensis*- and *goeldii*-group taxa; and in northern Peru, with *simonsi*-, *longicaudatus*-, and *goeldii*-group members. Despite the paucity of widely scattered locality records, these specimens share common bacular, palatal, counterfold, and karyotypic characters, the former being particularly divergent from other taxa in the genus *Proechimys*.

Because of similar bacular (but not karyotypic) features, the form from eastern Peru referred to *P. guyannensis* by Patton and Gardner (1972) is included here. This form is an enigma at the moment, and its placement must be considered provisional; it is not known with certainty from any locality other than Balta, Río Curanja, Ucayali, Peru (see map, fig. 4, and Patton & Gardner, 1972). Gardner and Emmons (1984) consider it closely related to *P. guyannensis,* perhaps even conspecific, but it does not share bacular or incisive foraminal characters with members of that group (see below).

trinitatus-group

Named forms in this group include:

> *trinitatus* (Allen and Chapman, 1893)
> *chrysaeolus* (Thomas, 1898)
> *mincae* (Allen, 1899)
> *urichi* (Allen, 1899)

FIG. 3. Geographic distribution of taxa of the *longicaudatus*-group (dots) and *trinitatus*-group (triangles). Type localities are indicated by stars.

guairae Thomas, 1901
ochraceous Osgood, 1912
poliopus Osgood, 1914
hoplomyoides Tate, 1939
magdalenae Hershkovitz, 1948

COMMENTS—Gardner and Emmons (1984) included *magdalenae* in their *brevicauda*-group and *chrysaeolus* in their *semispinosus*-group based on similarities of bullar septal patterns. Bacular and other characters, however, align these two taxa with others of the *trinitatus*-group as here defined. This group includes all members referred to as the "*guairae* complex" by Reig and co-workers, based on karyotypic data (see Benado et al., 1979; Reig et al., 1980; Reig, 1981), or as the *guairae*-group by Gardner and Emmons (1984).

Members of this group are distributed across northern South America, from Trinidad through the coastal mountains and upper llanos of Vene-zuela and Colombia, and including the isolated northern Andean valleys of Colombia (see map, fig. 3). Only *hoplomyoides* occurs south of the Río Orinoco in southeastern and southern Venezuela (see Gardner & Emmons, 1984). The included taxa are largely allopatric, or parapatric (see Reig et al., 1980; Reig, 1981), and are separated by rivers (upper llanos of Venezuela) or mountain ridges (northwestern Venezuela and northern Colombia). Sympatric contact between members of this group and other *Proechimys* occurs in several areas in northern Colombia: *chrysaeolus* with *semispinosus* and both *chrysaeolus* and *mincae* with *cani-collis*.

semispinosus-group

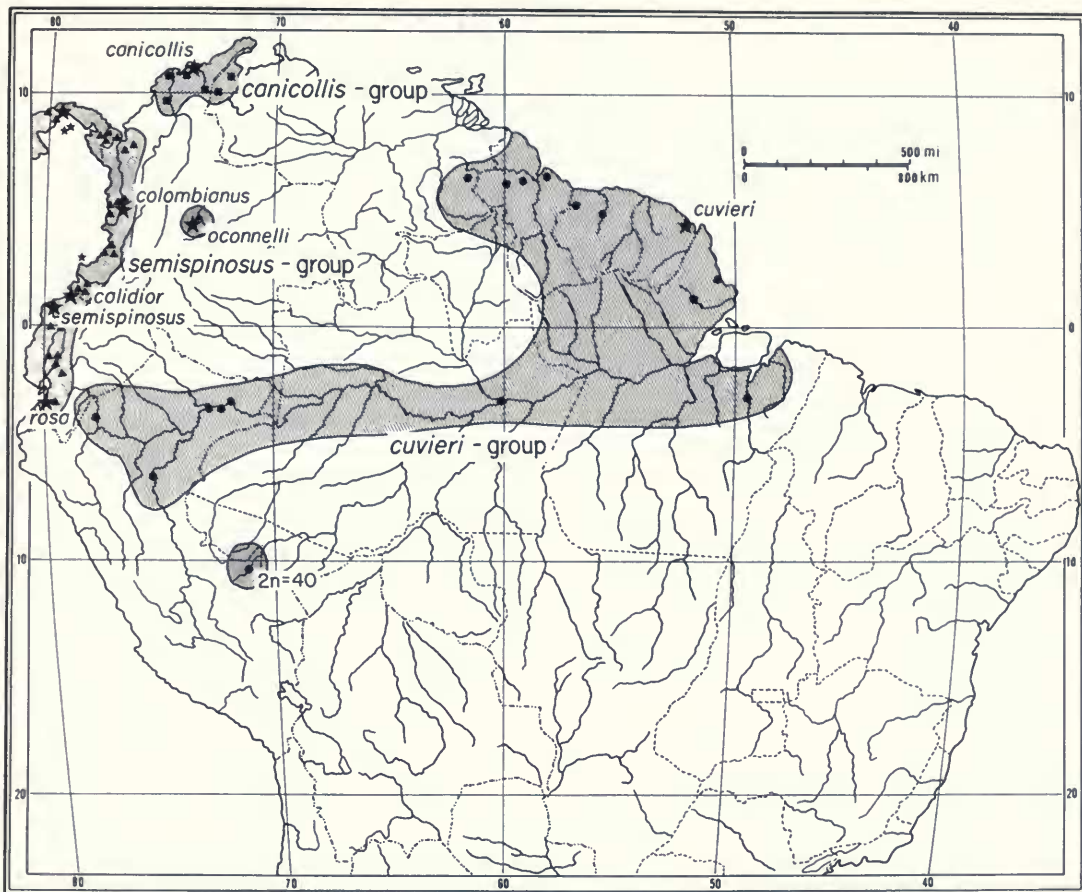Membership in this group includes the following named forms:

FIG. 4. Geographic distribution of taxa of the *cuvieri*-group (dots), *semispinosus*-group (triangles), and *canicollis*-group (squares). Type localities are indicated by stars.

semispinosus (Tomes, 1860)
centralis (Thomas, 1896)
rosa Thomas, 1900
chiriquinus Thomas, 1900
panamensis Thomas, 1900
burrus Bangs, 1901
gorgonae Bangs, 1905
calidior Thomas, 1911
oconnelli Allen, 1913
rubellus Hollister, 1914
colombianus Thomas, 1914
goldmani Bole, 1937
ignotus Kellogg, 1946

COMMENTS—Gardner (1983) reviewed the membership, distribution, and taxonomic history of this species group, and I concur with him. Gardner and Emmons (1984) expanded the group to include *oconnelli* and *chrysaeolus* based on common bullar septal patterns. I treat *oconnelli* as a component part of the *semispinosus*-group, but place *chrysaeolus* in the *trinitatus*-group based on bacular, palatal, and counterfold patterns (see below).

Members of the *semispinosus*-group are largely restricted in distribution to Central America and the Pacific lowlands of Colombia and Ecuador (see map, fig. 4). The only Amazonian representative is *oconnelli*, which is restricted to the limited area of Villavicencio in east-central Colombia, midway between the northernmost distributional extensions of members of the *goeldii*-, *simonsi*-, and *longicaudatus*-groups and the westernmost extension of the *trinitatus*-group.

canicollis-group

This group is limited to the nominate species:

canicollis (Allen, 1899)

COMMENTS—The species *P. canicollis* is one of the more readily recognizable in the entire genus *Proechimys* (see below), although on the basis of bullar septal patterns, Gardner and Emmons (1984) included it within their *brevicauda*-group. It is limited in its distribution to the coastal forested foothills from northern Bolívar, Colombia, to northwestern Zulia, Venezuela (see map, fig. 4). It is sympatric with *mincae* and *chrysaeolus* of the *trinitatus*-group.

decumanus-group

This group includes only the nominate species:

decumanus (Thomas, 1899)

COMMENTS—I consider this taxon to represent a separate species group, although Gardner and Emmons (1984) placed it in their *brevicauda*-group based on bullar septal patterns and karyotypic similarities. It is, however, readily distinguishable on external, palatal, and bacular grounds from other members of that group.

Proechimys decumanus is restricted to the Pacific lowland forests of extreme southwestern Ecuador and adjacent northwestern Peru (see map, fig. 2), where it is sympatric with the named form *rosa* of the *semispinosus*-group.

Bacular Structure and Characteristics

Didier (1962) described and figured bacular variants of echimyid rodents, with an emphasis on variation within the genus *Proechimys*. Bacular variants of *Proechimys* were also described by Martin (1970) and Patton and Gardner (1972). In the latter paper, bacular characters and karyotypes permitted the delineation of taxa sympatric at several localities in eastern Peru, suggesting that such structures could be of use in distinguishing taxa within the genus as a whole. Didier's (1962) material and the names he used were supplied by Philip Hershkovitz, from specimens in Field Museum collections. I have examined each of the bacula discussed by Didier, as well as the associated skulls and skins. Below, as I describe bacular variation in the context of the species groups recognized in this report, I will emend Didier's groupings according to this reexamination of materials.

A basic bacular type characterizes most species

in the genus *Proechimys,* as well as other echimyid genera, despite differences in overall size. This baculum is an elongated, narrow structure, with a rather rounded and broadened base and a shaft tapering distally. The distal tip shows only a weakly developed median depression, if any at all. This bacular type is characteristic of the dactylomyine genera *Thrinacodus, Kannabateomys,* and *Dactylomys,* species in the genera *Echimys, Makalata, Mesomys, Diplomys,* and *Isothrix* (see Didier, 1962; Patton & Emmons, 1985), and most species of *Proechimys.* It is also characteristic of most other caviomorphs examined to date (e.g., *Cavia, Abrocoma, Ctenomys, Agouti, Dasyprocta* [Didier, 1962; Hooper, 1961]). There are, however, both subtle as well as more marked differences among bacula of this general form, and these will be detailed below in the discussion of variation in *Proechimys.*

Overall size of the baculum of *Proechimys* depends strongly on age, although age does not noticeably affect shape. Hence, in the descriptions and summarized measurements given below, analyses are restricted to those individuals considered adults on the basis of tooth wear patterns (age classes 8 through 10 of Patton & Rogers, 1983). Bacula of each species group of *Proechimys* are illustrated in Figures 5–11, and measurements for geographic representatives of each group are summarized in Table 1. Figure 12 illustrates differences among the species groups in proportions of length and width. It is clear from this figure that there are two major classes of bacular variants in the subgenus *Proechimys.* Members of the *guyannensis*-, *simonsi*-, *trinitatus*-, *goeldii*-, *decumanus*-, and *canicollis*-groups have long and narrow bacula (despite differences in relative size and other characters), while taxa of the *semispinosus*-, *cuvieri*-, and *longicaudatus*-groups have massively long and broad bacula with well-developed distal apical wings or extensions.

guyannensis-group (Figure 5a–g)

Despite Didier's (1962) use of the name *guyannensis,* no specimen he examined can be referred to this group as defined here or as recognized by Gardner and Emmons (1984). The four bacular types Didier (1962, pp. 408–415) referred to *Proechimys guyannensis* in fact represent members of five different species groups, as follows: Type I (part *semispinosus*-group, part *cuvieri*-group), Type II (*longicaudatus*-group), Type III (*P.*
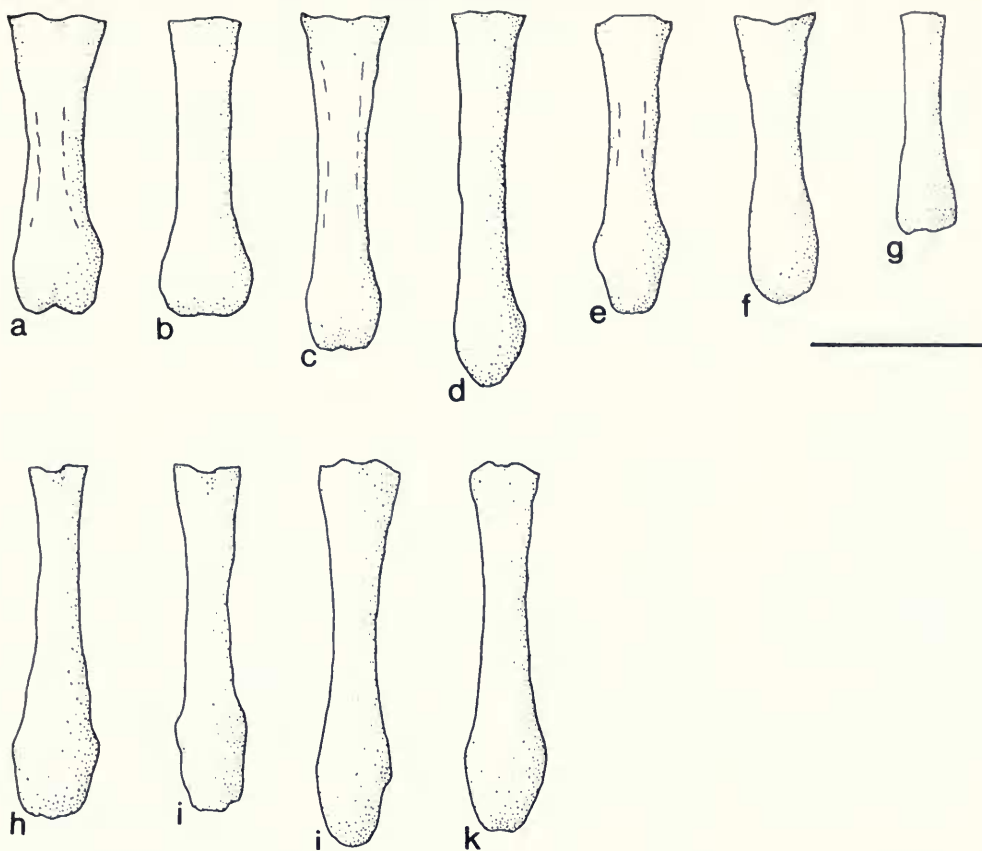
Fig. 5. Representative bacula of members of the *guyannensis*-group (a–g) and the *simonsi*-group (h–k); scale = 5 mm. **a,** BM[NH] 52.1124—Suriname: Zanderig. **b,** FMNH 95726—Suriname: Brokopando; Saramacca River, Loksie Hatti. **c,** AMNH 75803—Venezuela: Bolivár; Arabupu, Mt. Roraima (topotype of *arabupu* Moojen). **d,** AMNH 75451—Brazil: Roraima; Rio Cotingo, Limão. **e,** USNM 554847—Brazil: Amazonas; 72 km N Manaus. **f,** USNM 555653—Brazil: Pará; Altar da Chao, Rio Tapajós. **g,** BM[NH] 1.11.3.64—Brazil: Minas Gerais; Araguay, Rio Jordão (topotype of *roberti* Thomas). **h,** AMNH 71866—Peru: Loreto; Boca Río Curaray. **i,** USNM 461305—Peru: Ucayali; 59 km W Pucallpa. **j,** AMNH 213487—Peru: Pasco; Bermudas de Loma Linda. **k,** FMNH 84261—Peru: Madre de Dios; Itahuanía.

chrysaeolus of the *trinitatus*-group), and Type IV (part *goeldii*-group and part *semispinosus*-group).

The baculum is relatively long and narrow, averaging in adult specimens nearly 8 mm long and approximately 2 mm wide at both the proximal and distal extremities (see fig. 5a–g; table 1). The shaft is rather straight, with little dorsoventral curvature and only slightly tapered lateral indentations near mid-shaft. The proximal end is usually evenly rounded and paddle-shaped, although samples from every examined locality include bacula with a basal median notch of varying depth. The distal tip shows only slight development of apical wings and a moderate median depression. Except for topotypes of *P. roberti* from Minas Gerais, Brazil, there is no demonstrable geographic variation in length and width measurements among bacula

of the same age class from different geographic regions (see table 1). The few bacula examined of *P. roberti* are smaller in length and width relative to others of the group. However, *roberti* is a rather small animal (see Thomas, 1901), and the proportions of its baculum are similar to those of other members of the group (see fig. 12).

simonsi-group (Figure 5h–k)

Bacula of specimens referred to this group were described and figured by Didier (1962, pp. 416–417, 419, 422) as *Proechimys guyannensis brevicauda* and *P. hendeei*, and by Patton and Gardner (1972) as *P. hendeei*. Didier's supposed specimen of *guyannensis brevicauda* (FMNH 62095) is clearly

TABLE 1. Measurements of length, distal width, and proximal width of bacula (mean ± SD) of spiny rats, subgenus *Proechimys*. Data are presented only for adult individuals (age classes 8 through 10 of Patton & Rogers, 1983).

Species group/ region or taxon	Age	N	Length	Distal width	Proximal width
guyannensis-group					
Venezuela	8	2	6.38 ± 1.21	1.99 ± 0.12	2.17 ± 0.60
Guianas	8	8	7.44 ± 0.85	2.00 ± 0.30	2.06 ± 0.41
	9	12	8.09 ± 0.58	2.17 ± 0.35	1.94 ± 0.51
	10	9	8.87 ± 1.04	2.38 ± 0.36	1.83 ± 0.32
Central Brazil	8	8	6.81 ± 1.45	1.89 ± 0.23	1.87 ± 0.39
	9	4	6.91 ± 1.35	2.28 ± 0.18	2.29 ± 0.31
	10	4	8.12 ± 0.86	2.16 ± 0.16	2.37 ± 0.24
Southern Brazil	8	1	6.08	1.28	1.74
[*roberti*]	10	1	5.43	1.79	2.27
goeldii-group					
Colombia–Bolivia	8	24	7.21 ± 1.05	2.46 ± 0.41	2.45 ± 0.43
	9	31	7.11 ± 1.18	2.79 ± 0.45	2.57 ± 0.41
	10	21	8.17 ± 1.02	3.11 ± 0.42	2.93 ± 0.45
Venezuela–Brazil	8	5	6.58 ± 1.01	2.08 ± 0.20	2.06 ± 0.44
	9	9	7.44 ± 0.55	2.36 ± 0.44	2.58 ± 0.47
	10	3	8.36 ± 0.81	2.48 ± 0.68	2.62 ± 0.20
longicaudatus-group					
Colombia–Northern Peru	8	33	10.81 ± 1.73	5.13 ± 0.76	4.28 ± 0.62
	9	18	11.43 ± 1.61	5.75 ± 0.80	4.68 ± 0.69
	10	11	11.67 ± 1.90	5.87 ± 1.02	5.12 ± 0.87
Central Peru	8	8	7.79 ± 0.65	4.57 ± 0.55	3.72 ± 0.92
	9	11	9.30 ± 1.25	4.61 ± 0.45	4.10 ± 0.80
	10	7	10.11 ± 0.66	5.02 ± 0.68	4.08 ± 0.63
Southern Peru–Bolivia	8	4	8.66 ± 1.45	4.85 ± 0.50	4.41 ± 0.55
	9	6	9.60 ± 1.12	4.74 ± 0.79	4.46 ± 0.62
SE Bolivia–Brazil	8	2	10.17 ± 0.84	5.22 ± 0.82	4.43 ± 0.72
	9	2	11.01 ± 0.49	5.13 ± 0.40	3.20 ± 0.30
	10	4	11.08 ± 1.02	5.10 ± 0.32	5.02 ± 0.47
cuvieri-group					
Guianas	8	7	6.27 ± 0.49	5.51 ± 0.56	5.30 ± 0.50
	9	6	7.21 ± 0.84	5.94 ± 0.82	5.72 ± 0.84
	10	6	8.61 ± 0.80	7.09 ± 0.45	6.70 ± 0.58
Central Brazil	8	3	5.95 ± 1.29	5.18 ± 1.24	4.69 ± 1.08
	9	3	7.26 ± 0.41	6.02 ± 0.54	5.54 ± 0.45
	10	2	8.09 ± 1.45	6.14 ± 1.39	5.31 ± 1.05
Northern Peru	8	5	6.13 ± 0.85	5.82 ± 0.74	5.38 ± 0.50
	9	3	6.96 ± 0.45	6.88 ± 1.29	6.29 ± 0.45
	10	3	7.41 ± 0.75	7.40 ± 0.05	6.53 ± 0.49
2n = 40, Balta	8	1	7.27	5.76	4.45
	9	1	7.39	4.99	4.71
simonsi-group	8	8	8.42 ± 1.44	1.51 ± 0.21	1.93 ± 0.23
	9	11	9.02 ± 1.06	1.89 ± 0.38	2.05 ± 0.27
	10	11	10.09 ± 1.18	1.77 ± 0.22	2.50 ± 0.32
semispinosus-group					
semispinosus	8	9	8.54 ± 0.95	5.11 ± 0.91	4.21 ± 1.11
	9	11	9.16 ± 1.26	6.11 ± 0.67	4.67 ± 0.54
	10	9	9.66 ± 1.01	6.19 ± 0.31	4.94 ± 0.67
oconnelli	9	1	8.43	5.26	4.94
	10	1	8.16	4.63	4.93
trinitatus-group					
trinitatus	9	1	9.97	3.14	3.10
	10	1	10.46	3.32	3.15
magdalenae	8	2	8.07 ± 0.81	2.37 ± 0.41	2.56 ± 0.22
	10	2	10.47 ± 0.16	2.62 ± 0.30	2.88 ± 0.07

TABLE 1. *Continued.*

Species group/ region or taxon	Age	N	Length	Distal width	Proximal width
guairae	8	1	8.62	2.79	2.93
	9	1	9.25	2.78	3.57
	10	1	10.01	3.34	3.50
hoplomyoides	10	1	11.64	1.79	2.47
mincae	8	1	7.29	2.42	2.04
	9	3	9.98 ± 0.99	2.94 ± 0.18	2.17 ± 0.25
chrysaeolus	8	6	9.01 ± 0.94	2.34 ± 0.27	2.74 ± 0.23
	9	7	10.03 ± 0.73	2.34 ± 0.32	2.97 ± 0.44
	10	3	10.97 ± 1.35	2.63 ± 0.66	3.11 ± 0.31
decumanus-group	8	1	10.63	3.84	3.41
	9	2	9.16 ± 1.44	2.93 ± 0.64	2.80 ± 0.52
	10	3	11.83 ± 1.30	3.08 ± 0.34	2.92 ± 0.42
canicollis-group	9	1	7.74	2.80	2.55
	10	1	8.11	2.64	2.78

referable to *P. simonsi* by the cranial characters that distinguish this group from *P. brevicauda* (see below).

