

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 123

**The Glans Penis in Neotropical Cricetines
(Family Muridae) with Comments on
Classification of Muroid Rodents**

BY

EMMET T. HOOPER

AND

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ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
MARCH 18, 1964

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THE GLANS PENIS IN NEOTROPICAL CRICETINES
(FAMILY MURIDAE), WITH COMMENTS ON CLASSIFICATION
OF MUROID RODENTS

AMONG important recent contributions to knowledge of the South American cricetine fauna are those of Gyldenstolpe (1932), Osgood (1943), Simpson (1950, 1953), Pearson (1958), Cabrera (1961), and Hershkovitz (see Literature Cited). From the standpoint of the present report a late monograph by Hershkovitz (1962) is noteworthy because therein the author not only presents a detailed analysis of a large group of those rodents (the phyllotines) but, utilizing his impressive mass of data on South American forms and drawing on other published information, he also offers an estimate of evolution of the cricetines, with attention focused on Neotropical species. His estimate of interrelationships of the principal South American cricetine stocks constitutes a framework against which the many more data that are needed for understanding the fauna may be checked.

We refer to that framework in the present report in which we compare samples of 43 Neotropical cricetine species in regard to morphology of the glans penis. Since the 43 species represent most of the principal stocks of South American cricetines (Hershkovitz, *ibid.*) the data obtained from them not only indicate something of the types of phalli in those major lines but also may provide clues to interrelationships of those and other muroid rodents.

MATERIALS AND METHODS

Glandes that provide the basic data of this report are indicated below; the species are listed in systematic order, following Cabrera (1961) for South America and Miller and Kellogg (1955) for those North American species unlisted by Cabrera.

- Oryzomys palustris*: Florida, Oap. Locks, 2. Georgia, McIntosh Co., 1. Texas, Nueces and San Patricio counties, 2.
O. devius: Panamá, Chiriquí, 2.
O. fulvescens: México, Chiapas, 1; Puebla, 1.
O. albigularis: Colombia, Boyaca, 8. Panamá, Darien, 2. Venezuela, Aragua, 1; Paramo de Tama, 1.
O. alfaroi: Costa Rica, Cartago, 1. México, Guerrero, 1. Panamá, Chiriquí, 1; Darien, 2.
O. caliginosus: Colombia, Arauca, 12; Boyaca, 9; Magdalena, 1. Costa Rica, Cartago, 2; Heredia, 4. Panamá, Darien, 4.
O. capito: Colombia, Arauca, 1; Vaupes, 1. Panamá, Darien, 2; Los Santos, 4. Trinidad, San Rafael, 1.
O. concolor: Colombia, Boyaca, 3. Panamá, Darien, 1. Suriname, Lelydorppalan, 1. Venezuela, Aragua, 2.
O. flavescens: Argentina, Buenos Aires, 1. Uruguay, Canelones, 2.

- O. longicaudatus*: Chile, Arauco, 2; Malleco, 2.
O. melanotis: México, Jalisco, 1.
O. nigripes: Suriname, Finisanti, 1; Loksie Hattie, 1.
Neacomys guianae: Venezuela, Aragua, 5.
N. spinosus: Peru, Huanuco, 2.
Nectomys alfari: Panamá, Darien, 2.
Rhipidomys mastacalis: Brazil, Goyaz, 1.
Nyctomys sumichrasti: Laboratory-reared, 3. Panamá, Bocas del Toro, 1.
Thomasomys aureus: Peru, Cuzco, 1.
T. cinereus: Colombia, Antioquia, 1.
T. laniger: Colombia, Boyaca, 5.
Akodon arviculoides: Brazil, Rio de Janeiro, 1. Argentina, Misiones, 1.
A. azarae: Argentina, Buenos Aires, 2. Uruguay, Rocha, 1.
A. boliviensis: Peru, Cuzco, 2; Puno, 1.
A. obscurus: Argentina, Buenos Aires, 4.
A. orophilus: Peru, Ocabampa Valley, 1.
A. surdus: Peru, Idma, Santa Ana, 2.
A. urichi: Colombia, Arauca, 4; S. Negra, 1. Venezuela, Aragua, 1.
A. bogotensis: Colombia, Antioquia, 1.
Zygodontomys brevicauda: Colombia, Magdalena, 1; Meta, 1. Costa Rica, Puntarenas, 3. Suriname, Carolina Creek, 2; Loksie Hattie, 1. Venezuela, Aragua, 1.
Z. lasiurus: Brazil, Goyaz, 1.
Oxymycterus paramensis: Peru, Puno, 1.
O. rufus: Argentina, Buenos Aires, 4. Uruguay, Canelones, 1.
Notiomys valdivianus: Chile, Malleco, 3.
Scapteromys aquaticus: Argentina, Buenos Aires, 3.
S. tumidus: Uruguay, Canelones, 2.
Calomys callosus: Brazil, Mato Grosso, 1.
C. laucha: Argentina, Buenos Aires, 6.
Eligmodontia typus: Argentina, Neuguen, 3.
Phyllotis darwini: Peru, Arequipa, 1; Cuzco, 1.
P. pictus: Peru, Cuzco, 2; Puno, 1.
P. griseoflavus: Argentina, La Pampa, 2.
Holochilus brasiliensis: Peru, Loreto, 3. Suriname, Paranaribo, 1. Uruguay, Canelones, 1.
Rheomys hartmanni: Costa Rica, San José, 3.

Although most of the glandes are contained in the University of Michigan Museum of Zoology a few are the property of the American Museum of Natural History (AM), the Chicago Natural History Museum (CM), The Museum at Michigan State University (MSU), Museo Nacional de Historia Natural (MNHN) in Montevideo, Uruguay, and the U. S. National Museum (US). Curators of those collections and other persons have graciously taken special effort to provide us with specimens. For such consideration we are indebted to S. Anderson, R. H. Baker, J. A. Crespo, J. Dorst, J. K. Greer, C. O. Handley, Jr., P. Hershkovitz, A. Langguth, D. M. Lay, J. N. Layne, E. Massoia, J. Meester, O. Rossolimo, and R. Van Gelder. We are especially grateful for the assistance of Philip Hershkovitz who iden-

tified many specimens, instructed collectors for the Chicago Natural History Museum to preserve materials for us, and assisted in other ways. Our special thanks also go to Charles O. Handley, Jr., who likewise gave freely of his time and effort in furthering our studies. The excellent illustrations are the work of Suzanne Runyan, staff artist of the Museum of Zoology. The project received financial support from the National Science Foundation.

Measurements listed in Tables 1 and 2, all of adults, are described as follows:

LENGTH OF HIND FOOT.—Heel to claw-tip length.

LENGTH OF GLANS.—Distance from glans-prepuce junction to most distal part of glans as measured along dorsal midline.

DIAMETER OF GLANS.—Greatest diameter of glans including spines.

PROXIMAL BONE.—Length of main bone, the basal segment of the baculum.

MEDIAL DIGIT.—Midline length of the cartilage and/or bone which comprises the medial distal segment of the baculum; measured distad from the limits of the main bone.

TOTAL LENGTH OF BACULUM.—Distance from proximal face of main bone to tip of medial digit.

LATERAL DIGIT.—Length of one of the lateral pair of segments (cartilage and bone) of the baculum; measured distad from the limits of the main bone.

All of the glandes examined are of the complex type, basically like that described and figured for microtines (Hooper and Hart, 1962), but with another set of modifications of the basic structural plan. As in microtine and other complex glandes all are invested with spines and are more or less barrel-shaped. In some species there are well defined external lobes, the large dorsal ones of which are here termed the parotoid pair. Below the crater floor in each glans there is a pair of single or bilobed sacs which, apparently interconnected with similar tissues that extend distad into the bacular mounds, seem to be part of the erectile vascular system of the glans (Hooper, 1962:4). In the terminal crater there are typically a dorsal papilla, urethral flap and three bacular mounds which house three digits. Each of those structures varies in size, shape, and ornamentation, and one or more of them may be absent in a few species. In adults, while the proximal segment of the baculum is osseous in all species, the distal digits typically are cartilaginous, rarely osseous, and the lateral pair in several species is small or even absent. There are vascular cores in all bacular mounds, even in the lateral ones when they are small and contain minute bacular segments or none at all. Additional descriptions of the architecture of the complex glans, and variations therein, are found on the following pages and elsewhere (Hooper and Hart, 1962).