The baculum is elongate and narrow, with a rounded and slightly broadened base. In older specimens the base is often laterally expanded with thin wings of bone. The weakly expanded distal end is usually characterized by a small lateral platform on each side separated by a shallow median depression. In general aspects, the baculum of this group is similar to that described for the *guyannensis*-group, although it averages longer and narrower (see table 1). No geographic variation is apparent, but the samples are not adequate to document this.

goeldii-group (Figure 6)

Included in this group are bacula described and figured by Didier (1962) as *Proechimys guyannensis* Type IV and as *P. quadruplicatus,* both from Caquetá, Colombia. Specimens from Peru referred to *P. brevicauda* by Patton and Gardner (1972) also belong to this unit (see Gardner & Emmons, 1984, for the correct allocation of these specimens to *P. steerei*). One specimen figured by Martin (1970, p. 8; fig. 4d), from Riberalta, El Beni, Bolivia, is also referable to this group.

There is virtually no distinguishable geographic variation in the baculum of *goeldii*-group members among samples which range from southern Venezuela to Bolivia and from the Rio Tapajós to eastern Colombia and Peru (see fig. 6; table 1). In general form, this baculum is similar to that described for members of the *guyannensis*-group.

At similar cranial ages, it is nearly the same length but slightly wider both basally and distally, giving the baculum a somewhat stouter appearance. The base varies in shape from rounded to bilobed with a median notch, the sides are parallel to only slightly concave, and the tip shows only faint development of apical wings and a median depression. In lateral view, the baculum is straight to slightly convex dorsally and concave ventrally.

trinitatus-group (Figure 7)

Didier (1962, pp. 412, 417–418) described bacula of specimens referred to this group as *Proechimys guyannensis* Type III (which represent *P. chrysaeolus*) and as *P. guyannensis mincae.*

The baculum is long (averaging over 10 mm in adults; table 1) and narrow, but except for *hoplomyoides* it is considerably stouter than that of *simonsi*-group members which resemble them in overall length (see fig. 12). The lateral margins are only slightly concave; the base is broadened and rounded, usually with a distinct median notch; and the distal tip has only slightly developed apical wings and a median depression (fig. 7).

decumanus-group (Figure 8a–b)

The baculum of *Proechimys decumanus* has apparently not been described before. It is similar in general size and shape to that of the *trinitatus*-group (fig. 12; table 1), being elongate yet stout, and with rather parallel sides. The base is somewhat rounded and the distal tip only slightly ex-
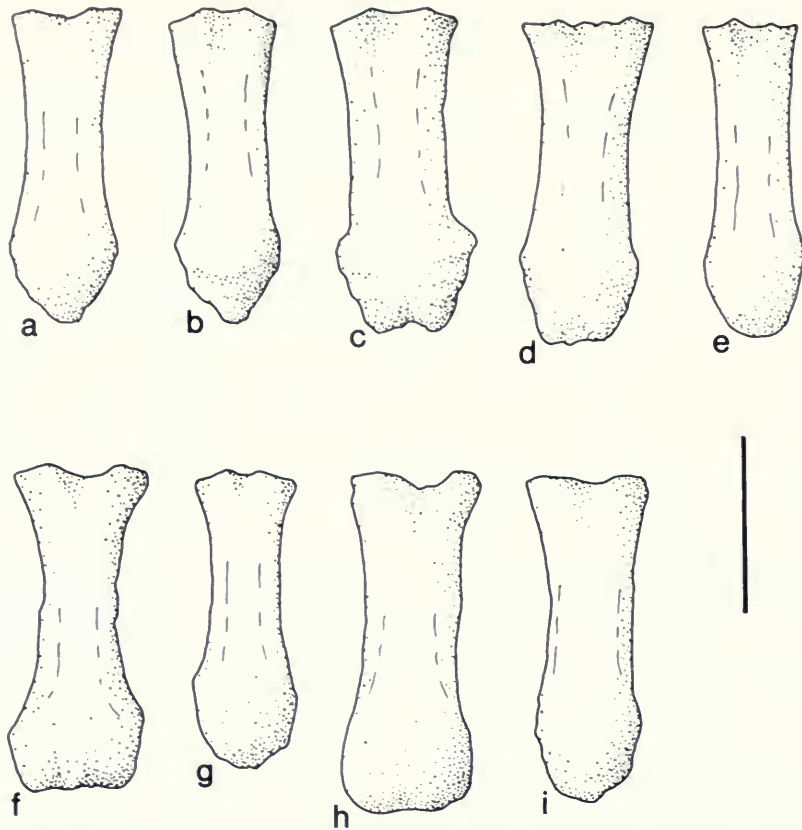
Fig. 6. Representative bacula of members of the *goeldii*-group; scale = 5 mm. **a,** FMNH 71178—Colombia: Caquetá; Florencia, Mantanito. **b,** MVZ 157955—Peru: Amazonas; La Poza, Río Santiago. **c,** AMNH 71592—Peru: Loreto; Boca Río Curaray. **d,** AMNH 76268—Peru: Loreto; Sarayacu. **e,** USNM 530931—Peru: Madre de Dios; Río Manu. **f,** AMNH 97017—Venezuela: Amazonas; Esmeralda. **g,** USNM 415117—Venezuela: Amazonas; Capibara, Casiquiare Canal. **h,** AMNH 92272—Brazil: Amazonas; Rosarinho, Río Madiera. **i,** AMNH 96828—Brazil: Pará; Ilha do Taiuno, Río Tocantins.

panded, with a weak median depression (fig. 8a–b).

canicollis-group (Figure 8c-d)

The baculum of *Proechimys canicollis* was described and figured by both Didier (1962, p. 419) and Martin (1970, p. 8). It is most similar to that of the *goeldii*-group in both shape and size, being relatively short and stout with a rounded base, weakly concave sides, and a rather flat distal tip with only weakly developed apical wings (see fig. 8c–d; table 1).

longicaudatus-group (Figure 9)

Bacula of this group were figured by Didier (1962, p. 410, fig. 2, p. 412) as *Proechimys guyannensis*

Type II (specimens from Caquetá, Colombia, and Santa Cruz, Bolivia), and by Martin (1970, p. 8, fig. 4c,e–k), also as *P. guyannensis,* from southeastern Peru, Bolivia, and southwestern Brazil. Patton and Gardner (1972) described and figured the bacula of Peruvian specimens of this group as *P. longicaudatus* (now referred to *P. brevicauda* [see Patton & Rogers, 1983; Gardner & Emmons, 1984]).

In general aspect, the baculum is elongate and broad, with well-developed apical wings (see fig. 9). 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; in others, the proximal base is evenly rounded. The shaft is arched dorsally from base to tip and transversely concave along its entire ventral length. While overall length varies considerably, as do width measures to a lesser extent (table 1), the uniform and character-
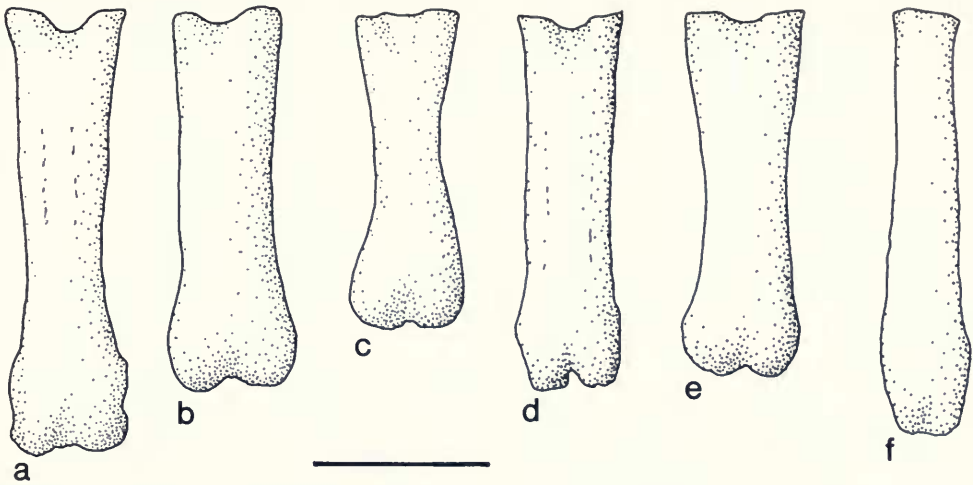
FIG. 7. Representative bacula of members of the *trinitatus*-group; scale = 5 mm. **a,** *P. chrysaeolus,* BM[NH] 12.4.2.4 — Colombia: Santander; Margarita. **b,** *P. chrysaeolus,* FMNH 69109 — Colombia: Bolivár; San Juan Nepomuceno. **c,** *P. guairae,* MVZ 168945 — Venezuela: Portuguesa; Sto. Domingo. **d,** *P. magdalenae,* USNM 499719 — Colombia: Antióquia; 22 km S and 22 km W Zaragoza. **e,** *P. trinitatus,* MVZ 168946 — Trinidad: Chaguaramas. **f,** *P. hoplomyoides,* AMNH 75827 — Venezuela: Bolivár; Arabupu, Mt. Roraima.

istic shape of the baculum renders members of this group easily identifiable. Geographically, samples allocated to *P. brevicauda* average larger and broader in the northern (e.g., southern Colombia, Ecuador, and northern Peru) than in more southern localities (e.g., southeastern Peru and adjacent Bolivia); samples from southeastern Bolivia and Brazil referred to *P. longicaudatus* approach the general size of northern samples of *P. brevicauda* (see table 1).

cuvieri-group (Figure 10)

Didier (1962, p. 411) recorded one specimen (FMNH 18198) of *Proechimys cuvieri* from Guyana in his *P. guyannensis* Type I bacular group. This group is otherwise made up of specimens of *P. semispinosus* (see below), although the bacula of *P. cuvieri* and some populations of *semispinosus* have similarities of shape in common (see figs. 10–11). Patton and Gardner (1972) figured and de-
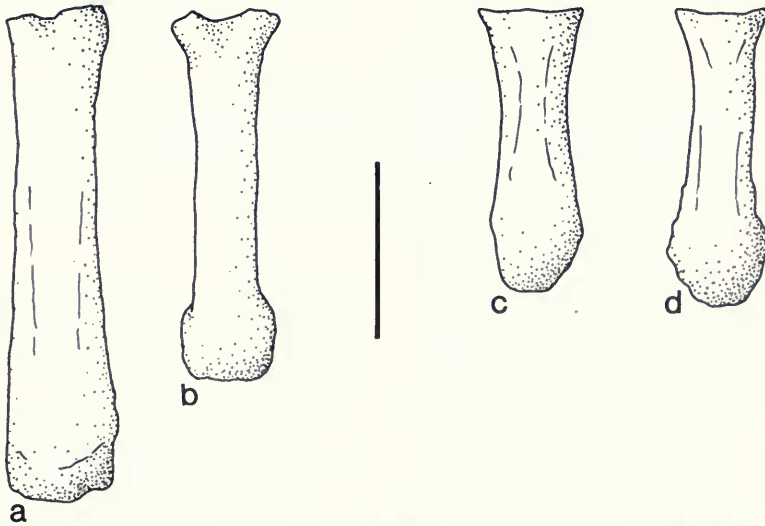

FIG. 8. Representative bacula of the *decumanus*-group (**a-b**) and *canicollis*-group (**c-d**); scale = 5 mm. **a,** FMNH 82023 — Peru: Piura; Laguna Lamadero. **b,** FMNH 81199 — Peru: Tumbes; Matapalo. **c,** USNM 280113 — Colombia: Magdalena; Río Cesar, opposite El Orinoco. **d,** USNM 280114 — Colombia: Magdalena; Río Cesar, opposite El Orinoco.
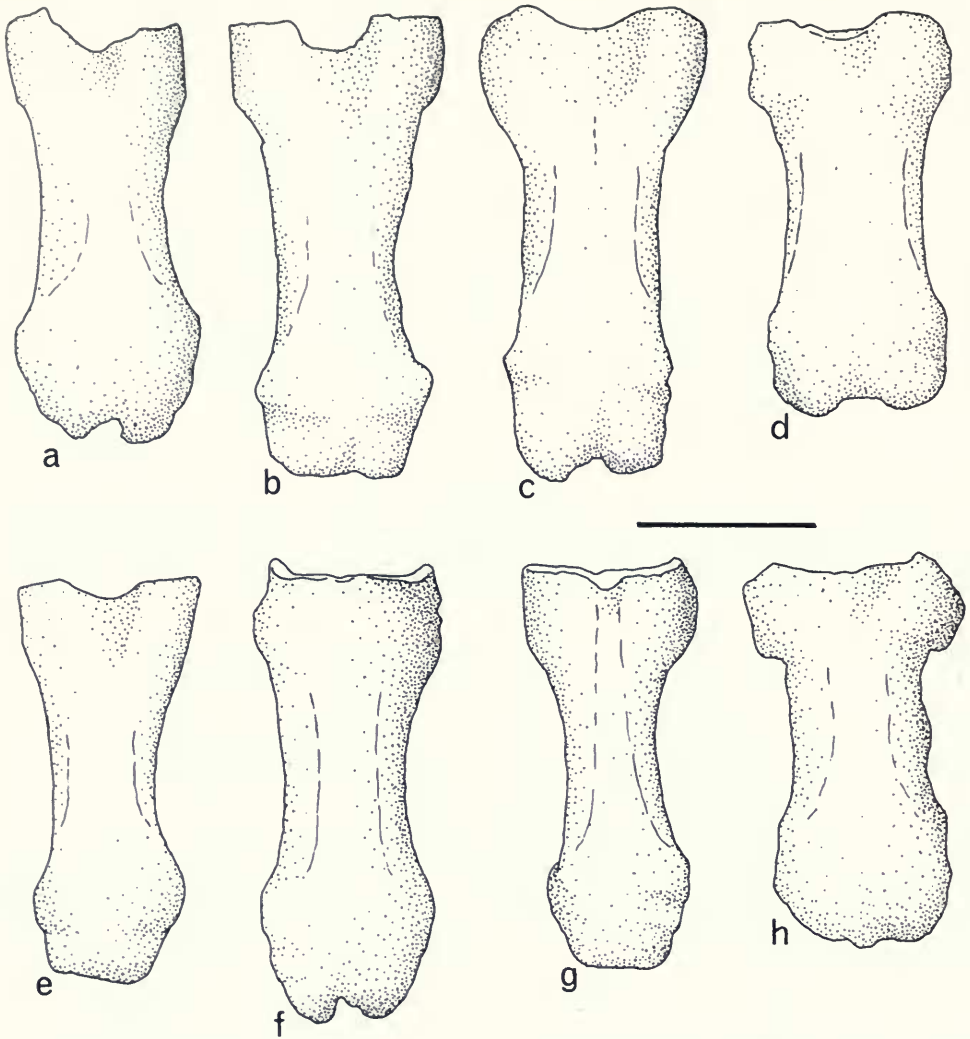
Fig. 9. Representative bacula of members of the *longicaudatus*-group; scale = 5 mm. **a,** FMNH 71174—Colombia: Caquetá; Florencia, Mantanita. **b,** MVZ 155034—Peru: Amazonas; Huampami, Río Cenepa. **c,** MVZ 157934—Peru: Amazonas; La Poza, Río Santiago. **d,** AMNH 71877—Peru: Loreto; Boca Río Curaray. **e,** MVZ 157854—Peru: Madre de Dios; Lago Sandoval. **f,** FMNH 119356—Bolivia: El Beni, San Pedro. **g,** BM[NH] 28.2.9.48—Bolivia: Santa Cruz; Buenavista. **h,** BM[NH] 3.7.7.94—Brazil: Mato Grosso; Serra de Chapada.

scribed bacula of specimens from eastern Peru with 2n = 40 karyotype that they referred to *P. guyannensis,* and that have this type of baculum.