TABLE 1
MEAN MEASUREMENTS (MM.) OF THE GLANS PENIS IN 39 SPECIES OF
NORTH AND SOUTH AMERICAN RODENTS

Species	No.	Hind Foot Length	Glans		Baculum, lengths			
			Length	Diameter	Proximal Bone	Medial Digit	Total Length	Lateral Digit
<i>Oryzomys</i>								
<i>palustris</i>	3	33	7.3	4.6	3.9	2.7	6.6	1.9
<i>albigularis</i>	11	35	6.1	3.4	4.1	2.2	6.3	1.7
<i>devius</i>	2	37	7.6	3.3	5.7	2.4	8.1	2.0
<i>capito</i>	9	31	5.2	3.0	3.3	1.7	5.0	1.4
<i>concolor</i>	6	29	5.7	3.3	3.5	1.8	5.3	1.4
<i>flavescens</i>	3	26	4.3	2.3	2.8	1.4	4.2	1.0
<i>fulvescens</i>	9	24	4.1	2.2	2.8	1.4	4.2	0.9
<i>nigripes</i>	1	23	4.6	2.4	2.9	1.6	4.5	1.1
<i>longicaudatus</i>	4	30	4.1	2.5	2.8	1.3	4.1	0.9
<i>caliginosus</i>	16	29	5.7	2.8	4.2	1.3	5.5	1.0
<i>alfaroi</i>	3	25	5.0	2.4	4.1	1.0	5.1	0.6
<i>melanotis</i>	1	27	4.9	2.0	3.7	0.9	4.6	0.6
<i>Neacomys</i>								
<i>guianae</i>	4	23	4.0	2.3	2.8	1.0	3.8	0.7
<i>Nectomys</i>								
<i>alfari</i>	2	38	7.0	2.3	4.4	1.2	5.6	0.8
<i>Rhipidomys</i>								
<i>mastacalis</i>	1	26	6.3	3.8	5.3	2.1	7.4	1.7
<i>Thomasomys</i>								
<i>aureus</i>	1	35	10.1	4.7	8.1	4.5	12.6	1.2
<i>cinereus</i>	1	31	5.4	3.1	4.6	1.8	6.4	1.5
<i>laniger</i>	5	26	4.9	3.2	4.3	1.0	5.3	0.4
<i>Nyctomys</i>								
<i>sumichrasti</i>	3	25	8.2	3.9	6.0	1.1	7.0	..
<i>Akodon</i>								
<i>boliviensis</i>	2	21	6.0	3.5	4.0	1.8	5.8	1.3
<i>arviculoides</i>	1	27	5.9	3.8	4.5	1.7	6.2	1.2
<i>azarae</i>	3	20	5.1	3.0	3.2	1.5	4.7	1.4
<i>surdus</i>	2	23	5.2	3.9	3.2	1.3	4.5	0.8
<i>urichi</i>	2	23	6.0	3.7	3.7	1.7	5.4	1.2
<i>obscurus</i>	1	21	3.9	1.9	2.2	1.2	3.4	0.6
<i>Notiomys</i>								
<i>valdivianus</i>	2	22	7.9	4.0	4.6	2.1	6.7	1.5
<i>Oxymycterus</i>								
<i>paramensis</i>	1	24	5.5	3.0	3.8	1.8	5.6	1.0
<i>rufus</i>	2	28	6.8	3.7	5.0	1.9	6.9	1.1
<i>Scapteromys</i>								
<i>aquaticus</i>	3	39*	9.1	4.5	5.9	..	6.9	1.0

TABLE 1 (Concluded)
 MEAN MEASUREMENTS (MM.) OF THE GLANS PENIS IN 39 SPECIES OF
 NORTH AND SOUTH AMERICAN RODENTS

Species	No.	Hind Foot Length	Glans		Baculum, lengths			
			Length	Diameter	Proximal Bone	Medial Digit	Total Length	Lateral Digit
<i>Calomys</i>								
<i>callosus</i>	1	22	5.7	3.0	3.1	1.9	5.0	1.4
<i>laucha</i>	3	16*	4.6	2.4	2.4	1.8	4.2	1.3
<i>Eligmodontia</i>								
<i>typus</i>	2	22	3.8	2.1	2.8	1.0	3.8	0.9
<i>Phyllotis</i>								
<i>darwini</i>	1	29	7.4	4.5	3.9	3.7	7.6	2.7
<i>griseoflavus</i>	2	28	5.8	3.1	3.1	2.1	5.2	1.3
<i>pictus</i>	1	26	5.4	3.8	3.9	2.2	6.1	1.1
<i>Zygodontomys</i>								
<i>brevicauda</i>	2	25	5.9	3.2	3.6	1.8	5.4	1.2
<i>lasiurus</i>	1	24	5.4	3.9	4.0	1.9	5.9	1.5
<i>Holochilus</i>								
<i>brasiliensis</i>	1	53*	9.9	5.3	6.3	3.0	9.3	2.0
<i>Rheomys</i>								
<i>hartmanni</i>	3	28	6.2	3.4	4.2	1.9	6.2	1.1

* Estimated (original measurement without claw length).

TABLE 2
 RATIOS (PER CENT) OF MEASUREMENTS LISTED IN TABLE 1
 Excepting those in one column (diameter: length of glans), all ratios are of lengths