The baculum is massive, with a broad shaft and a thickened and expanded base (see fig. 10; table 1). In cross section, the proximal two-thirds is convex dorsally and deeply concave ventrally. The distal end has a pair of diverging apical extensions separated by a wide median depression of varying depth. This is the most distinctive of any of the bacular types in *Proechimys*. It characterizes spec-

imens from widely scattered localities in the Guianas and along the entire length of the Amazon River, as well as the karyotypically differentiated 2n = 40 form from Balta, Río Curanjá, Ucayali, Peru (see Patton & Gardner, 1972). These latter specimens were considered to be conspecific with *P. guyannensis* by Gardner and Emmons (1984) on karyotypic grounds. In bacular characters, however, they are clearly different from *guyannensis*-group members and are placed here solely because of these uniquely shared bacula. The true taxo-
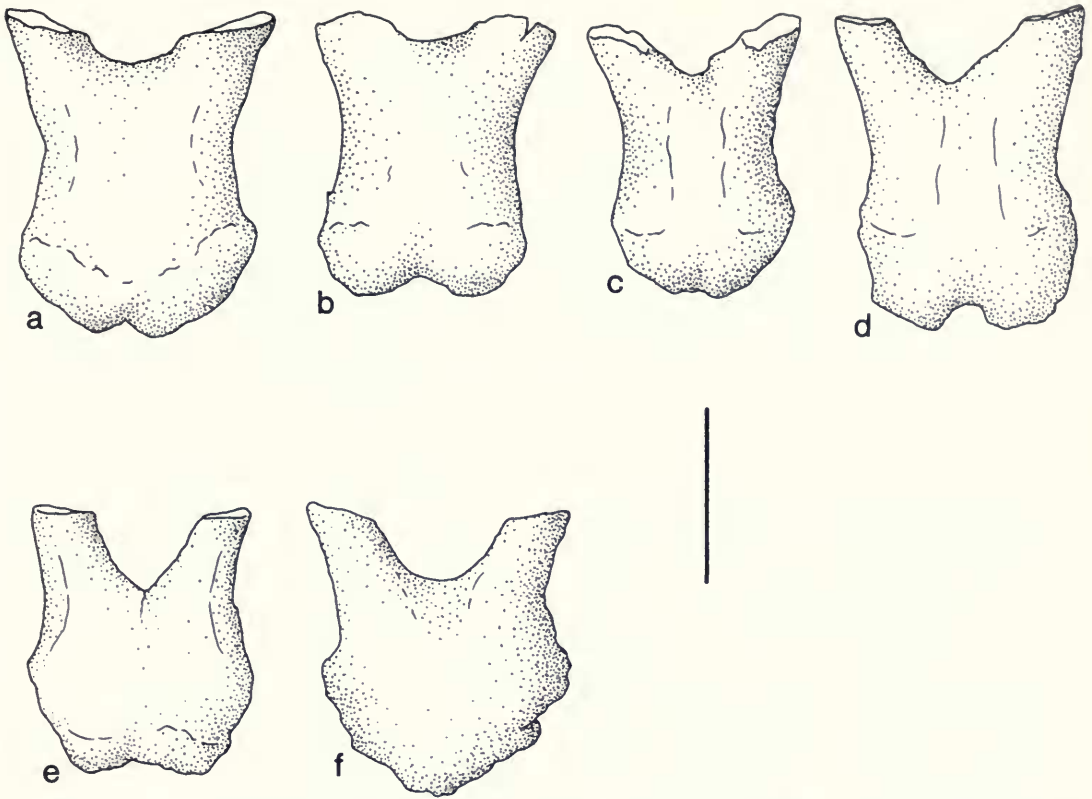
FIG. 10. Representative bacula of members of the *cuvieri*-group; scale = 5 mm. **a,** BM[NH] 7.6.20.5—Guyana: Hyde Park, Demarara River. **b,** AMNH 140540—Guyana: Kamakusa. **c,** AMNH 96844—Brazil: Pará; Ilha do Taiuno, Río Tocantins. **d,** AMNH 96867—Brazil: Pará; Ilha do Taiuno, Río Tocantins. **e,** MVZ 157874—Peru: Amazonas; La Poza, Río Santiago. **f,** AMNH 74091—Peru: Loreto; Orosa, Río Amazonas.

nomic position of these specimens remains an enigma, as material clearly assignable to this form has not been found elsewhere.

In the meager samples available, there appears to be little geographic variation in bacular size within *P. cuvieri,* although specimens from the Guianas average slightly larger than those from Brazil or Peru (table 1).

semispinosus-group (Figure 11)

Didier (1962, pp. 409–411) defined his *Proechimys guyannensis* Type I baculum based largely on specimens from western Colombia which represent the *semispinosus*-group as defined herein. Interestingly, three of the individuals he included in this group (FMNH 69063, 69064, 69071) were also listed as members of his *guyannensis* Type IV complex (Didier, 1962, p. 415), which is oth-

erwise composed of specimens here referred to the *goeldii*-group. All cranial characters, as well as bacular ones (see fig. 11b), show that these three specimens represent *P. semispinosus*. Patton and Gardner (1972, pp. 16–17) also described and figured specimens of *P. semispinosus* from Costa Rica. The additional specimens examined here do not differ importantly from the descriptions provided in these two papers.

In general aspects, the baculum is intermediate between the *longicaudatus* and *cuvieri* groups. The shaft is long and massive, with deeply concave margins, a broadly expanded and thickened base, and a wide distal portion with well-developed apical wings separated by a median depression. In cross section, the proximal and distal portions are convex dorsally and deeply concave ventrally. The width across the distal portion of the baculum typically exceeds that of the proximal portion (table 1), which is also characteristic of the *cuvieri-*
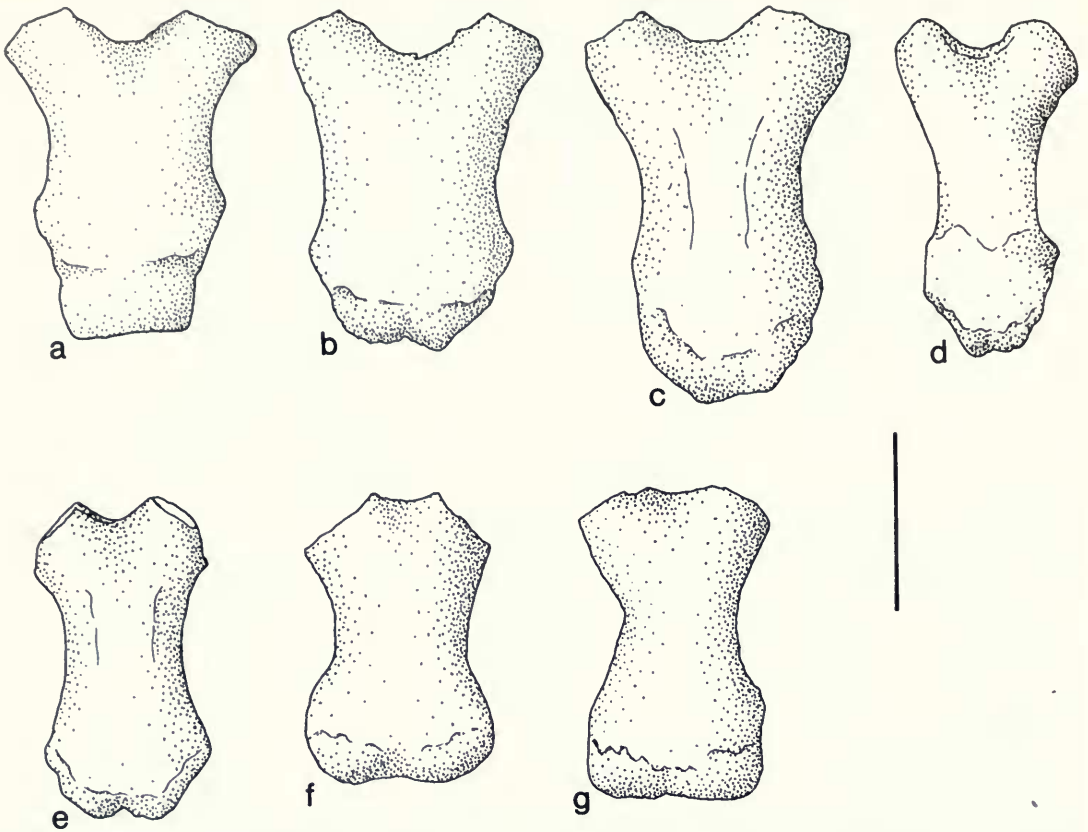
Fig. 11. Representative bacula of members of the *semispinosus*-group (*P. semispinosus* [a-e] and *P. oconnelli* [f-g]); scale = 5 mm. **a,** USNM 592694—Panama: Canal Zone. **b,** FMNH 69063—Colombia: Bolivár; Socorré, upper Río Sinu. **c,** FMNH 70085—Colombia: Choco; Unguía. **d,** FMNH 89525—Colombia: Nariño; La Guayacana. **e,** FMNH 90150—Colombia: Cauca; La Boca. **f,** MVZ 99680—Colombia: Meta; Villavicencio. **g,** FMNH 88050—Colombia: Meta; Los Micos, San Juan de Aramas.

group. However, specimens from the northern (Costa Rica and western Panama) and southern limits (Cauca, Colombia, and southward) of the range of *P. semispinosus,* as well as those of *P. oconnelli* (table 1), tend to be more symmetrical, those from central Panama south through Chocó, Colombia, more expanded distally (compare fig. 11a–d with 11e–g).

Qualitative Cranial Characters

The usual morphometric approach to specific and infraspecific taxonomy of small mammals has met with little success in studies of *Proechimys*. In part, this is due to the large age-related com-ponent of character variation within localities that obscures any geographic patterns and species differences (see Patton & Rogers, 1983). Use of qualitative characters has proven more successful, but only Patton and Gardner (1972) and Gardner and Emmons (1984) have marshalled such features as palatal structure, bullar septal pattern, temporal ridge development, and counterfold pattern on the cheekteeth into coherent patterns that identify geographically overlapping forms. Characters of the palate, in particular, proved to be concordant with bacular and karyotypic differences in delineating taxa in Peru (Patton & Gardner, 1972).

Here, I focus on the qualitative description of five cranial features that prove useful in the discrimination of sympatric taxa and in the definition of homogeneous regional units. These include (see Patton & Gardner, 1972; Gardner & Emmons,
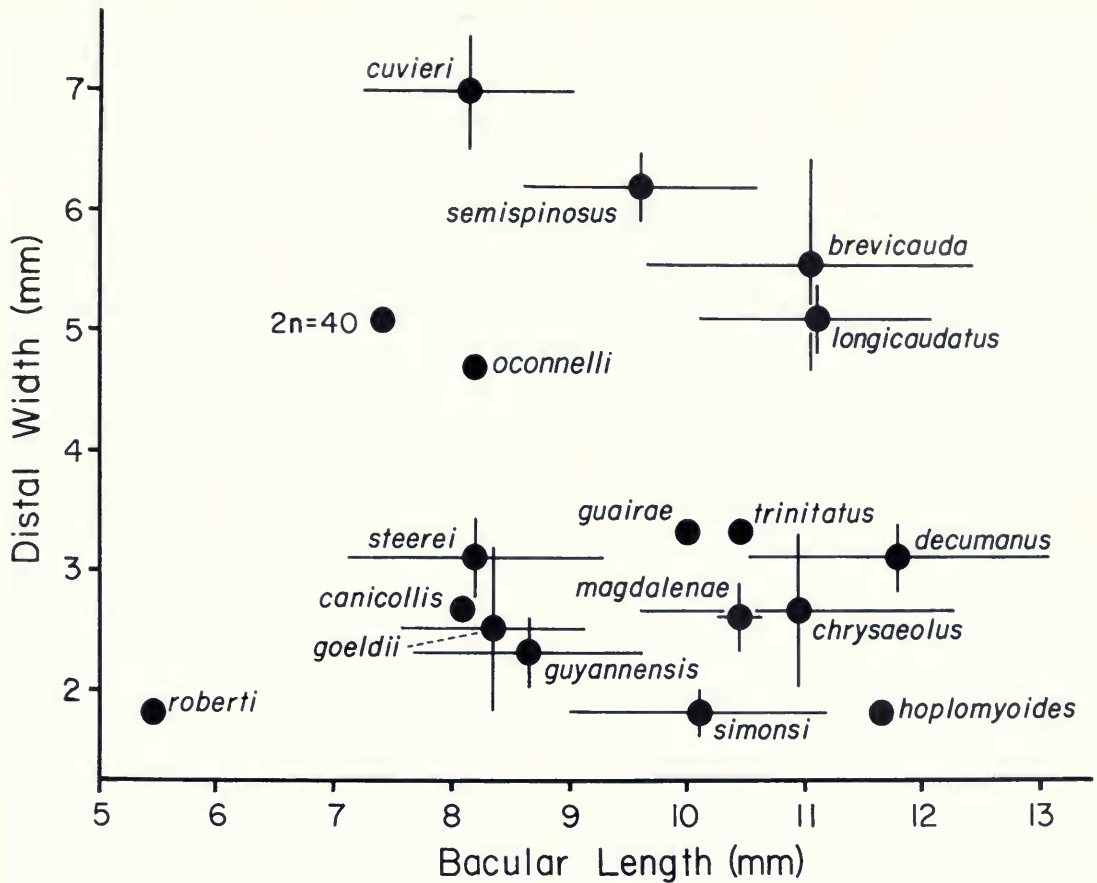
FIG. 12. Bivariate plot of distal bacular width and bacular length measurements for taxa of spiny rats, subgenus *Proechimys*. All individuals represent age class 10 of Patton and Rogers (1983). Circles indicate means, vertical and horizontal lines indicate standard deviations. See text for the allocation of taxa into species groups.

1984): (1) shape and structure of the incisive foramen; (2) angle and depth of mesopterygoid fossa; (3) degree of development of a bony groove in the floor of the infraorbital foramen; (4) degree of development of the temporal ridges across the parietals; and (5) the counterfold pattern of the upper and lower cheekteeth. These structures were used by Moojen (1948) with limited success to segregate sympatric taxa in Brazil, but he failed to use them to group regional samples into consistently defined morphological entities. Hence, his analysis appears to show that these features are much more variable, and thus of less utility, than actually proves to be the case.

Other qualitative features of the cranium, such as the size and shape of the bullae, the size and position of the hamular processes of the pterygoids, and the degree of lateral indentation of the

paroccipital processes, need further examination (see, e.g., Patton & Gardner, 1972). My preliminary analysis of each of these features indicates strong concordance with those characters used here to define taxonomic limits.

Shape and Structure of the Incisive Foramen

Specimens of each recognized species group were analyzed for the following characteristics of the incisive foramen: (1) general shape and size [lyre-shaped, constricted posteriorly; oval; evenly tapered posteriorly or parallel sided]; (2) presence or absence of grooves extending onto the anterior portion of the palate; (3) flanged or flat postero-lateral margins of the foramen; (4) degree of development of the maxillary and premaxillary por-
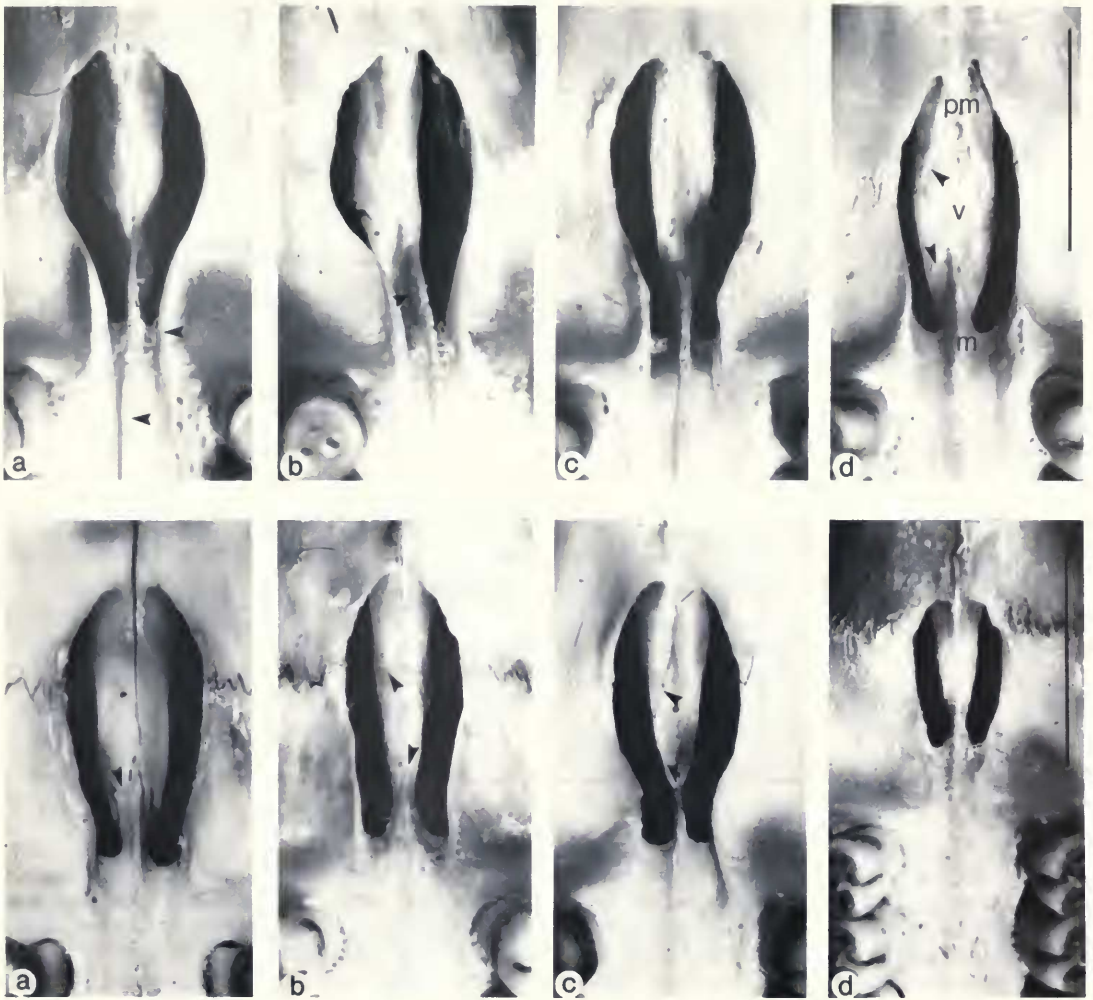
Fig. 13 (**top**).   Representative incisive foramina of specimens of *P. brevicauda* of the *longicaudatus*-group; scale =
5 mm. **a,** MVZ 153596 — Peru: Amazonas; Huampami, Río Cenepa. Arrows indicate median palatal ridge and elevated
flange marking posterolateral foraminal margins. **b,** Same specimen as in **a,** emphasizing the strongly keeled maxillary
portion of the foraminal septum (arrow). **c,** MVZ 153607 — Peru: Amazonas; Huampami, Río Cenepa. **d,** MVZ 157855 —
Peru: Amazonas; La Poza, Río Santiago. The premaxillary (pm), vomerine (v), and maxillary (m) portions of the
foraminal septum are identified; arrows indicate sutures between these elements.

Fig. 14 (**bottom**).   Representative incisive foramina of specimens of the *cuvieri*-group (*P. cuvieri* [**a-c**] and the
2n = 40 karyotypic form from Balta, eastern Peru [**d**]); scale = 5 mm. **a,** FMNH 95720 — Suriname: Brokopando;
Saramacca River, Loksie Hattie. Arrow indicates direct contact between premaxillary and maxillary portions of the
septum. Note that only a small part of the vomerine portion is visible ventrally. **b,** MVZ 160091 — Venezuela: Bolívar;
69 km S Río Cuyuni. An expanded vomerine portion of the septum is evident (arrows identify vomerine contact
with the premaxilla and maxilla). **c,** MVZ 157874 — Peru: Amazonas; La Poza, Río Santiago. The vomerine portion
of the septum is visible ventrally, widely separating the premaxillary and maxillary components (arrows). **d,** LSU
14425 — Peru: Ucayali; Balta, Río Curanja. Note the small size of this specimen relative to the others, and the
elongated premaxillary portion of the septum.

tions of septum; (5) whether the vomerine portion
of septum is visible ventrally; (6) whether or not
the maxillary portion of the septum is keeled; and
(7) whether the anterior portion of the palate has
a median ridge. Descriptions of the incisive fo-
ramina for representatives of each of the species
groups are given below and are illustrated in Fig-
ures 13–20; examples were chosen to express the

full range of character variation for each group, regardless of the specific localities from which specimens were collected.

longicaudatus-group (Figure 13a-d)

The general features of this type of incisive foramen were given by Patton and Gardner (1972, p. 10). Figure 13 illustrates the range of form typical for members of the group. The most diagnostic features include: a lyre-shaped foramen, usually with a strongly constricted posterior portion; the maxillary terminus of the foramen deeply grooved onto the anterior palate; the posterolateral margins of the foramen strongly flanged; an expanded, long premaxillary portion of the septum, usually extending more than one-half its length; a well-developed and strongly keeled maxillary portion of the septum (see fig. 13b), the maxillary keel extending onto the anterior palate resulting in a well-developed median ridge; and a vomerine portion of the septum exposed ventrally between the premaxillary and maxillary components.