Species	Diam. Glans	Glans	Baculum	Baculum	Proximal Bone	Medial Digit
	Len. Glans	Foot	Foot	Glans	Glans	Proximal Bone
<i>Oryzomys</i>						
<i>palustris</i>	61	22	21	93	55	71
<i>albigularis</i>	55	18	18	102	67	51
<i>devius</i>	41	21	21	103	75	42
<i>capito</i>	59	17	16	98	65	52
<i>concolor</i>	60	19	18	93	62	49
<i>flavescens</i>	55	17	16	99	66	49
<i>fulvescens</i>	55	17	18	103	70	49
<i>nigripes</i>	52	20	20	98	67	55
<i>longicaudatus</i>	62	14	14	100	68	46
<i>caliginosus</i>	50	20	19	95	72	33
<i>alfaroi</i>	48	20	19	101	84	24
<i>melanotis</i>	41	18	16	90	76	24
<i>Neacomys</i>						
<i>guianae</i>	59	18	17	96	72	34
<i>Nectomys</i>						
<i>alfari</i>	30	19	15	80	63	28
<i>Rhipidomys</i>						
<i>mastacalis</i>	60	24	28	117	84	40
<i>Thomasomys</i>						
<i>aureus</i>	47	29	37	130	80	56
<i>cinereus</i>	57	17	21	120	85	39
<i>laniger</i>	65	17	21	110	89	36
<i>Nyctomys</i>						
<i>sumichrasti</i>	47	32	27	77	73	18
<i>Akodon</i>						
<i>boliviensis</i>	59	29	29	98	67	46
<i>arviculoides</i>	64	22	23	95	76	38
<i>azarae</i>	60	25	23	92	63	47
<i>surdus</i>	75	22	20	87	62	41
<i>urichi</i>	62	26	23	94	62	45
<i>obscurus</i>	49	19	16	87	56	55
<i>Notiomys</i>						
<i>valdivianus</i>	50	36	30	85	58	47
<i>Oxymycterus</i>						
<i>paramensis</i>	55	23	23	102	69	47
<i>rufus</i>	55	25	25	86	74	39
<i>Scapteromys</i>						
<i>aquaticus</i>	50	24	18	75	65	..

TABLE 2 (Concluded)

RATIOS (PER CENT) OF MEASUREMENTS LISTED IN TABLE 1

Excepting those in one column (diameter: length of glans), all ratios are of lengths

Species	Diam. Glans	Glans	Baculum	Baculum	Proximal Bone	Medial Digit
	Len. Glans	Foot	Foot	Glans	Glans	Proximal Bone
<i>Calomys</i>						
<i>callosus</i>	53	26	23	88	54	61
<i>laucha</i>	53	29	27	92	52	75
<i>Eligmodontia</i>						
<i>typus</i>	55	17	17	100	75	38
<i>Phyllotis</i>						
<i>darwini</i>	61	25	26	103	53	92
<i>griseoflavus</i>	53	21	18	89	54	71
<i>pictus</i>	70	21	23	113	72	56
<i>Zygodontomys</i>						
<i>brevicauda</i>	54	24	22	90	61	50
<i>lasiurus</i>	72	23	25	109	74	48
<i>Holochilus</i>						
<i>brasiliensis</i>	54	19	18	94	64	48
<i>Rheomys</i>						
<i>hartmanni</i>	55	23	22	98	67	47

DESCRIPTIONS OF GLANDES

The following accounts are arranged approximately in accordance with Cabrera's checklist (1961) except where otherwise indicated. We make use of several suprageneric terms employed by various authors in their studies of Neotropical cricetines and have grouped our oryzomyine, thomasomyine, akodont, oxymycterine, scapteromyine, phyllotine, sigmodont, and ichthyomyine representatives under appropriate headings following Hershkovitz (1944, 1955, 1962). Whether the phallic data accord with these groupings, each now defined primarily on dental and other cranial characters, is given attention where appropriate.

ORYZOMYINE GROUP

Of the 43 species sampled in this study 15 are oryzomyine rodents as follows: *Neacomys guianae* and *spinosus*; *Nectomys alfaroi*; *Oryzomys* (*Melanomys*) *caliginosus*; *Oryzomys* (*Oecomys*) *concolor*; *Oryzomys* (*Oligoryzomys*) *flavesens*, *fulvescens*, *longicaudatus*, and *nigripes*; and *Oryzomys* (*Oryzomys*) *albigularis*, *alfaroi*, *capito*, *devius*, *melanotis*, and *palustris*.

To judge from the samples, most of these species are distinguishable in glans and baculum and, further, they form distinctive phallic subgroups

which cut across some generic lines, but as an assemblage they are less diverse in regard to glans and baculum than are current phyllotines, sigmodonts, and thomasomyines.

Although the group is fairly homogeneous it is rather weakly characterized. Only a few slight changes would be required in the following diagnosis to make it fit only part of the group (some species of *Oryzomys* and *Nectomys*, for example) or to encompass some species (of *Holochilus* for example) that are now excluded from the group.

Glans comparatively plain externally, with no more than four weakly to moderately defined lobes (these fewer and less prominent than in *Sigmodon* for example); rim of terminal crater bordered by a band of nonspinous tissue, this abutting against the medial mound and in some species covering the lateral mounds; all three well-developed mounds erect or slightly incurved and comparatively simple (without elaborations as seen in species of *Phyllotis*, *Rhipidomys*, and *Reithrodon* for example), their bacular segments mostly or entirely cartilaginous and the incurved lateral pair at least three-fourths as long as the erect medial one; urethral flap bifurcate distally, its two processes erect or gently curved; dorsal papilla, the only one in the crater, finger-like or triangular in dorsal view and spinous or spineless. No spines present on crater walls and floor, on bacular mounds, or on urethral flap.

The glandes of these oryzomyine rodents are compared below, the species accounts arranged by genera for convenience in reference and, within each genus, on the basis of phallic criteria such that species with similar glandes are approximately in sequence.

Oryzomys

On the basis of structure of glans the species of *Oryzomys* may be arranged in two groups which for convenience we term the *albigularis* and *alfaroi* subgroups.

ALBIGULARIS SUBGROUP

Included here are the following species: *palustris*, *albigularis*, *devius*, *concolor*, *capito*, *flavescens*, *fulvescens*, *nigripes*, and *longicaudatus*.

These species are characterized as follows: glans short—in respect both to its diameter (more than one-half its length) and to the hind foot length (see measurements); parotoid lobes moderately well defined; terminal crater directed distad (not somewhat ventrad as in *Neacomys*), its opening bordered by a broad ring of spineless tissue. Baculum approximately as long as glans, its digits long with respect to the main bone (medial digit exceeding 40 per cent of bone in length).

O. palustris.—The following set of characters distinguishes *O. palustris* from the other oryzomyine rodents examined: glans perhaps the most robust and longest relative to foot length (Tables 1, 2); dorsal parotoid lobes prominent (Fig. 1), the dorsolateral trough bounding each extending distad to the rim of the terminal crater; dorsal and lateral faces of dorsal papilla studded with numerous spines, a condition approached (among *Oryzomys* examined) only in *flavescens*, *fulvescens*, *nigripes*, and *longicaudatus*; a subapical lobule present on the ventral face of each urethral process (Fig. 1)—a configuration seen in no other species of *Oryzomys*.

Baculum shorter than glans but long relative to foot length (exceeded only by *O. devius*), similar in configuration to that of other oryzomyine species, but the main bone much deeper than wide and keeled ventrally in the middle half of its length, expanded apically and either concave or convex proximally; medial digit unusually long (Table 2) and lateral segments more robust and more abruptly incurved distally than in other oryzomyine species; a small ossicle present in the middle one-third of the medial digit of one specimen, likely the oldest of the four at hand.

O. albigularis.—This species is phallically more similar to *devius* and *capito* than to *palustris*. Glans slightly smaller, less robust, and with less prominent lobation than in *palustris* (Fig. 1); dorsal papilla a broad-based conical mound with a spine at its tip but none elsewhere; urethral flap comparatively broad and short (greatest length approximately equal to width and about one-half the length of a lateral digit of the baculum), each of its distal processes stubby and simple, without a subapical lobule (Fig. 1); medial bacular mound, slightly taller but smaller in diameter than each lateral one, projecting beyond the crater rim.

Baculum about equal to glans in length; its proximal segment rather robust, the moderately broad basal part deeply concave between dorsolateral condyles—its proximal outline (as viewed ventrally) gently curved but not deeply emarginate medially—and its distal half deeper than wide; medial digit deeper than wide (with slight distal taper) and scarcely longer than the gently curved and more robust lateral segments; in ventral view the entire distal mass of the baculum is circular in outline.

O. devius.—The phallus of *devius* apparently is essentially an elongate replica of that of *albigularis*. In present samples the glans and baculum of *devius* are slightly larger in all measurements except diameter of glans (Table 1); thus, most proportions of the two species are closely comparable except diameter/length ratio and baculum/glans ratio (Table 2); the two ratios, respectively, reflect the slim glans and disproportionately longer bone in *devius*. The urethral flaps are relatively shorter (approximately one-third the length of a lateral digit of the baculum), but this difference