This is one of the more consistently recognizable types of incisive foramina within the genus *Proechimys,* varying mostly in the degree of constriction at the posterior margins, hence in the degree of the general lyre-shape.

cuvieri-group (Figure 14a-d)

The incisive foramen of *Proechimys cuvieri* is most similar in structure to that of the *longicaudatus*-group. The general conformation is weakly to strongly lyre-shaped with strongly developed posterolateral flanges. The anterior palate, however, is only weakly to moderately grooved resulting in a slight median ridge. The premaxillary portion of the septum is strongly developed, extending more than one-half its length; the maxillary portion varies from stout to attenuate, but is always short and is only weakly keeled. The vomer is varyingly exposed ventrally (compare fig. 14a with 14b–c).

The 2n = 40 specimens from Balta which have bacula similar to *P. cuvieri* share only some foraminal characters with that taxon (fig. 14d). The foramen is weakly lyre-shaped and the posterolateral margins are only weakly flanged, hence the anterior palate is scarcely grooved. Nevertheless, the premaxillary portion of the septum is elongated and broad, similar in shape and structure to

that of *P. cuvieri.* The maxillary portion is well developed and appears to contact directly the premaxillary portion.

goeldii-group (Figure 15a-d)

The general features of this foraminal type were provided by Patton and Gardner (1972, p. 4) under *P. brevicauda.* The foramen is usually only weakly lyre-shaped, or with margins tapering slightly posteriorly or parallel-sided. The premaxillary portion of the septum is short, usually one-half or less of the length of the foramen; the maxillary portion varies greatly, being usually rather weak and attenuate, often not in contact with the premaxillary portion (fig. 15d) but sometimes broadly spatulate and filling much of the foramen (fig. 15a). Nevertheless, the vomer is only rarely exposed ventrally, being completely enclosed in the premaxillary sheath. The maxillary portion of the septum often exhibits a median vacuity (fig. 15b); it may be slightly ridged, but is never strongly keeled, and seldom does this ridge extend onto the anterior palate (fig. 15b). Thus, there are only moderately developed grooves onto the anterior palate, and the posterolateral margins of the foramen are only moderately flanged.

semispinosus-group (Figure 16a-d)

Specimens of this group from Costa Rica were described by Patton and Gardner (1972, p. 15). Foraminal shape varies from rather evenly tapered margins to moderately lyre-shaped ones. The posterolateral margins are usually strongly flanged, creating deep grooves extending onto the anterior palate despite only moderate development of a medial ridge (compare fig. 16b with 16c). The premaxillary portion of the septum is dominant, usually broadly filling the foramen and extending well over one-half its length. The maxillary portion varies from moderately developed to attenuate, but is almost always in direct contact with the premaxillary portion. The vomer is completely encased within the premaxilla and thus is not visible in ventral aspect.

simonsi-group (Figure 17a-d)

Again, the incisive foramen of the *simonsi*-group was described fully by Patton and Gardner (1972,
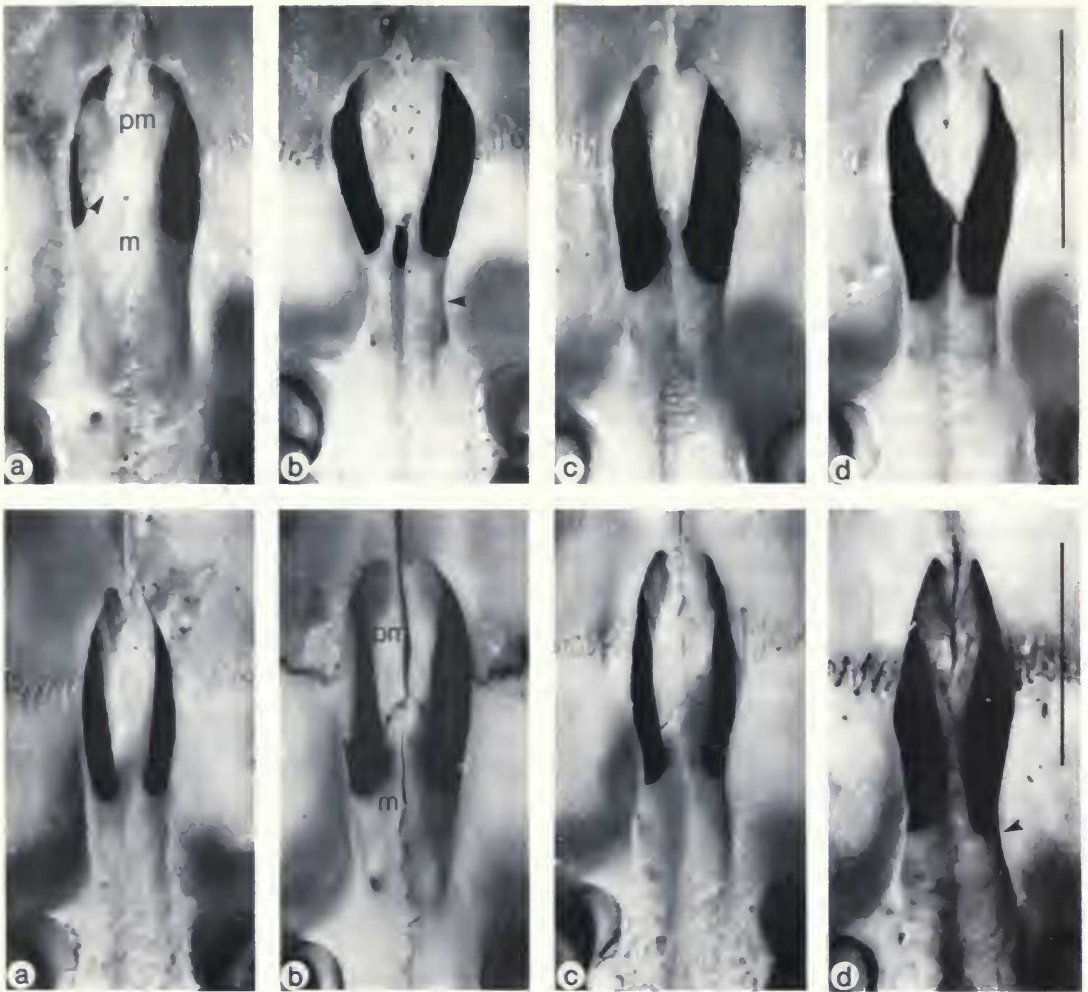
FIG. 15 (top). Incisive foramina of *P. steerei* of the *goeldii*-group. All are from La Poza, Río Santiago, Amazonas, Peru; scale = 5 mm. **a,** MVZ 157949. Note the enlarged maxillary portion of the septum (m) and the direct contact (arrow) between it and the premaxillary portion (pm). **b,** MVZ 157956. Note the moderately developed posterolateral flange (arrow). **c,** MVZ 157861. **d,** MVZ 157869. Note the attenuate maxillary portion of the septum and the lack of contact between it and the premaxilla portion.

FIG. 16 (**bottom**). Incisive foramina of *P. semispinosus* of the *semispinosus*-group; scale = 5 mm. **a,** MVZ 165794—Panama: Panamá; 0.8 km N Paraiso. **b,** FMNH 90169—Colombia: Chocó; Río Baudo. Note the direct contact between the premaxillary (pm) and maxillary (m) portions of the septum. **c,** FMNH 90177—Colombia: Chocó; Río Baudo. **d,** FMNH 70080—Colombia: Chocó; Unguía. Note the well-developed posterolateral flange (arrow).

p. 19). This is a distinctive foraminal type, as all specimens examined were consistent in most features despite variation in overall shape. The foramen is oval in general shape, although often asymmetrical in anteroposterior direction (fig. 17b). The premaxillary portion of the septum is rather short, usually no more than one-half the length of the foramen. The maxillary portion is usually weak and attenuate, only rarely in contact with the premaxillary portion. When the septum is complete (fig. 17a), the vomer is either completely enclosed

by the premaxilla or barely visible (fig. 17c). The posterolateral margins are flat, not flanged, and no groove extends onto the anterior palate. Rather, the palate is noticeably flat and smooth, without a medial ridge.

guyannensis-group (Figure 18a-d)

This foraminal type is virtually indistinguishable from that described for the *simonsi*-group.
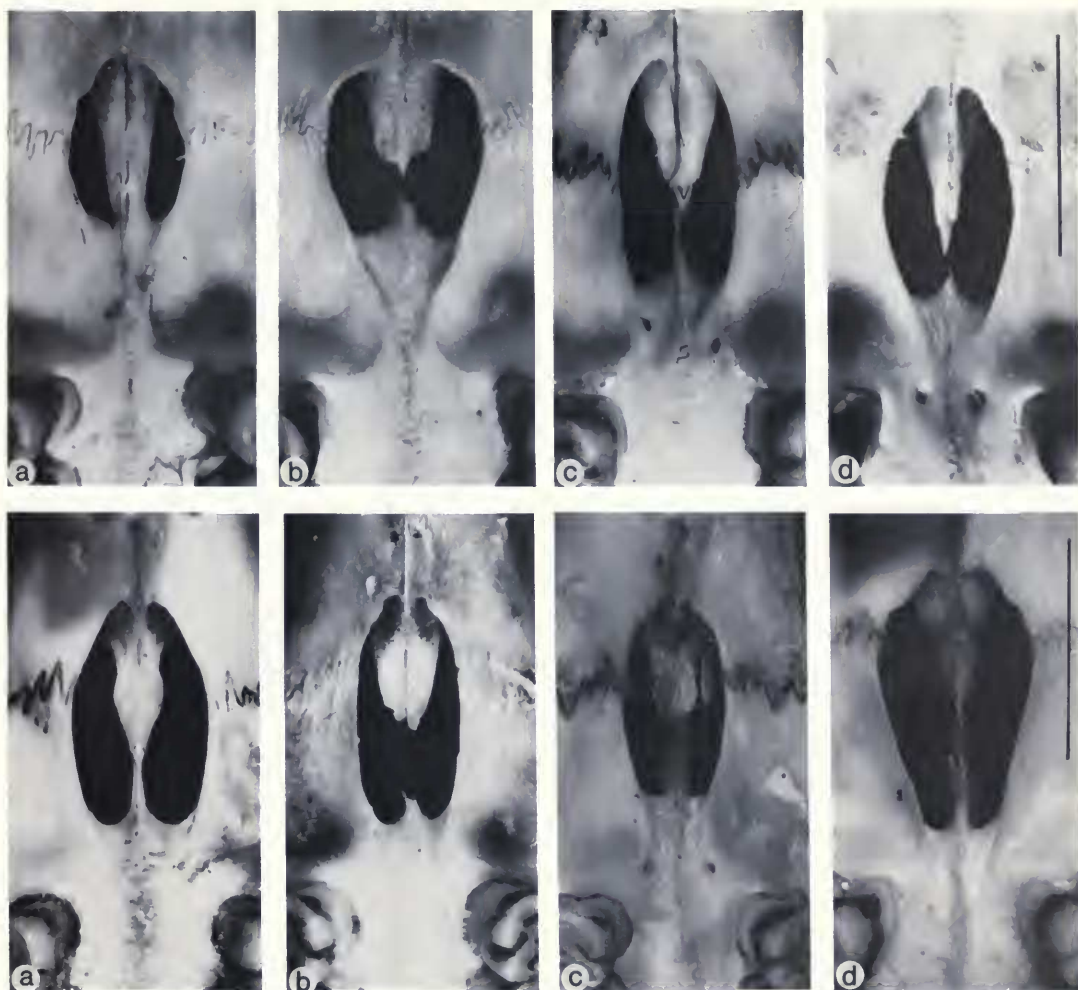
FIG. 17 (**top**).   Incisive foramina of *P. simonsi* of the *simonsi*-group; scale = 5 mm. **a,** MVZ 155045—Peru: Amazonas; headwaters of Río Kagka. Note lack of posterolateral flanges or palatal grooves. **b,** MVZ 157914—Peru: Amazonas; La Poza, Río Santiago. **c,** MVZ 136654—Peru: Ucayali; Balta, Río Curanja. Note slightly exposed vomer (v) and attenuate maxillary portion of septum. **d,** MVZ 168955—Peru: Madre de Dios; Albergue, Río Madre de Dios.

FIG. 18 (**bottom**).   Incisive foramina of the *guyannensis*-group (**a-b**, *arabupu*; **c**, *oris*; and **d**, *roberti*); scale = 5 mm. **a,** AMNH 139741—Venezuela: Bolívar; Auyantepui. Note lack of posterolateral flanges and anterior palatal grooves, and the attenuate maxillary portion of the septum. **b,** MVZ 160094—Venezuela: Bolívar; 4 km E El Paují. Note the lack of contact between the premaxillary and maxillary portions of the septum. **c,** AMNH 93997—Brazil: Pará; Faro, north bank Río Amazon. Note weakly developed posterolateral flanges. **d,** AMNH 134309—Brazil: Goiás; Anápolis.

The shape is oval, although often unequal (fig. 18d). The anterior palate is flat, without grooves or a median ridge, and the posterolateral margins of the foramen are not flanged, or only weakly flanged (fig. 18c shows maximal development of flanges). The premaxillary portion of the septum is relatively short, usually less than one-half the length of the foramen, and the maxillary portion is attenuate, usually not in contact with the pre-maxillary portion. The vomer generally does not contribute to the ventral aspect of the septum.

trinitatus-group (Figure 19a-d)

Members of this species group generally exhibit the most enlarged foramina within the subgenus *Proechimys*. Specimens referred to *mincae, polio-*
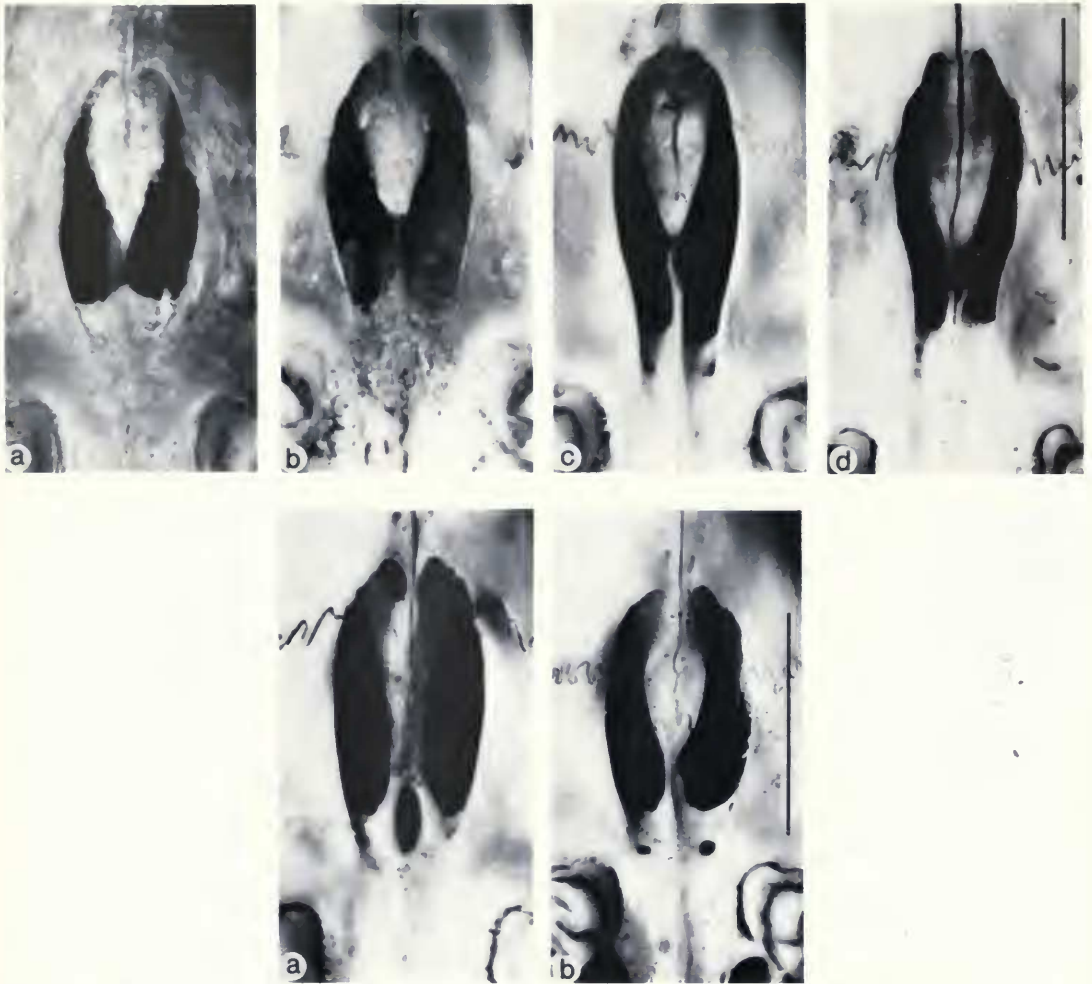
FIG. 19 (**top**). Incisive foramina of the *trinitatus*-group; scale = 5 mm. **a,** *P. mincae,* FMNH 13203—Colombia: Magdalena; Minca (topotype). **b,** *P. ochraceous,* FMNH 18688—Venezuela: Zulia; El Panorama, Río Aurare (topotype). **c,** *P. guairae,* FMNH 92588—Colombia: Arauca; Río Cobaria. **d,** *P. chrysaeolus,* FMNH 69037—Colombia: Bolívar; San Juan Nepumoceno.

FIG. 20 (**bottom**). Incisive foramina of the *decumanus*- and *canicollis*-groups; scale = 5 mm. **a,** *P. decumanus,* FMNH 82024—Peru: Piura; Laguna Lamadero. **b,** *P. canicollis,* FMNH 69111—Colombia: Bolívar; San Juan Nepumoceno.

pus, and *ochraceous* have smoother, less ridged palates and ovoid foramina lacking posterolateral flanges (fig. 19a–b); those referred to *guairae, trinitatus, urichi, hoplomyoides,* and *chrysaeolus* have somewhat more lyre-shaped foramina with weakly to moderately flanged posterolateral margins which define grooves extending onto the anterior palate (fig. 19c–d). In all forms the premaxillary portion of the septum is enlarged, usually extending one-half or more of the length of the foramen, while the maxillary portion is attenuate, most often not in direct contact with the premaxillary portion.