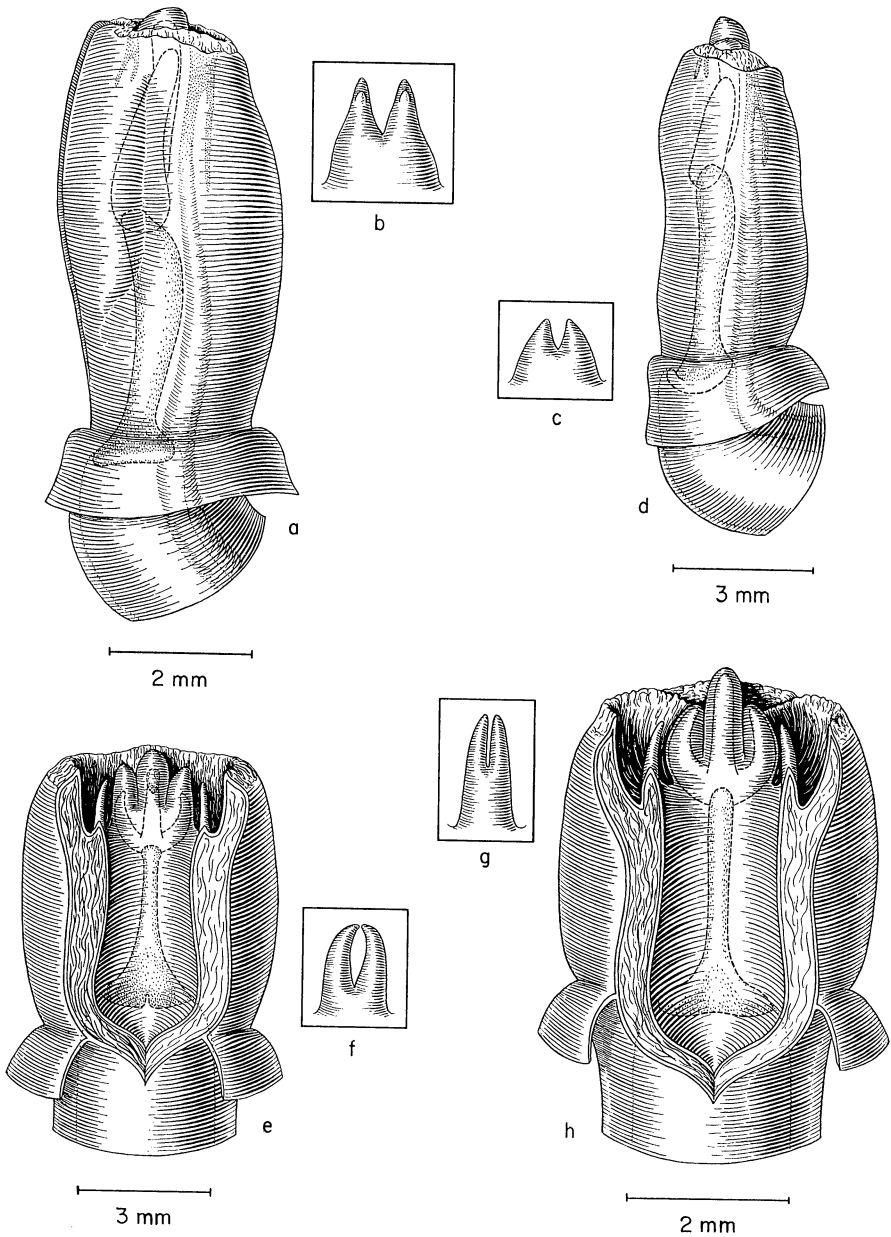


FIG. 1. Views of glans penis (lateral and ventral aspects, the glans incised midventrally in *e*, *h*) and of urethral flap (enlarged, ventral aspect) in four species of *Oryzomys*: *a*, *b*, *palustris* (110388), Texas; *c*, *d*, *albigularis* (CM 18663), Venezuela; *e*, *f*, *concolor* (UMMZ P-3900), Panamá; *g*, *h*, *flavescens* (110444), Argentina.

also may be a function of the greater length of glans in *devius*. The two species are phallically similar.

O. capito.—In morphology of glans and baculum this species fits between *albigularis* and *concolor*, variously resembling each of those species but smaller than both (Tables 1, 2). External parotoid lobes indistinct (much as in *albigularis*); tips of lateral bacular mounds incompletely covered by spineless tissue of crater rim; urethral flap moderate in length (shorter than lateral segments of baculum), its two processes similar to those in *albigularis*. Baculum as long as glans, the osseous part comprising approximately two-thirds of that length, as in *concolor* and *albigularis*; basal part of bone broad and angular, with prominent dorsolateral condyles, the proximal face of the bone (as seen ventrally) strongly convex but medially emarginate; digits essentially as in *concolor*.

O. concolor.—The specimens of *O. concolor* resemble the examples of *O. albigularis* except in the following details: glans slightly smaller in all measurements, but perhaps more stubby (Tables 1, 2) and with slightly more prominent parotoid lobes; dorsal papilla, usually spine-tipped, more elongate and finger-like; urethral processes relatively longer, the length of each about that of a lateral bacular digit (Fig. 1); lateral bacular mounds shorter, completely covered by spineless tissue of crater rim.

Baculum slightly shorter than glans (Table 2); basal part of the bone relatively broader and usually deeply emarginate proximally (Fig. 1); medial digit, as wide as deep and tapered evenly from base to tip, distinctly longer than each lateral segment; a small ossicle present in the tip of the medial digit of one specimen.

O. flavescens.—As indicated in the following diagnosis the phallus of *flavescens* is readily distinguishable from that of *capito* and that of other species of this subgroup of *Oryzomys*. Glans among the smallest seen in our oryzomyine species (Table 1); parotoid lobes well developed, the dorsolateral troughs notching the crater rim (as in *O. palustris*); dorsal part of shelf of nonspinous tissue (rimming the crater) inset approximately on a level with the dorsal papilla (a condition also seen in *Neacomys*); the relatively large, wider than deep, dorsal papilla studded with spines dorsally (2 to 5 spines per papilla in specimens at hand); urethral flap relatively long (length about that of a lateral digit of the baculum), its two processes attenuate. Lateral digits of baculum much shorter than the medial one; the bone like that of other *Oryzomys*, but its broad basal part less angular, the outline (as viewed ventrally) of its proximal face essentially straight or slightly concave, not strongly concave, convex, or deeply emarginate (Fig. 1).

O. fulvescens.—The specimens of *fulvescens* and *flavescens* are closely

similar. The urethral flap in *fulvescens* is broader and shorter than that in *flavescens*, but this variation is slight, possibly of the sort within a single species.

O. nigripes.—Glans of the only adult specimen at hand, although slightly larger and more elongate (Table 1), is closely similar to those of *flavescens* and *fulvescens*; the slight differences possibly represent intraspecific variation.

O. longicaudatus.—The specimens of this species resemble those of *fulvescens* and *flavescens* except that the glans and baculum are slightly shorter with respect to both foot length and diameter of glans (Table 2), external lobes are less prominent, the ventral face of the bone is more deeply concave and the proximal face in ventral view is either entire or emarginate.

ALFAROI SUBGROUP

Grouped here by reason of resemblances of their glandes are three species of *Oryzomys*: *caliginosus*, *alfaroi*, and *melanotis*. Many of their characters which distinguish them as a group from other species of *Oryzomys* are also evident in *Nectomys alfaroi*.

This subgroup is characterized by an elongate glans (diameter/length ratio not exceeding .50) with a comparatively open terminal crater, its rim bordered by a narrow ring of nonspinous tissue, and by a distinctive baculum comprised of a long bone (more than 70 per cent of glans in length) and short digits, the medial one (less than 34 per cent of the proximal bone in length) a slim cylinder much less robust than each of the lateral pair (its dorsoventral diameter one-fourth to one-third that of a lateral digit).

O. caliginosus.—The glans of *caliginosus* resembles that of *albigularis* in external dimensions (Table 1) and configuration; in both species the glans is exteriorly plain, with only traces of dorsal lobes and dorsolateral troughs. Internally, however, there is less resemblance both with *albigularis* and with other species of the *albigularis* subgroup of *Oryzomys*: meatus of crater comparatively large, the surrounding narrow ring of nonspinous tissue not covering the three subequal bacular mounds; dorsal papilla elongate (finger-like), tipped with a single spine; and urethral flap shallowly bifurcate, the two processes curved laterad (Fig. 2).

Baculum slightly shorter than glans, three-fourths of that length contributed by the proximal segment; shaft (distal one-half of bone) comparatively short, only slightly deeper than wide and expanded distally; base of bone gross, its outline in ventral view essentially an equilateral triangle with a medial notch on the proximal face; distal digits short (Table 2),

the three approximately equal in length, but the medial one a thin rod (its dorsoventral thickness approximately one-third that of a lateral digit) strongly contrasted in ventral view with the robust, horn-shaped, lateral pair.

O. alfaroi.—In the following diagnosis *O. alfaroi* is compared especially with *O. caliginosus* which is but slightly larger than *alfaroi* (Table 1) and resembles it in exterior configuration: spine-tipped dorsal papilla possibly relatively larger; urethral flap short (width and height approximately equal) and shallowly cleft, the two short processes erect, not out-curved as in *caliginosus* (Fig. 2).

Proximal segment of baculum unusually long (Table 2), its slim rod-like shaft with small terminal head making up more than the distal one-half of the bone; its base comparatively narrow (Fig. 2); distal digits among the shortest seen in oryzomyines, the medial one slim and the laterals robust in ventral aspect (as in *caliginosus*).

O. melanotis.—The available specimens of this species, all improperly preserved, warrant few comments. The best example, measurements of which are listed in Table 1, resembles specimens of *O. alfaroi*.

Neacomys

N. guianae.—To judge from specimens examined the small stubby glans of *N. guianae* with its dorsal "hood," which directs the crater mouth somewhat ventrad instead of entirely distad, deeply cleft urethral flap, short bacular digits and angular bone, is readily distinguishable from that of all other oryzomyine species examined save possibly *Neacomys spinosus*.

In the following diagnosis, *guianae* is compared especially with *O. flavescens* and *O. fulvescens*, two forms which differ from it in proportions of baculum (Table 2) but which resemble it in size and some other characters: glans stubby (Table 2) and strongly lobate, the parotoid lobes perhaps relatively the largest seen in the oryzomyine samples; these lobes produced distad forming a terminal hood which is so situated as to direct the crater opening more ventrad than is seen in the other oryzomyines (Fig. 2); a shelf of nonspinous tissue present within the crater; medial bacular mound decidedly taller than each lateral one, but the three approximately equal in diameter; dorsal papilla a short spine-tipped cone; urethral flap moderately long (length about that of a lateral digit of the baculum) and deeply cleft, each attenuate process comprising approximately three-fourths the length of the flap.