Only in specimens referred to *guairae* and *trinitatus* does the maxillary portion of the septum show a medial ridge (fig. 19c).

decumanus-group (Figure 20a)

This foraminal type is oval in shape and large, with poorly defined posterolateral flanges and weak grooves extending onto the anterior palate. The premaxillary portion of the septum is long, but tapering posteriorly and in direct contact with a

Fig. 21. Patterns of temporal ridge development in *Proechimys*; scale = 5 mm. **a,** *P. semispinosus,* FMNH 90145—Colombia: Cauca; Río Saija. Note extreme development of ridge 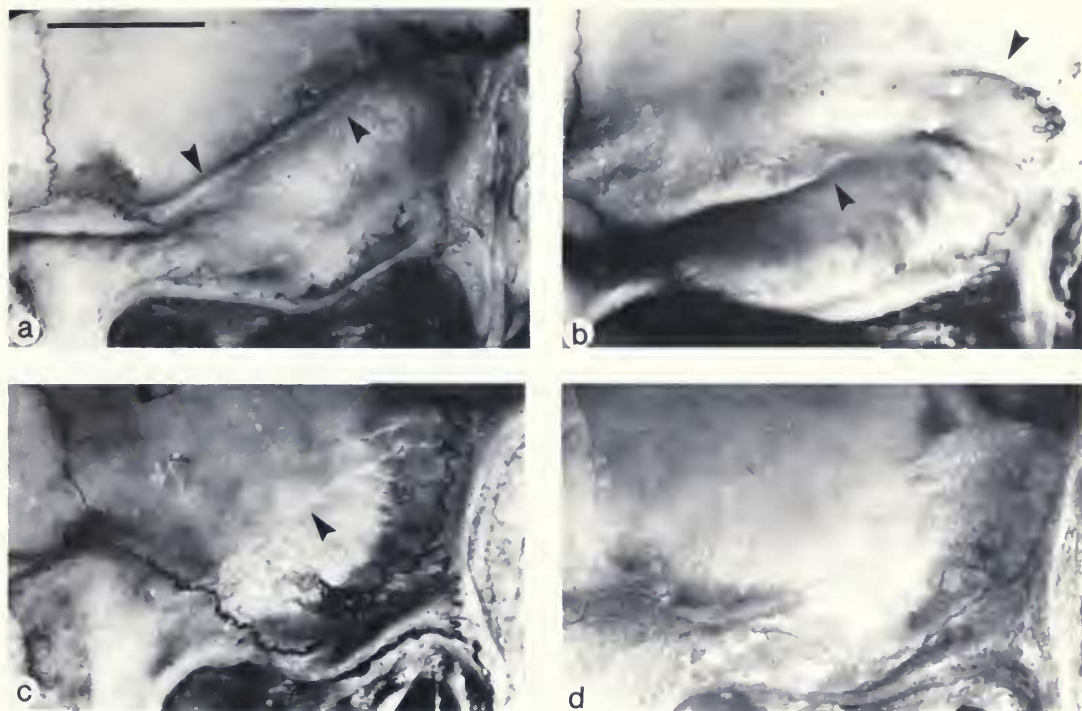across parietals continuous between the supraorbital ledge and the lambdoidal ridge (arrows). **b,** *P. steerei,* MVZ 157955—Peru: Amazonas; La Poza, Río Santiago. Note separation of temporal ridge into an anterior part distinctly ventral to a posterior section (arrows). **c,** *P. quadruplicatus,* UMMZ 80069—Ecuador: Napo; San Francisco, Río Napo. Note barely perceptible temporal ridge (arrow). **d,** *P. cuvieri,* MVZ 160091—Venezuela: Bolivár; 69 km S Río Cuyuní. Note relatively smooth parietal with only an anterior temporal ridge extension.

short but wide (and often perforated) maxillary portion. The vomer is not visible ventrally.

canicollis-group (Figure 20b)

The shape and structure of this foramen is similar to that described for *P. decumanus.* The opening is oval in shape, posterolateral flanges are weakly developed, and the anterior palate shows only faint grooves. The premaxillary portion of the septum is broad and extends to one-half the length of the foramen; the maxillary portion is moderately developed and in direct contact with the premaxilla. Hence, the vomer does not form part of the ventral aspect of the septum.

Development of the Temporal Ridge

Four conditions of temporal ridge development were recognized, as follows:

1. Ridge well developed, extending across the parietals from the supraorbital ledge to the lambdoidal ridge (fig. 21a).

2. Ridge moderately developed, but with an anterior parietal portion separated from and distinctly ventral to the posterior lambdoidal portion (fig. 21b).

3. Ridge continuous across parietals, but weakly developed, being a barely perceptible change in the lateral curvature of the parietals (fig. 21c).

4. No ridge development, or only a weak ridge extending from the supraorbital ledge onto the anterior parietals (fig. 21d).

Representatives of each species group were scored for these conditions, and the patterns are indicated in Table 2. Only *P. semispinosus* of the *semispinosus*-group displays complete and well-developed ridges, a characteristic noted by Gardner and Emmons (1984). *P. oconnelli* of this group, however, does not exhibit temporal ridges. The remainder of the species groups, however, show

TABLE 2. Frequency classes of the development of the temporal ridge of spiny rats, subgenus *Proechimys*. See text for explanation of character-states.

Species group/ region or taxon	Ridge score				
	N	1	2	3	4
semispinosus-group					
Central America	82	0.82	0.18	···	···
Northern Colombia	63	0.94	0.06	···	···
Central Colombia	31	1.00	···	···	···
Northern Ecuador	19	0.95	0.05	···	···
Southern Ecuador	29	1.00	···	···	···
oconnelli	20	···	···	···	1.00
longicaudatus-group					
Colombia–Ecuador	6	···	0.33	0.17	0.50
Northern Peru	145	···	0.53	0.27	0.20
Central Peru	39	···	0.58	0.19	0.23
SE Peru–Bolivia	35	···	0.46	0.36	0.18
Bolivia–Brazil	32	···	0.39	0.36	0.26
cuvieri-group					
Guianas	3	···	···	1.00	···
Central Brazil	37	···	0.35	0.50	0.15
Peru	4	···	0.25	0.50	0.25
2n = 40, Balta	5	···	···	0.40	0.60
goeldii-group					
Northern Peru	104	···	0.17	0.77	0.06
Central Peru	31	···	0.24	0.76	···
SE Peru–Bolivia	17	···	···	0.89	0.11
Venezuela–Brazil	21	···	···	0.61	0.39
Central Amazon	63	···	0.07	0.70	0.23
Eastern Amazon	123	···	0.07	0.81	0.12
guyannensis-group					
Goiás, Brazil	20	···	0.05	0.05	0.90
Pará, Brazil	50	···	0.13	0.12	0.75
Central Amazon	31	···	···	0.12	0.88
Venezuela–Brazil	129	···	0.01	···	0.99
Suriname	1	···	···	···	1.00
simonsi-group					
Colombia–Ecuador	5	···	···	···	1.00
Northern Peru	32	···	···	···	1.00
Central Peru	15	···	···	···	1.00
SE Peru–Bolivia	27	···	···	···	1.00
trinitatus-group					
chrysaeolus	5	···	···	0.25	0.75
mincae	19	···	···	0.05	0.95
trinitatus	12	···	···	0.08	0.92
urichi	8	···	···	···	1.00
guairae	3	···	···	···	1.00
ochraceous	1	···	···	···	1.00
poliopus	1	···	···	···	1.00
hoplomyoides	1	···	···	···	1.00
canicollis-group	13	···	···	···	1.00
decumanus-group	17	···	0.59	0.29	0.12

considerable overlap in the expression of this feature, although *decumanus*-, *longicaudatus*-, *goeldii*-, and *cuvieri*-group members consistently show some ridge development while taxa of the *guy-* *annensis*-, *simonsi*-, *trinitatus*-, and *canicollis*-groups characteristically do not (table 2).

Ventral Canal of the Infraorbital Foramen

The infraorbital nerve courses near the medial floor of the infraorbital foramen, producing a canal of varying distinctness in many caviomorph rodents, including *Proechimys* (Woods, 1984). Both Moojen (1948) and Gardner and Emmons (1984) suggested that the presence and degree of development of this canal or groove has taxonomic significance in the genus. To evaluate this view, several grades of notch development were scored for representatives of each species group:

1. No groove present (fig. 22c)
2. Groove present, with moderately developed lateral flange (fig. 22b)
3. Groove present, with extreme development of a lateral flange (fig. 22a)

Intermediate levels between each of these classes were also recognized, providing five scores ranging from 1.0 to 3.0 in half increments.

The degree of groove development for geographic and taxonomic representatives of each species group is given in Table 3. While groove development varies widely within the genus, each species group displays a relatively narrow range. Members of the *longicaudatus*-, *trinitatus*-, *cuvieri*-, and *guyannensis*-groups exhibit the least development of a groove, the *longicaudatus*-group rarely showing any groove at all. The *goeldii*- and *simonsi*-groups show moderate development of the groove, while a notch is most strongly developed in the *semispinosus*-group. Specimens of *P. oconnelli* of the *semispinosus*-group consistently displayed the most extensive lateral flange development.

Geographic variation in the expression of groove development within each species group is virtually absent. The *longicaudatus*- and *semispinosus*-groups, with the lowest and highest mean scores, respectively, are the most uniform geographically; the *guyannensis*- and *goeldii*-groups are most variable (table 3).

Angle and Depth of the Mesopterygoid Fossa

The angle formed by the anterior margins of the mesopterygoid fossa was measured with a pro-

FIG. 22. Degrees of development of the canal or groove on the medial floor of the infraorbital foramen that accommodates the infraorbital nerve; see text for description of scoring system used; scale = 5 mm. **a,** Score = 3.0, *P. oconnelli,* MVZ 99685—Colombia: Meta; Villavicencio. **b,** Score = 2.0, *P. oconnelli,* MVZ 99684—Colombia: Meta; Villavicencio. **c,** Score = 1.0, *P. quadruplicatus,* UMMZ 80069—Ecuador: Napo; San Francisco, Río Napo.

TABLE 3. Mean scores and ranges for the development of the infraorbital foramen canal of spiny rats, subgenus *Proechimys.* See text for explanation of scoring system.

| Species group/ region or taxon	N	Mean	Range
longicaudatus-group			
Colombia–Ecuador	6	1.1	1.0–1.5
Northern Peru	145	1.1	1.0–1.4
Central Peru	39	1.1	1.0–1.5
SE Peru–Bolivia	35	1.1	1.0–1.5
Southern Bolivia–Brazil	32	1.0	1.0–1.5
cuvieri-group			
Guianas	3	1.4	1.0–1.5
Central Amazon	37	1.3	1.0–2.0
Peru	4	1.4	1.0–2.0
2n = 40, Balta	5	1.4	1.0–2.0
semispinosus-group			
Central America	82	2.6	1.0–3.0
Northern Colombia	63	2.7	1.5–3.0
Central Colombia	31	2.6	2.0–3.0
Northern Ecuador	19	2.7	2.0–3.0
Southern Ecuador	29	2.7	1.5–3.0
oconnelli	20	2.8	2.0–3.0
goeldii-group			
Northern Peru	104	2.1	1.0–3.0
Central Peru	31	1.8	1.0–3.0
SE Peru–Bolivia	17	1.5	1.0–2.0
Venezuela–Brazil	21	1.8	1.0–3.0
Central Amazon	63	1.5	1.0–2.5
Eastern Amazon	123	1.9	1.0–3.0
guyannensis-group			
Goiás, Brazil	20	1.2	1.0–1.5
Pará, Brazil	50	1.1	1.0–1.5
Central Amazon	31	2.0	1.0–3.0
NW Brazil	34	2.0	1.5–3.0
SE Venezuela–Brazil	95	1.5	1.0–3.0
Suriname	1	2.5	···
simonsi-group			
Colombia–Ecuador	5	2.0	···
Northern Peru	32	2.1	1.5–3.0
Central Peru	15	1.6	1.0–2.0
SE Peru–Bolivia	27	1.8	1.0–2.5
trinitatus-group			
chrysaeolus	7	1.7	1.0–2.0
mincae	19	1.8	1.0–2.0
trinitatus	12	1.9	1.5–3.0
urichi	6	1.3	1.0–2.0
guairae	3	2.0	1.5–3.0
ochraceous	1	1.5	···
poliopus	1	1.5	···
hoplomyoides	1	1.0	···
canicollis-group	13	1.2	1.0–1.5
decumanus-group	17	1.4	1.0–2.0
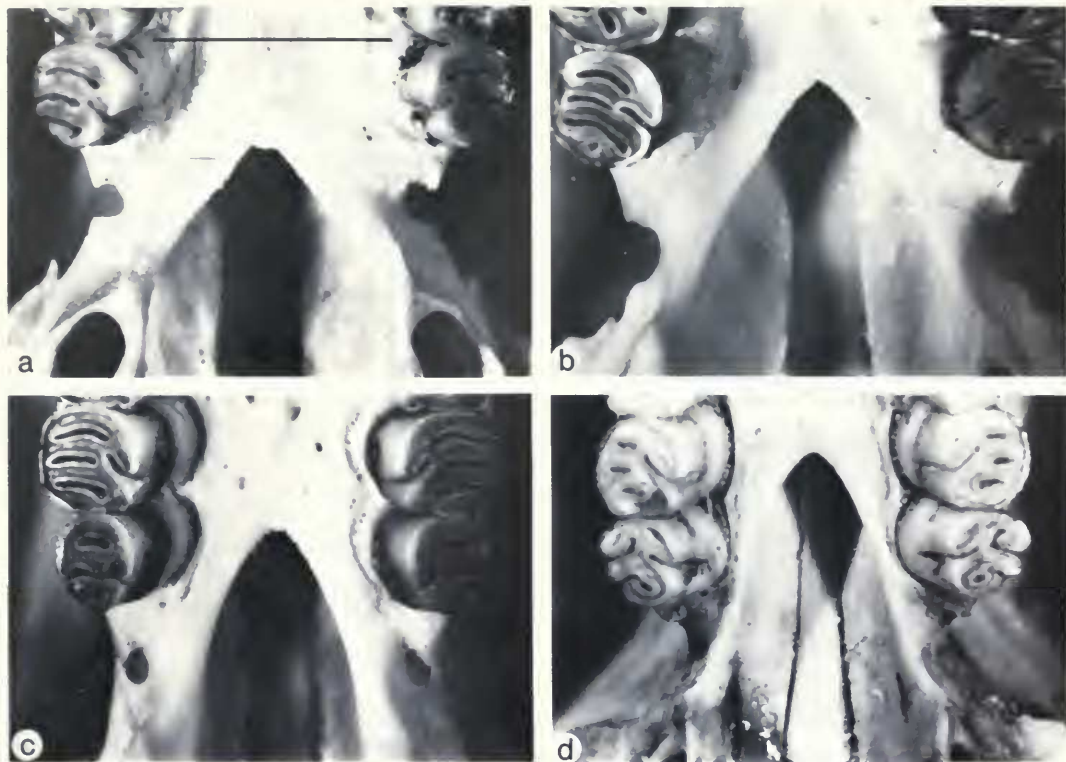
FIG. 23. Angle and extent of the mesopterygoid fossa for representative taxa of *Proechimys*; scale = 5 mm. **a,** *P. brevicauda,* MVZ 157854—Peru: Amazonas; La Poza, Río Santiago. **b,** *P. steerei,* MVZ 157888—Peru: Amazonas; La Poza, Río Santiago. **c,** *P. simonsi,* MVZ 157950—Peru: Amazonas; La Poza, Río Santiago. **d,** *P. guyannensis,* AMNH 75820—Venezuela: Bolivár; Arabupu, Mt. Roraima (topotype of *arabupu*).

tractor to the nearest degree, and the maximal penetration of the fossa into the palate was scored relative to the cheekteeth, as follows:

1. Not extending to the posterior margins of M3
2. Extending to the posterior one-half of M3
3. Extending to anterior one-half of M3
4. Extending to posterior one-half of M2
5. Extending to anterior one-half of M2

These two characters, angle and depth, are correlated in that the greater the depth usually the more acute the angle (fig. 23).

Table 4 provides data for the mesopterygoid fossa characters for representatives for each recognized species group of *Proechimys*. Members of the *longicaudatus*-group consistently have the broadest angle with the most shallow fossa (fig. 23a); those of the *simonsi*-group have the most acutely-angled fossa and, with members of the *guyannensis*-group, the deepest penetration into the palate (fig. 23c–d). Most other groups show moderate angles and degree of penetration. Except

for the *guyannensis*-group, where samples referred to *P. oris* (Pará state, Brazil) and *P. roberti* (Goiás and Minas Gerais states, Brazil) are quite different from other samples examined (table 4), there is little geographic variation in the expression of mesopterygoid fossa characters within each species group.

Counterfold Pattern of the Cheekteeth

Early attempts to establish systematic relationships within *Proechimys* placed considerable emphasis on variation in counterfolds of the cheekteeth, both in number and pattern (e.g., Hershkovitz, 1948; Moojen, 1948). In general, these earlier studies indicated that fold number and pattern are quite variable geographically within taxa. As a result, counterfolds have been used primarily to recognize taxa sympatric at given localities rather than as a character complex capable of uniting distinct populations into cohesive and

TABLE 4. Mesopterygoid fossa (MPF) angle (in degrees) and depth scores of spiny rats, subgenus *Proechimys*. See text for detailed descriptions of character-states.

Species group/region or taxon	N	MPF angle		MPF depth	
		Mean ± SD	Range	Mean	Range
longicaudatus-group					
Colombia–Ecuador	6	79.0 ± 8.9	64–89	2.0	1–3
Northern Peru	145	79.6 ± 5.8	64–107	2.0	1–3
Central Peru	39	78.7 ± 7.1	64–93	1.9	1–3
SE Peru–Bolivia	35	72.7 ± 6.3	60–90	1.9	1–3
Southern Bolivia–Brazil	32	77.6 ± 8.5	60–91	2.2	1–3
cuvieri-group					
Guianas	3	69.7 ± 4.9	64–73	2.0	⋯
Central Brazil	37	72.8 ± 5.6	57–92	2.2	1–3
Peru	4	66.7 ± 5.7	59–71	2.0	1–3
2n = 40, Balta	5	56.4 ± 3.2	52–60	3.2	2–4
semispinosus-group					
Central America	82	56.4 ± 6.4	45–73	2.6	1–3
Northern Colombia	63	57.7 ± 6.1	45–72	2.5	2–4
Central Colombia	31	57.1 ± 5.6	46–62	2.8	2–4
Northern Ecuador	19	62.6 ± 6.8	53–75	3.0	⋯
Southern Ecuador	29	62.1 ± 4.8	53–71	2.8	2–4
oconnelli	20	63.3 ± 5.3	56–72	2.9	2–4
goeldii-group					
Northern Peru	104	60.6 ± 7.0	49–80	2.7	1–4
Central Peru	31	65.3 ± 7.1	45–76	2.6	2–3
SE Peru–Bolivia	17	67.9 ± 7.0	55–79	2.4	2–3
Venezuela–Brazil	21	68.2 ± 6.2	56–80	2.7	2–4
Central Brazil	63	62.1 ± 5.1	52–78	2.9	2–4
Eastern Brazil	123	65.3 ± 5.1	50–80	2.6	1–4
guyannensis-group					
Goiás, Brazil	20	67.7 ± 6.1	54–78	2.8	2–3
Pará, Brazil	50	64.2 ± 6.2	44–82	3.0	2–4
Central Brazil	31	56.1 ± 4.9	45–66	3.7	3–5
Venezuela–Brazil	129	47.5 ± 6.3	34–67	3.9	2–5
Suriname	1	58.0	⋯	4.0	⋯
simonsi-group					
Colombia–Ecuador	5	49.3 ± 6.9	39–53	3.6	3–4
Northern Peru	32	51.1 ± 3.3	47–62	4.1	2–5
Central Peru	15	53.3 ± 4.6	46–62	3.8	3–5
SE Peru–Bolivia	27	51.2 ± 4.5	45–64	3.2	2–4
trinitatus-group					
chrysaeolus	7	59.3 ± 9.9	53–67	2.3	1–3
mincae	19	56.7 ± 3.2	53–64	3.7	3–4
trinitatus	12	52.8 ± 4.9	48–65	3.4	3–4
urichi	6	56.3 ± 4.9	48–64	3.3	3–4
guairae	3	55.7 ± 3.1	53–58	3.3	3–4
ochraceous	2	48.5 ± 3.5	46–51	4.0	⋯
poliopus	2	47.0 ± 1.4	46–48	3.5	3–4
hoplomyoides	1	40.0	⋯	4.0	⋯
canicollis-group	13	54.2 ± 2.9	50–61	3.0	⋯
decumanus-group	17	52.9 ± 3.5	46–59	3.1	2–4

definable groups. While there is geographic variation in counterfold pattern and number within taxa of spiny rats, these characters can be used to form groups which are consistently separable from others. In this respect, the counterfold pattern and number reinforces group membership delineated by other morphological features, such as bacula and palatal characters.

Illustrations of counterfold patterns for both upper and lower toothrows for each species group

Fig. 24.   Upper (left) and lower (right) toothrows of *P. semispinosus* of the *semispinosus*-group of *Proechimys*; scale = 5 mm. **a,** FMNH 90143—Colombia: Cauca: Río Saija. **b,** FMNH 70072—Colombia: Chocó; Unguía.

(with the exception of the *decumanus*-group) are presented in Figures 24–30. As with other character complexes I examined, these examples were chosen to illustrate the range of variation. Geographic variation within each group is summarized in Table 5.

Counterfold number and, to a lesser extent, pattern change with increasing age. Obviously, folds become obliterated in advanced age, but even in moderately aged individuals smaller folds easily can become lost, and coalescence or isolation of folds occurs (see Moojen, 1948). These age-related
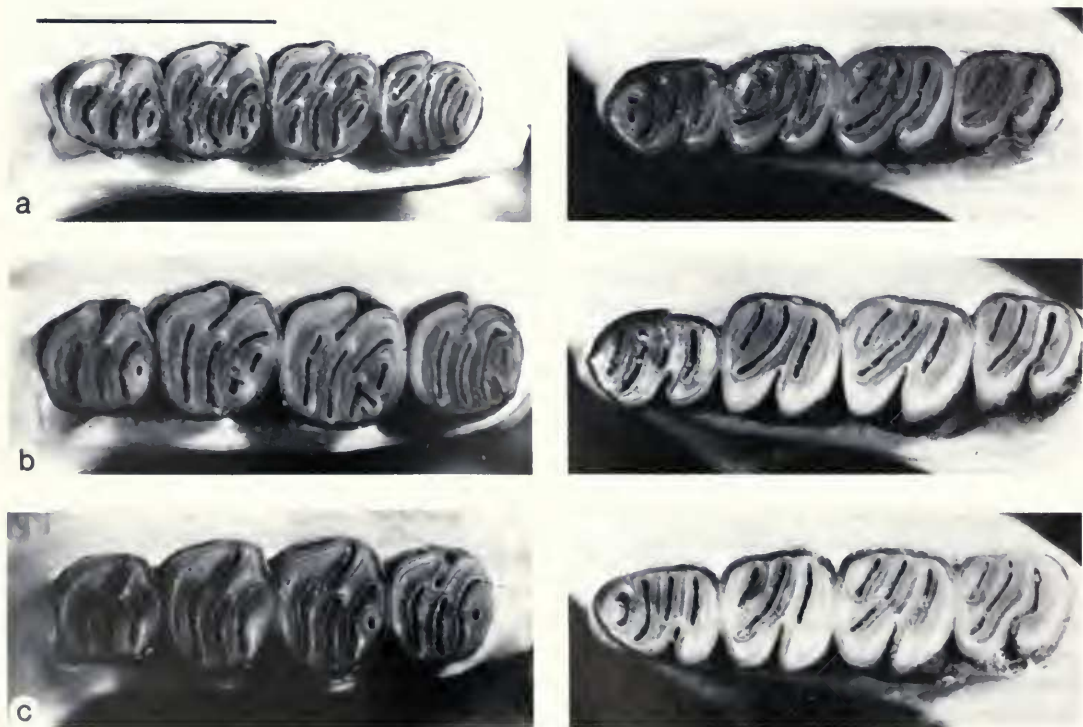

Fig. 25.   Upper (left) and lower (right) toothrows of *P. steerei* of the *goeldii*-group; all specimens from La Poza, Río Santiago, Amazonas, Peru; scale = 5 mm. **a,** MVZ 157871. **b,** MVZ 157863. **c,** MVZ 157861.
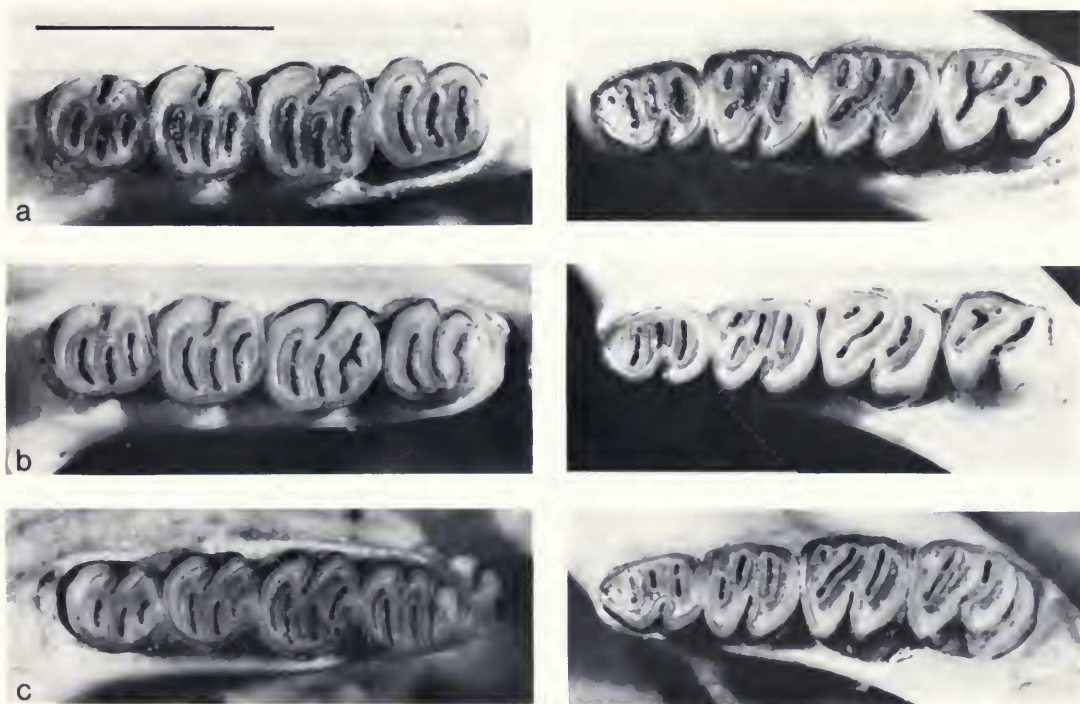
FIG. 26. Upper (left) and lower (right) toothrows of *P. brevicauda* (**a-b**) and *P. longicaudatus* (**c**) of the *longicaudatus*-group; scale = 5 mm. **a**, MVZ 157584—Peru: Amazonas; La Poza, Río Santiago. **b**, MVZ 157855—Peru: Amazonas; La Poza, Río Santiago. **c**, JRS 222—Paraguay: Chaco; 54 km E Agua Dulce (specimen to be deposited in National Museum, Asunción, Paraguay).

phenomena create difficulties in counting folds and clearly are partly responsible for some of the variability observed within and between samples. To minimize this extraneous variation, the data assembled here are based on individuals in age classes 8 or 9 (as defined by Patton & Rogers, 1983) where folds are still mostly confluent with the sides of each tooth.

Taxa of the *semispinosus*-group (fig. 24; table 5), followed by those of the *goeldii*-group (fig. 25),
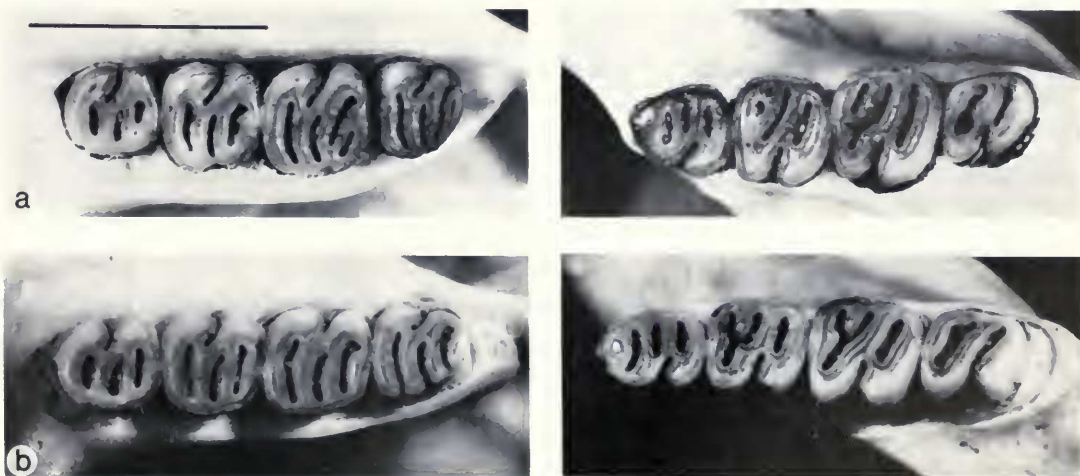

FIG. 27. Upper (left) and lower (right) toothrows of *P. cuvieri* of the *cuvieri*-group; scale = 5 mm. **a**, MVZ 157874—Peru: Amazonas; La Poza, Río Santiago. **b**, MVZ 160091—Venezuela: Bolivár; 69 km S Río Cuyuní.

TABLE 5. Counterfold patterns of the cheekteeth of spiny rats, subgenus *Proechimys*. Folds are given as frequencies for each tooth, based largely on specimens of the age classes 8 and 9 (Patton & Rogers, 1983).

Species group/ region or taxon	N	dPM⁴			M¹			M²		
		2	3	4	2	3	4	2	3	4
semispinosus-group										
Central America	76	⋯	1.00	⋯	⋯	0.92	0.08	⋯	0.70	0.30
Northern Colombia	36	⋯	1.00	⋯	⋯	0.89	0.11	⋯	0.71	0.29
Central Colombia	12	⋯	0.67	0.33	⋯	0.58	0.42	⋯	0.30	0.70
Northern Ecuador	10	⋯	0.80	0.20	⋯	0.30	0.70	⋯	⋯	1.00
Southern Ecuador	29	⋯	1.00	⋯	⋯	0.97	0.03	0.05	0.85	0.10
oconnelli	19	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
goeldii-group										
Colombia–Ecuador	9	⋯	0.25	0.75	⋯	0.12	0.88	⋯	0.08	0.92
Northern Peru	91	⋯	0.36	0.64	⋯	0.30	0.70	⋯	0.10	0.90
Central Peru	13	⋯	0.85	0.15	⋯	0.75	0.25	⋯	0.55	0.45
SE Peru–Bolivia	18	⋯	0.92	0.12	⋯	0.78	0.22	⋯	0.22	0.78
Brazil–Venezuela	21	⋯	0.79	0.21	⋯	0.58	0.42	⋯	0.25	0.75
Central Amazon	61	⋯	0.86	0.14	⋯	0.72	0.28	⋯	0.57	0.43
Eastern Amazon	108	⋯	1.00	⋯	⋯	1.00	⋯	⋯	0.98	0.02
longicaudatus-group										
Colombia–Ecuador	7	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
Northern Peru	134	⋯	1.00	⋯	⋯	1.00	⋯	⋯	0.97	0.03
Central Peru	19	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
SE Peru–Bolivia	36	⋯	1.00	⋯	⋯	1.00	⋯	⋯	0.95	0.05
Southern Bolivia–Brazil	37	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
cuvieri-group										
Guianas	3	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
Brazil	24	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
Peru	20	⋯	1.00	⋯	⋯	1.00	⋯	⋯	0.80	0.20
2n = 40, Balta	5	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
simonsi-group										
Colombia–Ecuador	12	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
Northern Peru	39	⋯	1.00	⋯	⋯	1.00	⋯	⋯	0.88	0.12
Central Peru	24	⋯	1.00	⋯	⋯	0.98	0.02	⋯	0.76	0.24
SE Peru–Bolivia	31	⋯	1.00	⋯	⋯	1.00	⋯	⋯	0.68	0.32
guyannensis-group										
Goiás	20	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
Pará	50	⋯	1.00	⋯	⋯	1.00	⋯	⋯	0.98	0.02
Central Amazon	31	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
NW Brazil–Venezuela	34	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
SE Venezuela	95	⋯	1.00	⋯	0.02	0.98	⋯	0.03	0.97	⋯
Suriname	17	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
trinitatus-group										
chrysaeolus	12	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
mincae	19	⋯	1.00	⋯	⋯	1.00	⋯	0.16	0.84	⋯
trinitatus	12	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
urichi	6	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
guairae	2	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
hoplomyoides	1	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
decumanus-group	17	⋯	1.00	⋯	⋯	1.00	⋯	⋯	1.00	⋯
canicollis-group	13	⋯	1.00	⋯	1.00	⋯	⋯	1.00	⋯	⋯

* Five folds occur on dpm₄ with frequencies of 0.02 and 0.01, respectively.

exhibit the most complex counterfold patterns. Specimens of *P. semispinosus* from central Colombia south into northern Ecuador have the highest average number of folds per tooth, particularly of the maxillary row (table 5); this number decreases slightly to the north and south. *Proechimys oconnelli* shows the lowest counterfold number for this group. In the *goeldii*-group, specimens from Co-

TABLE 5. *Continued.*

\	M³	\	\	dpm₄	\	\	m₁	\	\	m₂	\	\	m₃	\
2	3	4	2	3	4	2	3	4	2	3	4	2	3	4
...	0.91	0.09	...	0.62	0.38	0.01	0.99	...	0.05	0.90	0.05	0.18	0.81	0.01
...	0.77	0.23	...	0.44	0.56	...	1.00	...	...	0.97	0.03	0.20	0.73	0.07
...	0.83	0.17	...	...	1.00	...	1.00	...	...	1.00	...	...	0.83	0.17
...	...	1.00	...	...	1.00	...	1.00	...	...	0.90	0.10	...	1.00	...
0.05	0.85	0.10	...	0.25	0.75	...	1.00	...	...	1.00	...	0.48	0.52	...
0.04	0.96	...	...	1.00	...	0.18	0.82	...	0.22	0.78	...	0.85	0.15	...
...	0.28	0.72	...	...	1.00	...	1.00	...	...	1.00	...	...	1.00	...
...	0.14	0.86	...	...	0.98*	...	0.95	0.05	...	0.93	0.07	...	1.00	...
...	0.23	0.77	...	...	1.00	...	1.00	...	...	1.00	...	...	1.00	...
...	0.58	0.42	...	...	1.00	...	1.00	...	...	1.00	...	...	1.00	...
...	0.54	0.46	...	...	1.00	...	1.00	...	...	1.00	...	0.07	0.93	...
...	0.70	0.30	...	0.06	0.93*	...	1.00	...	0.02	0.98	...	0.05	0.95	...
0.06	0.92	0.02	...	0.33	0.67	0.01	0.99	...	0.10	0.90	...	0.50	0.50	...
...	1.00	...	...	0.70	0.30	...	1.00	...	...	1.00	...	0.23	0.77	...
...	0.98	0.02	...	0.74	0.26	...	1.00	...	0.02	0.98	...	0.26	0.74	...
...	1.00	...	...	0.75	0.25	...	1.00	...	0.11	0.89	...	0.46	0.54	...
...	0.98	0.02	...	0.71	0.29	0.02	0.98	...	0.02	0.98	...	0.43	0.57	...
...	1.00	...	...	0.98	0.02	0.14	0.86	...	0.10	0.90	...	0.69	0.31	...
...	1.00	...	...	0.67	0.33	...	1.00	...	0.18	0.82	...	0.33	0.67	...
...	1.00	...	...	0.94	0.06	0.02	0.98	...	0.24	0.76	...	0.33	0.67	...
...	0.98	0.02	...	0.25	0.75	...	1.00	...	...	1.00	...	0.95	0.05	...
...	1.00	...	...	0.79	0.21	...	1.00	...	...	1.00	...	1.00	...	...
0.04	0.96	...	...	0.75	0.25	...	1.00	...	...	1.00	...	...	1.00	...
...	0.97	0.03	...	0.70	0.30	...	1.00	...	0.01	0.99	...	0.15	0.84	0.01
...	1.00	...	...	0.42	0.58	0.03	0.97	...	...	1.00	...	0.21	0.79	...
...	0.79	0.21	...	0.29	0.71	...	1.00	...	...	1.00	...	0.11	0.89	...
0.08	0.92	...	...	1.00	...	0.52	0.48	...	0.75	0.25	...	1.00	...	...
0.11	0.89	...	...	0.85	0.15	0.33	0.67	...	0.39	0.61	...	0.96	0.04	...
0.11	0.89	...	...	0.91	0.09	0.75	0.25	...	0.75	0.25	...	0.92	0.08	...
0.12	0.88	...	...	0.90	0.10	0.67	0.33	...	0.62	0.38	...	0.84	0.16	...
0.36	0.64	...	...	1.00	...	0.78	0.22	...	0.85	0.15	...	0.97	0.03	...
...	1.00	...	...	1.00	...	1.00	...	...	1.00	...	...	1.00	...	...
...	1.00	...	...	0.97	0.03	...	1.00	...	0.35	0.65	...	0.50	0.50	...
0.62	0.38	...	...	1.00	...	0.98	0.02	...	0.98	0.02	...	0.97	0.03	...
0.05	0.95	...	...	1.00	...	0.18	0.82	...	0.22	0.78	...	0.30	0.70	...
0.21	0.95	...	...	1.00	...	0.25	0.75	...	0.30	0.70	...	0.71	0.29	...
1.00	...	...	...	1.00	...	1.00	...	...	1.00	...	...	1.00	...	...
...	1.00	...	...	1.00	...	...	1.00	...	...	1.00	...	...	1.00	...
0.04	0.96	...	...	1.00	...	0.04	0.96	...	0.63	0.37	...	0.98	0.02	...
1.00	...	...	1.00	...	...	1.00	...	...	1.00	...	...	1.00	...	...

lombia south to northern Peru and east into Venezuela and adjacent Brazil have the highest fold counts (table 5); those from Ecuador represent *quadruplicatus*, which was named by Hershkovitz (1948) for its high fold number. Counts decrease slightly to the south into Bolivia and central and eastern Brazil (table 5).

The *longicaudatus*-group members have a con-

FIG. 28. Upper (left) and lower (right) toothrows of *P. simonsi* of the *simonsi*-group; scale = 5 mm. **a**, MVZ 157950—Peru: Amazonas; La Poza, Río Santiago. **b**, MVZ 166035—Peru: Madre de Dios; Albergue, Río Madre de Dios.

sistent fold count for the upper teeth throughout their ranges (fig. 26; table 5). The lower cheekteeth, however, show a decrease in fold number from north to south: samples referred to *P. longicaudatus* are characterized by only two folds on the last molar; specimens referred to *P. brevicauda* typically have the first and second medial folds on m_3 displaying degrees of coalescence (see fig. 26a–b). The *cuvieri*-group shows a fold count similar to that of the *longicaudatus*-group (table 5), and these two groups cannot be distinguished in pattern (compare fig. 26 with fig. 27). Taxa of the *simonsi*-group are somewhat intermediate between the *goeldii*- and *longicaudatus*-groups in fold number (fig. 28). The upper cheekteeth, particularly M^2, show a slight increase in number of folds

from north to south, as does dpm_4 (table 5). This geographic pattern is the reverse of that seen in both the *goeldii*- and *longicaudatus*-groups over the same part of the western Amazon Basin.

Taxa of the *guyannensis*-group are uniform in number and pattern of counterfolds throughout their range (fig. 29; table 5). They are characterized by having three folds on most teeth, often with two folds on the lower molars, and only rarely four folds on dpm_4. Members of the *trinitatus*-, *decumanus*-, and *canicollis*-groups display the lowest counterfold number (table 5) and, hence, the simplest pattern (fig. 30). Specimens of *P. canicollis* have the least complex cheekteeth of any taxon in the subgenus *Proechimys*, with two folds on each tooth the general rule.
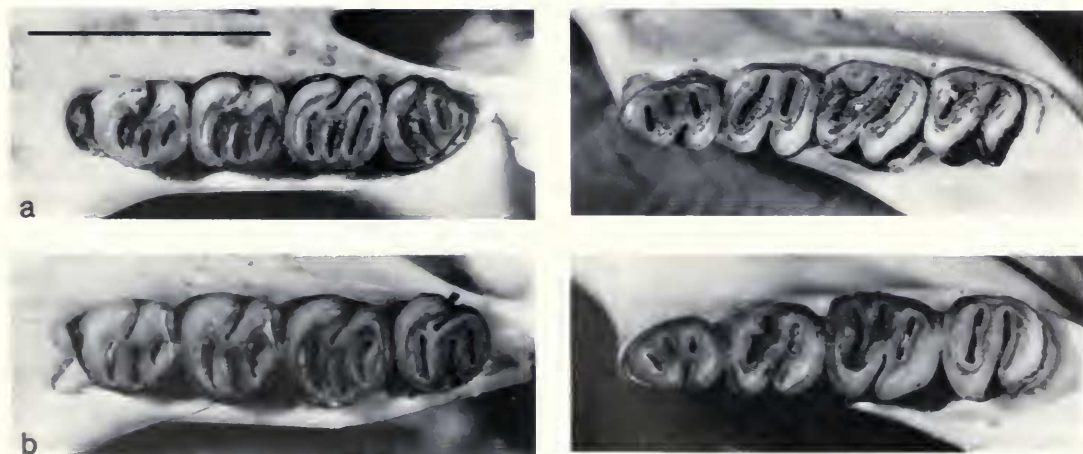

FIG. 29. Upper (left) and lower (right) toothrows of *P. guyannensis* (**a**) and *P. roberti* (**b**) of the *guyannensis*-group; scale = 5 mm. **a**, AMNH 130737—Venezuela: Bolívar; Auyantepui. **b**, AMNH 134309—Brazil: Goiás; Anápolis.

Fig. 30. Upper (left) and lower (right) toothrows of representatives of the *trinitatus* (**a-c**) and *canicollis* (**d**) groups; scale = 5 mm. **a,** *P. chrysaeolus,* FMNH 69039—Colombia: Bolívar; San Juan Nepumoceno. **b,** *P. mincae,* FMNH 13203—Colombia: Magdalena; Minca (topotype). **c,** *P. guairae,* FMNH 92588—Colombia: Arauca; Río Cobaria. **d,** *P. canicollis,* FMNH 69109—Colombia: Bolívar; San Juan Nepumoceno.

Remarks and Prospectus

Nine species groups of spiny rats (subgenus *Proechimys*) are defined herein, and 59 of the 67 names which have been proposed are allocated to one or another of these groups. Although the defined groups differ from those proposed recently by Gardner and Emmons (1984), it is reassuring that we have grouped taxa similarly, with only minor exceptions, despite our use of different suites of characters. Our common conclusions indicate that characters are not hopelessly chaotic geographically (see, for example, Thomas, 1928), but that consistent patterns are recognizable.

The preceding discussion, however, neither suggests the number of species that are likely present in each of the groups defined, nor comments on the phyletic relationships among them. I would like here to summarize my opinions as to the likely number and distribution of the species contained within each group. It remains for future work, both in the field and in the museum, to verify the accuracy of these hypotheses.

The *decumanus-, canicollis-,* and *simonsi-*groups are considered monotypic; certainly the restricted ranges and uniform character distributions of both *Proechimys decumanus* and *P. canicollis* support this view. Despite a much broader geographic range, character variation among populations assigned to the *simonsi-*group is either negligible or clinal in nature. Indeed, this is perhaps the most consistently recognizable group of spiny rats because of this character uniformity (see also Gardner & Emmons, 1984). Even the karyotype is invariant throughout the species range, based on samples available from southern Colombia (Reig

& Useche, 1976) to southern Peru (Patton & Gardner, 1972; Gardner & Emmons, 1984). By seniority, the single species in the *simonsi*-group should be recognized as *P. simonsi* Thomas, with the names *hendeei* Thomas and *nigrofulvus* Osgood considered synonyms.

The *guyannensis*-group members are close to *P. simonsi* in most salient features described here. Their bacula are nearly indistinguishable, as are characters of the incisive foramina and mesopterygoid fossa. Differences exist in counterfold pattern, but these could represent nothing more than geographic variation. Only the analysis of samples from the hiatus in western Brazil between the known distributions of these taxa (see fig. 1) will permit such a determination. Certainly, of the groups defined herein, the *simonsi*- and *guyannensis*-groups are more similar in examined characters than any of the others. Future work may indicate that these groups should be condensed into one.

More than one species is likely present, however, in my *guyannensis*-group. Karyotypic variation is large, as diploid number ranges from 44 to 30 among the limited geographic samples (see Gardner & Emmons, 1984). Moreover, there are some seemingly striking geographic differences in some of the characters examined, although not in all. For example, specimens from eastern Pará, Goiás, and Minas Gerais states of Brazil (referred to *oris* Thomas and *roberti* Thomas) have broader and shallower mesopterygoid fossae and a less developed infraorbital canal than do those from elsewhere in the group's range. Clearly, a more refined and critical examination of detailed geographic variation in these characters is needed; the view provided here is simply too general to judge adequately the significance of this variation.

The *goeldii*-group varies more over its geographic range than any other; nevertheless, much of the variation in counterfold pattern, for example, appears clinal, and abrupt character shifts which might signal species-level demarcations are not readily apparent in the characters I examined. Known karyotypic variation also appears limited, with samples examined from southern Venezuela ($2n = 26$, FN = 42; Reig & Useche, 1976), Ecuador and northern Peru ($2n = 28$, FN = 42–44; Gardner & Emmons, 1984), and central and southern Peru ($2n = 24$, FN = 42; Patton & Gardner, 1972; Gardner & Emmons, 1984). Specimens from the western Amazon Basin and from the Casiquiare region of southern Venezuela appear fairly homogeneous in counterfold and pelage color char-

acters. There does, however, appear to be relatively sharp transition of some characters, particularly those of the pelage (not examined in this report), in the central Amazon Basin between the lower Río Negro and the Río Tapajós. It is probable that at least two species are present in this group, a western one to which the name *steerei* Goldman would apply, and an eastern one to which the senior name *goeldii* Thomas applies.

The character summaries provided in this paper tend to minimize the difficulties that I had in assigning individual specimens to species groups, and thus may provide a sense of false security. This is particularly true for specimens of the *goeldii* and *guyannensis* groups from the eastern parts of both ranges, primarily in Pará state, Brazil. There are more individual question marks regarding group assignments for specimens from this region than for any other area or group, and much more detailed effort is necessary to confirm the character differences described herein.

Within the *longicaudatus*-group there appears to be at least two species, *Proechimys longicaudatus* Rengger from eastern Bolivia east through adjacent Brazil into northern Paraguay; and *P. brevicauda* Gunther, which occupies the remainder of the group range as depicted in Figure 3. An area of rather sharp character transition, particularly in pelage color and color pattern but also in bacular measurements, for example, occurs in the upper Río Iténez and Río Mamoré of southern El Beni and Santa Cruz in Bolivia. The limited samples of *P. longicaudatus* examined show little variation throughout its range. Samples of *P. brevicauda* from southern Colombia to northern Bolivia are, however, quite variable, and more than one species may be represented here. Gardner and Emmons (1984) suggested that the Ecuadoran populations referred to *gularis* are specifically distinct from northern Peruvian *brevicauda* based on karyotypic differences ($2n = 30$, FN = 48 without large subtelocentric autosomes, versus $2n = 30$, FN = 48 with two pairs of large subtelocentrics). They also suggested that the central and southern Peruvian populations might represent a valid subspecies of *P. brevicauda,* to which the name *elassopus* would apply, based both on karyotypic ($2n = 28$, FN = 50) and color pattern differences. A thorough analysis of geographic variation within this group is certainly warranted.

No more than two species appear to be represented in the *semispinosus*-group; *P. semispinosus* (Tomes) is distributed from Nicaragua south along the Pacific lowlands to southern Ecuador, and *P.*

oconnelli is restricted to the western llanos in the vicinity of Villavicencio, Colombia. Karyotypic variation occurs in *P. semispinosus,* but such is minimal (2n = 30, FN = 50–54); *P. oconnelli* differs only by a single fusion/fission (Gardner & Emmons, 1984). A more detailed examination of geographic variation in *P. semispinosus* is needed before the intraspecific status of the large number of named forms referred to this group can be properly evaluated.

As mentioned previously, the *cuvieri*-group is clearly divisible into two biological units. The widespread species *P. cuvieri* Petter is uniform in its characters, including karyotype, from the Guianas to northern Peru. The status of the 2n = 40 karyotypic form from Balta in eastern Peru, however, is an enigma at present. It is clearly specifically distinct from *cuvieri* and is only placed in this group because of similar bacular design. I do not believe that it is a relative of *guyannensis*-group taxa, as suggested by both Patton and Gardner (1972) and Gardner and Emmons (1984). I have also not been able to identify this form with certainty anywhere except at Balta.

Finally, I have treated the various taxa assigned to my *trinitatus*-group as though they were species, primarily because I have examined relatively few specimens from only scattered localities. Nevertheless, it is likely that a number of species exist in this group. Karyotypic variation is extensive (see reviews by Reig et al., 1980; Reig, 1981), and both karyotypic and electromorphic data (Benado et al., 1979) differentiate a *guairae* superspecies (including *guairae, poliopus, ochraceous,* and *mincae* [see Gardner & Emmons, 1984]) and a *trinitatus* superspecies (composed of *trinitatus* and *urichi*). *Proechimys hoplomyoides* is clearly a species distinct from the above, as indicated by Gardner and Emmons (1984). These latter authors included *chrysaeolus* in their *semispinosus*-group and *magdalenae* in their *brevicauda*-group, positions which are not supported by the bacular characters covered here. If their true relationships do lie with the *trinitatus*-group, they too are probably separate species. Certainly, *chrysaeolus* is the most distinctive member of my *trinitatus*-group in incisive foraminal and counterfold characters.

Acknowledgments

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Appendix: Specimens Examined

Repositories for specimens examined in this study are as follows: American Museum of Natural History (AMNH), British Museum (Natural History) (BM[NH]), Field Museum of Natural History (FMNH), Louisiana State University Museum of Zoology (LSU), University of California Museum of Vertebrate Zoology (MVZ), University of Michigan Museum of Zoology (UMMZ), and National Museum of Natural History (USNM).

canicollis-group

COLOMBIA: Atlántico: Cienaga de Guajaro, Sabana Larga (1, USNM). **Bolívar:** San Juan Nepumoceno (9, FMNH). **Magdalena:** Bonda (29, AMNH; 1, FMNH; 8, USNM; 2, BM[NH]); Bonda, Finca Veracruz (2, USNM); Mamatoca (11, AMNH; 7, FMNH); Minca Road (1, AMNH); El Líbano plantation (6, AMNH); Santa Marta (11, AMNH; 1, FMNH); Río Guaimaral, Valledupar (13, USNM); Aguas Verdes, Valledupar (26, USNM); Parmarito, Valledupar (2, USNM); El Orinoco, Río Cesar, Valledupar (14, USNM); Villanueva, Valledupar (33, USNM).

VENEZUELA: Zulia: Perijá, Río Cogollo (7, FMNH); Río Cachiri (1, MVZ).

cuvieri-group

P. CUVIERI

BRAZIL: Pará: Ilha do Taiuno, Rio Tocantins (25, AMNH); Vila Bela Imperatriz, Serra de Parintins, Rio Amazonas (1, AMNH).

GUYANA: Kamakusa (1, AMNH); Kalacoon (1, AMNH); Kartabo (8, AMNH); Minehaha Creek (1, AMNH); Samin Island, Mazarani River (6, AMNH); Maracai Creek, Demarara River (1, BM[NH]); Demarara River (2, BM[NH]); Supinaam River (2, BM[NH]).

PERU: Amazonas: La Poza, Río Santiago (1, MVZ). **Loreto:** Pebas, Río Amazonas (5, BM[NH]);

Orosa, Río Amazonas (14, AMNH); Pto. Indiana, Río Amazonas (1, AMNH); Santa Luisa, Río Nanay (3, FMNH); Sarayacu, Río Ucayali (3, AMNH).

SURINAME: Carolinakreek (5, FMNH); Wilhelmina Mts., West River (1, FMNH); Finisanti, Saramacca River (1, FMNH); Lelydorppplan (2, FMNH); La Poule (2, FMNH); Dirkshoop (3, FMNH).

$2n = 40$

PERU: Ucayali: Balta, Río Curanja (5, LSU).

decumanus-group

ECUADOR: El Oro: Santa Rosa (2, AMNH). **Guayas:** Chongón (4, BM[NH]): Chongoncito (10, AMNH); Cerro Manglar Alto (3, AMNH); Cerro Baja Verde (1, AMNH); Los Pozos (25, AMNH). **Los Ríos:** Vinces, Hda. Pijigual (2, AMNH). **Manabí:** Bahia de Caraques, Río Briseno (7, AMNH).
PERU: Piura: Quebrada Bandarrango (1, FMNH); Laguna Lamadero (2, FMNH). **Tumbes:** Matapalo (6, FMNH).

goeldii-group

BOLIVIA: El Beni: Riberalta, Vaca Diez (13, USNM); 13 km W Riberalta (11, USNM); 3.5 km NW Riberalta (2, USNM); 5 km NW Riberalta (3, USNM); Río Mamoré, 4 km below Santa Cruz (2, AMNH); 6 km S Buena Hora (1, AMNH); Río Mamoré, 7 km N Lagionha (2, AMNH); Río Mamoré, 5 km S Guayaramarin (1, AMNH); Río Mamoré, 5 km S Guayaramarin (1, AMNH); Río Mamoré (2, AMNH); Río Mamoré, opposite Cascajal (1, AMNH); Río Mamoré, 17 km NNW Nuevo Berlín (1, AMNH).
BRAZIL: Acre: Sena Madureira, Mandel Urbano (1, USNM); Rio Branco, 3–4 km S Rio Branco (2, USNM). **Amazonas:** Faro, Rio Yurnunda [= Nhamunda] (2, BM[NH]); Faro, Paraiso (2, AMNH); Acajutuba, Rio Negro (2, BM[NH]); Mirapinima, Rio Negro (5, AMNH); Cacauo Pereira Igarapé, Rio Negro (9, AMNH); Yucabi, Rio Negro (1, AMNH); Tatu, Rio Uaupés (3, AMNH); Itamarati, Rio Uaupés (1, AMNH); Tahuapunta, Rio Uaupés (2, AMNH); Manacapurú, Rio Solimões (2, BM[NH]); Maturaca Mission, northern Amazonia (1, USNM); Humaitá, km 886–990, Br 230 (3, USNM); São Antonio de

Amatari (1, AMNH); Borba, Rio Madeira (2, AMNH); Auara Igarapé, Rio Madeira (15, AMNH); São Antonio de Uayara (9, AMNH); Rosarinho, Rio Madeira (11, AMNH); Ipixuna, Rio Purus (1, USNM); Rio Purus, Hyutanahan (4, USNM). **Mato Grosso:** Serra da Chapada (4, BM[NH]); Utiariti, Rio Papagaio (1, AMNH). **Pará:** Cametá, Rio Tocantins (2, BM[NH]); Manapiri Island, Rio Tocantins (2, BM[NH]); Ilha do Taiuno, Rio Tocantins (57, AMNH); Mocajuba, Rio Tocantins (1, AMNH); Baião, Rio Tocantins (3, AMNH); Urucum de Corumbá (1, FMNH); Tuary, Rio Tapajós (1, FMNH; 11, AMNH); Aramanay, Rio Tapajós (6, AMNH); Piquiatuba, Rio Tapajós (7, AMNH); Igarapé Amorim, Rio Tapajós (30, AMNH); Igarapé Brabo, Rio Tapajós (2, AMNH); Farinicatuba, Rio Tapajós (1, AMNH); Aquiatuba, Rio Tapajós (1, AMNH); Limoal, Rio Tapajós (1, AMNH); Inajatuba, Rio Tapajós (1, AMNH); Fordlandia, Rio Tapajós (5, AMNH); Santarém (1, BM[NH]); km 84, Santarém-Cuiabá hwy (27, USNM); km 212, Santarém-Cuiabá hwy (4, USNM); km 216, Santarém-Cuiabá hwy (3, USNM); Itaituba, Rio Tapacurazinho (9, USNM); Mojui Dos Campos (15, USNM); km 19, Itaituba-Jacaréacanga hwy (12, USNM); km 25, Itaituba-Altamira hwy (4, USNM); Itaituba (6, USNM); 54 km S, 150 km W Altamira (3, USNM); Agrovila, km 43 Itaituba-Altamira rd (2, USNM); Vila Bela Imperatriz, south bank Rio Amazonas (3, AMNH); Serra de Parintins, Vila Bela Imperatriz, south bank Rio Amazonas (7, AMNH); Porto de Moz, Rio Xingu (2, AMNH); Vilarinho do Monte, Rio Xingu (4, AMNH). **Rondônia:** Pista Nova, 8 km N Porto Vêlho (4, USNM).
COLOMBIA: Caquetá: La Tagua, Tres Troncos, Río Caquetá (13, FMNH); Río Mecaya (1, FMNH); Florencia, Mantanito (3, FMNH); La Murelia, Río Bodoquera (2, FMNH).
ECUADOR: Napo: San Francisco, Río Napo (8, UMMZ); Llunchi, Río Napo (5, UMMZ).
PERU: Amazonas: La Poza, Río Santiago (128, MVZ). **Huánuco:** San Antonio, Río Pachitea (1, BM[NH]); Port Leguia, Río Pachitea (1, BM[NH]). **Loreto:** Yurimaguas (1, FMNH); Orosa, Río Amazonas (14, AMNH); Boca Río Curaray (2, AMNH); Pto. Indiana, Río Amazonas (27, AMNH); Río Mazán (2, AMNH); Río Panduro (6, AMNH); Pampa Chica, Iquitos (1, AMNH); Santa Rita, Iquitos (5, FMNH); Santa Luisa, Río Nanay (9, FMNH); Santa Elena, Río Samiria (11, FMNH); Río Samiria (10, FMNH); San Lorenzo, Río Marañón (1, FMNH; 4, BM[NH]); Boca Río Peruate, Río Amazonas (2, FMNH); Lagunas (10, FMNH; 1, BM[NH]); Quistacocha, Maynas (4, FMNH); Río Tigre, 1 km above Río Tigrillo (7, FMNH); Pebas, Río Amazonas (1,

BM[NH]); Sarayacu, Río Ucayali (16, AMNH); San Jeronimo, Río Ucayali (1, BM[NH]); Cantamana (3, BM[NH]); Lago Mirano, Río Napo (6, BM[NH]). **Madre de Dios:** La Pastora, Maldonado (1, FMNH); Tambopata, Puerto Maldonado (3, USNM); Itahuania (1, FMNH). **Ucayali:** Yarinacocha (6, FMNH; 9, LSU); Chicosa, upper Río Ucayali (6, BM[NH]); 59 km W Pucallpa (1, USNM); Pucallpa (2, AMNH); Santa Rosa, Río Ucayali (12, AMNH); Fernando Stahl Mission (14, AMNH); Cumaria (5, BM[NH]); Tushemo, Masisea, Río Ucayali (1, BM[NH]); Balta, Río Curanja (1, LSU).

VENEZUELA: Amazonas: 68 km SE Esmeralda (9, USNM); Río Orinoco, Tamatama (13, USNM); Casiquiare Canal, Capibara (14, USNM); 30 km SSE Puerto Ayacucho, Coromoto (8, USNM); 18 km SSE Puerto Ayacucho (2, USNM); Mt. Duida, Río Casiquiare, Quemapure (2, AMNH); Mt. Duida, 8 mi from Río Orinoco (2, AMNH); Mt. Duida, Esmeralda (11, AMNH); Mt. Duida, Caño Seco (1, AMNH); Mt. Duida, El Merey (2, AMNH); Río Orinoco, Paripari (1, AMNH); Río Orinoco, Boca del Río Ocamo (3, AMNH).

guyannensis-group

BRAZIL: Amapá: Serra do Navio (3, USNM); Calicoene (1, USNM); Capoeira (1, USNM). **Amazonas:** Hd. Rio Tucaro (1, USNM); Serra de Neblina (1, USNM); Rio Uaupés, Tauarate (1, AMNH); Rio Uaupés, Tahuapunta (10, AMNH); Rio Negro, Tatu (1, AMNH); Rio Negro, Uacara (1, AMNH); Rio Negro, Camanaos (1, AMNH); Rio Negro, Pira-pocú (1, AMNH); Rio Negro, Manaus (1, AMNH); Faro, north bank Rio Amazonas (10, AMNH); Rio Paratucu (2, AMNH); Rio Nhamundá, Castanhal (20, AMNH); Rio Nhamundá, São José (3, AMNH). **Goiás:** Fazenda Cangalha (1, USNM); Anápolis (79, AMNH). **Minas Gerais:** Rio Jordão, Araguari (1, FMNH; 10, BM[NH]). **Pará:** Providência (1, FMNH); Cametá, Rio Tocantins (1, FMNH; 1, AMNH); Ilha do Taiuno, Rio Tocantins (1, AMNH); Baião, Rio Tocantins (1, AMNH); Manapiri Island, Rio Tocantins (1, AMNH); Maranhão, Alto Parnaíba (1, FMNH); km 84, Santarém-Cuiabá hwy (53, USNM); km 212, Santarém-Cuiabá hwy (1, USNM); km 217, Santarém-Cuiabá hwy (4, USNM); km 19, Itaituba-Jacaréacanga hwy (2, USNM); Rio Tapacurazinho (10, USNM); Agrovila, Altamira (6, USNM); km 43, Itaituba-Altamira hwy (5, USNM); Marabá, Serra Norte (7, USNM); Jatobal (11, USNM); Itupiranga (1, USNM); Belém (46, USNM; 1, AMNH); Igarapé-Açu (13, AMNH);

Tury-Açu, Maranhão (1, BM[NH]); Abaeté (8, BM[NH]); Patagônia (15, AMNH); Capim (10, AMNH); Igarapé Amorim, Rio Tapajós (17, AMNH); Inajatuba, Rio Tapajós (1, AMNH); Igarapé Brabo, Rio Tapajós (4, AMNH); Limoal, Rio Tapajós (1, AMNH); Vila Bela Imperatriz, south bank Rio Amazonas, Lago Andina (1, AMNH); Vila Bela Imperatriz, south bank Rio Amazonas, Boca Rio Andina (3, AMNH); Vila Bela Imperatriz, south bank Rio Amazonas, Serra de Parintins (3, AMNH). **Roraima:** Uaico, Rio Uraricoera (3, AMNH); Rio Cotingo, Limão (64, AMNH).

SURINAME: Brokopondo: Carolinakreek (4, FMNH); Lawa Mission, Lawa River (1, AMNH); Loksie Hattie, Saramacca River (4, FMNH); Finisanti, Saramacca River (8, FMNH).

VENEZUELA: Amazonas: 68 km SE Esmeralda, Mavaca (2, USNM); 68 km SE Esmeralda, Boca Masiaca (1, USNM); Río Canucunuma, Belén (26, USNM); Casiquiare Canal, Capibara (3, USNM); San Juan, Río Manapiari (17, USNM); Río Orinoco (2, USNM); Río Orinoco, Boca del Río Ocamo (5, AMNH); Río Casiquiare, El Merey (6, AMNH); Río Casiquiare, Buena Vista (4, AMNH); Río Casiquiare, Solano (2, AMNH); Río Casiquiare (1, AMNH); Río Casiquiare, 2 mi W Tamasu (1, AMNH); Mt. Duida, foothills camp (1, AMNH); Mt. Duida, middle camp (7, AMNH); Mt. Duida, Valle de los Monos (2, AMNH); Mt. Duida, Playa del Río Base (6, AMNH); Mt. Duida, Caño Seco (1, AMNH); Mt. Duida, Pie del Cerro (1, AMNH); Mt. Duida, La Lajo, Río Orinoco (1, AMNH).

longicaudatus-group

BOLIVIA: El Beni: 6 km S Buena Hora (1, AMNH); Río Machupo, 15 km above Horquilla (1, AMNH); San Ignacio (47, USNM); 3.6 km NNE San Ignacio (9, USNM); Riberalta (2, FMNH); Riberalta, Vaca Diez (4, USNM); Fortaleza (2, USNM); San Marco, 3.2 km SW San Joaquín (3, USNM; 22, FMNH); San Joaquín (7, USNM; 90, FMNH; 4, AMNH); 20 km S San Joaquín, Est. Yutiole (1, AMNH); Cafetal, 20 km SE San Ramón (4, USNM); Río Iténez, opposite Príncipe da Beira (3, AMNH); Río Mamoré, 5 km NE Río Grande mouth (5, AMNH); Río Mamoré, 1 mi NW Guayaramarin (5, AMNH); Guayaramarin (1, AMNH); Río Mamoré, 5 km S Guayaramarin (2, AMNH); Río Mamoré (1, AMNH); Río Mamoré, opposite Cascajal (2, AMNH); Río Mamoré, 2 km SE Puerto Siles (5, AMNH); 10 km E San Antonio (1, AMNH); Rurrenabaque (1, AMNH);

Lago Victoria (1, USNM; 14, FMNH); La Esperanza, 42 km NE San Joaquín (1, USNM); Est. Barranquita, 20 km S San Joaquín (3, FMNH); El Carmen (20, FMNH); Azunta (27, FMNH); Santo Dios (10, FMNH); San Pedro (2, FMNH); Caravana (17, FMNH); San Pablo (8, FMNH); Filadelfia (6, FMNH); Acapulco (1, FMNH); Buena Vista (1, FMNH); Arruda (2, FMNH); Centenela (1, FMNH); Cinco (4, FMNH); Las Pavas (6, FMNH); Providencia (1, FMNH); Puerto Siles (1, FMNH); San Andrés (2, FMNH); San Juan (3, FMNH); Tapera Jorillo (3, FMNH); Veintedos (1, FMNH); Huchulu (1, USNM); Las Penas (1, USNM); Pampitas (1, USNM). **Cochabamba:** El Mojón (4, FMNH); San Rafael, 19 km SW Villa Tunari (2, USNM); 4 km SE Villa Tunari (1, USNM); 2 km E Villa Tunari (2, AMNH); Todos Santos (3, FMNH; 13, AMNH); Mission San Antonio, Río Chimore (8, AMNH); El Palmar (5, FMNH); Charuplaya, upper Río Secure (5, BM[NH]). **La Paz:** 5 km SE Guanay, Río Challana (2, UMMZ); Caranavi (4, UMMZ); Mapiri (4, AMNH; 3, BM[NH]); Ticunhuaya (5, AMNH); San Ernesto (2, BM[NH]). **Pando:** Río Nareuda (2, AMNH). **Santa Cruz:** Buenavista (4, FMNH; 10, BM[NH]); Ascención de Guarayos (12, FMNH); Río Surutu (1, BM[NH]); Río Ichilo, 54 km S Boca Río Chaparé (12, AMNH); Río Ichilo, 52 km S Boca Río Chaparé (2, AMNH); Río Ichilo, 34 km S Boca Río Chaparé (4, AMNH); Río Ichilo, 30 km S Boca Río Chaparé (1, AMNH); Río Mamoré, 2 km from Boca Río Chaparé (2, AMNH); Warnes (2, USNM); 1.3 km NE Warnes (8, USNM); 1 km NNW Warnes (9, USNM); 3 km SW Warnes, Santa Rosita (6, USNM); Florida, near Floripondio (2, FMNH); Cerro Hosana (1, FMNH).

BRAZIL: Acre: Sena Madureira, Mandel Urbano (1, AMNH); Rio Branco, 3–4 km S Rio Branco (2, USNM). **Mato Grosso:** Tapirapuã, Rio Siputuba (2, AMNH); Urucum (2, AMNH); Serra da Chapada (6, BM[NH]); Fazenda Acurizal (2, USNM); Aripuanã, Humboldt-Aripaunã (8, USNM); Corumbá (7, USNM); 7 km SE Corumbá (1, USNM); 22 km S Corumbá (2, USNM); Sta. Theresa, 7 km WSW Urucum (7, USNM); Cuiabá, 10 km N Cuiabá (1, USNM); Limão, 48 km W Cáceres, Rio Jauru (15, USNM). **Rondônia:** Pista Nova, 8 km N Porto Vêlho (6, USNM); Porto Vêlho (1, FMNH).

COLOMBIA: Caquetá: Río Mecaya (2, FMNH); Florencia, Mantanito (17, FMNH); Florencia (17, AMNH); La Murelia, Río Bodoquera (15, AMNH).

ECUADOR: Napo: San Francisco, Río Napo (17, UMMZ); Intillama, Río Napo (2, UMMZ); Llunchi, Río Napo (2, UMMZ); near Río Napo, Oriente (4, BM[NH]); San José Abajo (6, AMNH); Río Suno Abajo (2, AMNH). **Pastaza:** Canelos, Río Bobonaza

(2, BM[NH]); Río Pastaza (2, BM[NH]); Río Pindo Yacu (2, FMNH); Río Yana Rumi (1, FMNH); Río Capihuara (3, FMNH); Río Copataza (3, FMNH); Río Lipuno (1, AMNH); Sarayacu (4, AMNH); Canelos (1, AMNH).

PERU: Amazonas: Huampami, Río Cenepa (173, MVZ); La Poza, Río Santiago (38, MVZ). **Huánuco:** Port Leguia, Río Pachitea (3, BM[NH]); San Antonio, Río Pachitea (1, BM[NH]); 35 km NE Tingo María, Sta. Elena (2, LSU); Tingo María (5, BM[NH]; 1, LSU; 9, FMNH); Chinchavita (10, BM[NH]). **Loreto:** Yurimaguas (2, USNM; 2, BM[NH]; 25, FMNH); Pebas, Río Amazonas (10, BM[NH]); Boca Río Curaray (32, AMNH); Iquitos, Río Amazonas (1, BM[NH]); Santa Luisa, Río Nanay (1, FMNH); San Fernando, Río Yavari (1, FMNH); Cantamana (3, BM[NH]). **Madre de Dios:** Tambopata, Puerto Maldonado (23, USNM); Lago Sandoval, Río Madre de Dios (3, MVZ); La Pastora, Puerto Maldonado (5, FMNH); Albergue, Río Madre de Dios (8, MVZ). **Pasco:** Nevati Mission (54, AMNH); San Pablo (32, AMNH). **Puno:** Santo Domingo [= Inca Mines] (1, BM[NH]; 5, AMNH; 6, FMNH). **San Martín:** Achinamiza, Río Huallaga (1, AMNH). **Ucayali:** Yarinacocha (1, FMNH); Pucallpa (1, FMNH); 59 km W Pucallpa (21, USNM); Fernando Stahl Mission (2, AMNH); Balta, Río Curanja (18, LSU; 10, MVZ).

semispinosus-group

P. SEMISPINOSUS

COLOMBIA: Antióquia: Urabá, Villa Arteaga, Río Curulao (23, FMNH). **Cauca:** Río Saija (16, FMNH); El Papayo, Río Saija (3, FMNH); La Boca, Río Saija (3, FMNH); San José (1, FMNH; 11, AMNH); Novita trail, western Andes (1, AMNH). **Chocó:** Condoto (1, BM[NH]); Río Docampado (12, FMNH); Río Saudo (16, FMNH); Unguía (24, FMNH); Bagado (4, AMNH); Andaqueda (1, AMNH). **Córdoba:** Socorre, upper Río Sinú (4, FMNH). **Nariño:** La Guayacana (15, FMNH); La Candelilla (4, FMNH); Isla Gorgona (5, BM[NH]; 2, FMNH); Barbacoas (8, AMNH). **Valle de Cauca:** Sabaleta 2, FMNH).

COSTA RICA: Alajuela: San Carlos (2, FMNH). **Limón:** Cariari (5, LSU); Finca La Lola (1, LSU); 4.6 km W Limón (2, MVZ). **Puntarenas:** San Geronimo (2, FMNH; 2, AMNH); Rincón de Osa (1, LSU); Palmar Sur (2, LSU); Palmar (28, AMNH). **San José:** 16.3 km SE San Isidro (2, MVZ); 34.7 km SE San Isidro (2, MVZ); 1.6 km W Villa Colón (2, MVZ);

2.8 km W Villa Colón (1, MVZ); 14.5 km N Quepos, Río Damitas (1, LSU); Caspirola (1, LSU).

ECUADOR: Esmeraldas: San Javier (6, BM[NH]; 1, FMNH); Esmeraldas (3, AMNH). **Manabí:** Río Mongaya (2, FMNH). **Pichincha:** Santo Domingo (9, BM[NH]). **El Oro:** Santa Rosa (3, BM[NH]; 4, AMNH); Pasaje (4, AMNH). **Los Ríos:** Bucay (1, AMNH); Puente de Chimbo, Bucay (2, AMNH); Cague, El Destino (6, AMNH); Limón, Balsapampa to Babahoyo road (7, AMNH); Ventura (1, AMNH).

NICARAGUA: Rivas: Río Grande (11, AMNH). **Zelaya:** Toro Rapids (2, AMNH); Bluefields (5, MVZ).

PANAMA: Canal Zone: Barro Colorado Island (3, AMNH); Gatun (20, AMNH); Maxim Ranch (3, AMNH); Buena Vista Peninsula (6, LSU); Río Chagres (2, AMNH); Balboa (1, AMNH). **Chiriquí:** Boquerón (1, BM[NH]; 12, FMNH; 56, AMNH); Bugaba (6, BM[NH]). **Darién:** Cituro (4, AMNH); El Real (8, AMNH); Boca de Cupe (4, AMNH); Tapaliza (3, AMNH); Tacarcuna (2, AMNH). **Panamá:** Tocumen (3, BM[NH]); Gobernador Island (7, BM[NH]); Savanna near Panamá (3, BM[NH]); 0.8 km N Paraíso (4, MVZ); Cebaco Island (5, BM[NH]); San Miguel Island (3, FMNH; 5, AMNH).

P. OCONNELLI

COLOMBIA: Meta: Quaicaramo (3, AMNH; 15, USNM); Mambita (2, USNM); La Aguadita (1, AMNH); Barrigona (2, AMNH); Restrepo (12, AMNH); Villavicencio (26, AMNH; 2, USNM; 10, UMMZ; 4, MVZ); 3 km N Villavicencio (1, USNM); Los Micos, San Juan de Arama (16, FMNH).

simonsi-group

BOLIVIA: El Beni: Río Mamoré (1, AMNH). **Cochabamba:** Yungas (1, AMNH). **Pando:** Río Nareuda (1, AMNH).

COLOMBIA: Caquetá: Río Mecaya (9, FMNH); La Murelia, Río Bodoquera (1, AMNH).

ECUADOR: Napo: Intillana, Río Napo (5, UMMZ); near Río Napo (1, BM[NH]); San José Abajo (3, AMNH); Río Suno Abajo (1, AMNH). **Pastaza:** Río Pindo Yacu (4, FMNH); Río Bobonaza, Montalvo (3, FMNH); Río Bobonaza (2, BM[NH]); Río Yana Rumi (1, FMNH); Río Capihuara (2, FMNH); Río Pastaza (5, BM[NH]); Río Tigre (4, BM[NH]). **Zamora:** Gualaquiza (1, BM[NH]).

PERU: Amazonas: Huampami, Río Cenepa (3, MVZ); headwaters Río Kagka (2, MVZ); La Poza,

Río Santiago (3, MVZ); Yambrasbamba (1, FMNH; 5, BM[NH]). **Cajamarca:** Huarandosa (1, AMNH). **Cuzco:** 40 km E Quincemil above Río Marcapata (2, LSU); Cosñipata, Hda. Villa Carmen (4, FMNH); Urubamba (1, BM[NH]). **Junín:** Río Perené (1, BM[NH]). **Loreto:** Yurimaguas (3, FMNH); Santa Luisa, Río Nanay (5, FMNH); Boca Río Curaray (22, AMNH); Orosa, Río Amazonas (1, AMNH); Cerro Azul, Cantamana, Río Ucayali (4, BM[NH]); Cantamana (1, BM[NH]). **Madre de Dios:** Itahuanía (4, FMNH); Tambopata, Puerto Maldonado (4, USNM); Aguas Calientes, Río Alto Madre de Dios (10, MVZ); Hda. Erika, Río Alto Madre de Dios (3, MVZ); Albergue, Río Madre de Dios (7, MVZ). **Pasco:** Mairo, Río Palcazu (2, BM[NH]); San Juan (1, USNM); Bermudas de Loma Linda (13, AMNH); San Pablo (3, AMNH). **San Martín:** Puca Tambo, 50 mi E Chachapoyas (10, BM[NH]). **Ucayali:** Balta, Río Curanja (2, MVZ; 17, LSU); Yarinacocha (1, FMNH); 59 km W Pucallpa (33, USNM).

trinitatus-group

P. CHRYSAEOLUS

COLOMBIA: Antióquia: Puri, above Cáseres (8, FMNH); Medellín (1, BM[NH]). **Bolívar:** San Juan Nepumoceno (26, FMNH); Coloso (20, FMNH); Margarita (3, BM[NH]). **Boyacá:** Muzo (3, FMNH; 2, BM[NH]). **Cauca:** Río Chili (2, BM[NH]). **Córdoba:** Catival, upper Río San Jorge (4, FMNH); Socorre, upper Río Sinu (18, FMNH). **Tolima:** Santana (3, BM[NH]).

VENEZUELA: Táchira: San Cristóbal (1, BM[NH]).

P. GUAIRAE

COLOMBIA: Arauca: Río Cobaria (22, FMNH); Río Bojaba (5, FMNH); Río Arauca (18, FMNH); Fatima, Río Cobaria (12, FMNH). **Boyacá:** La Argentina, Río Cubugón (4, FMNH); El Porvenir, Río Cubugón (3, FMNH).

VENEZUELA: Barinas: Guaquitas (1, MVZ). **Portuguesa:** Sto. Domingo (1, MVZ).

P. HOPLOMYOIDES

VENEZUELA: Bolívar: Mt. Roraima, Arabupu (1, AMNH); Mt. Roraima, Rondon camp (1, AMNH).

P. MAGDALENAE

COLOMBIA: Antióquia: near La Providencia, SW Zaragoza (1, USNM); 25 km S and 22 km W Zaragoza (48, USNM). **Bolívar:** Norosi, Mompos, Río San Pedro (18, USNM).

P. MINCAE

COLOMBIA: Magdalena: Minca (2, BM[NH]; 6, USNM; 78, AMNH); Bonda (12, AMNH; 2, USNM); Onaca (4, AMNH); Buritaca (1, AMNH); Don Dago (1, AMNH); Cuaco (1, AMNH); Masinga Vieja (1, AMNH); Manzanares (2, USNM); Colonia Agrícola de Caracolicito (1, USNM); El Salado (5, USNM).

P. OCHRACEOUS

VENEZUELA: Zulia: El Panorama, Río Aurare (2, FMNH).

P. POLIOPUS

VENEZUELA: Táchira: San Juan de Colón (1, FMNH). **Zulia:** Kasmera (1, MVZ).

P. TRINITATUS

TRINIDAD: Caparo (2, FMNH); Princestown (2, FMNH; 1, AMNH); Turure Forest (2, AMNH); Cumaca (1, AMNH); Oropuche Heights (2, FMNH); Chaguaramas (1, MVZ).
VENEZUELA: Monagas: 2 km N and 4 km W Caripe (1, USNM). **Sucre:** 5 km S and 25 km E Carúpano (1, USNM).

P. URICHI

VENEZUELA: Sucre: San Estéban (2, FMNH); Quebrada Seca (1, FMNH; 1, AMNH); Campo Alegre (1, AMNH); Los Palmales (1, AMNH).