Baculum slightly shorter than glans, its proximal segment in lateral view similar to that of *flavescens* and *fulvescens*, but in ventral view the

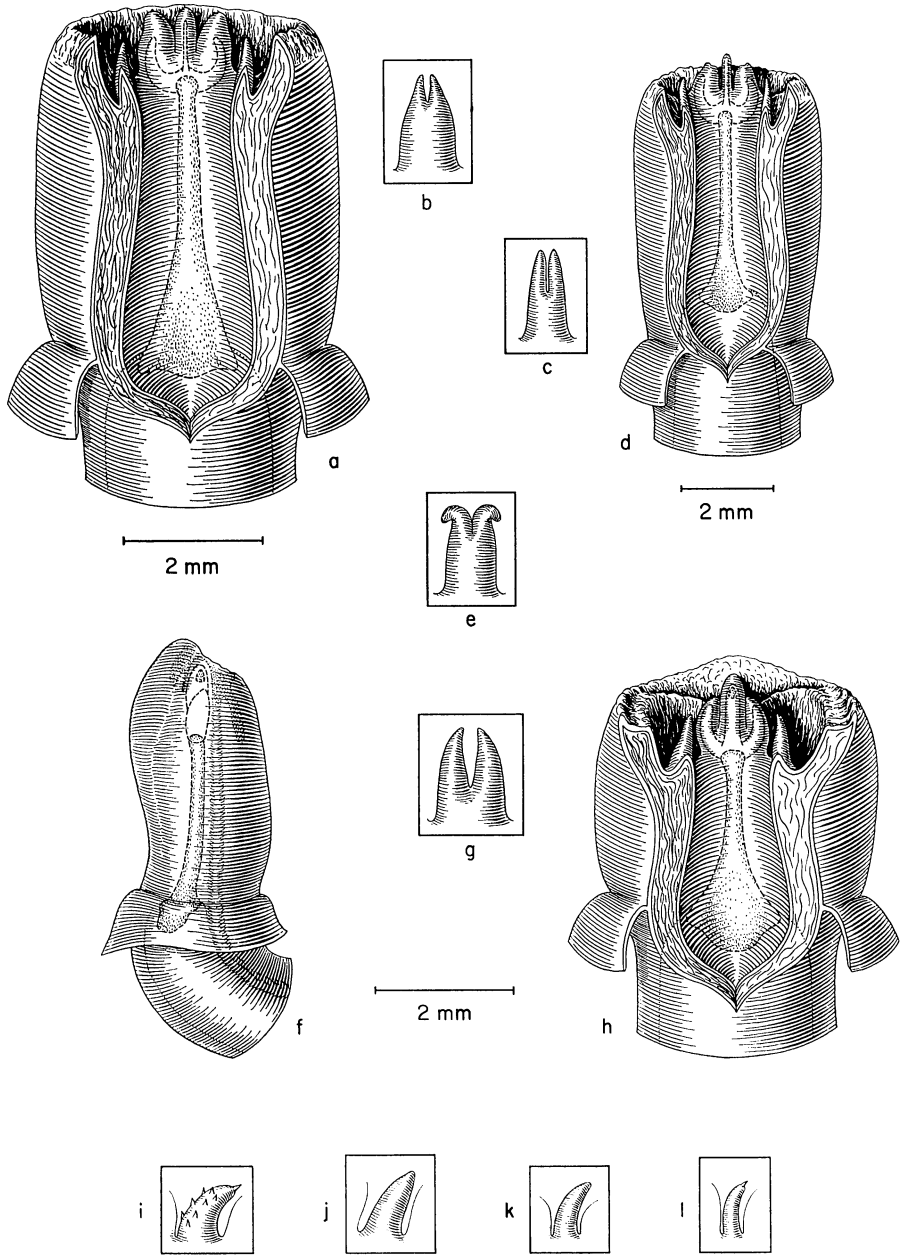


FIG. 2. Views of glans penis (lateral and ventral aspects, the glans incised midventrally in *a*, *d*, *h*), of urethral flap (enlarged, ventral aspect), and of dorsal papilla (enlarged, lateral aspect) in six species: *a*, *b*, *k*, *Oryzomys alfaroi* (UMMZ P-3905), Panamá; *c*, *d*, *l*, *Nectomys alfaroi* (UMMZ P-3903), Panamá; *e*, *O. caliginosus* (UMMZ P-3911), Panamá; *f*, *g*, *h*, *Neacomys guianae* (UMMZ P-4003), Venezuela; *i*, *O. palustris* (110388), Texas; *j*, *O. albicularis* (CM 18663), Venezuela.

slender shaft with its broader tip more strongly contrasted with the long, broad, triangular base of the bone; distal digits shorter and more delicate (Fig. 2), the laterals shorter than the medial one. In one specimen there is a small ossicle in the tip of the medial unit; in another, bony tissue occurs in the basal part of each lateral segment.

N. spinosus.—Of the two examples of *N. spinosus* at hand, the adult specimen is damaged and somewhat unsatisfactory for study. The undamaged young specimen is essentially a larger replica of a juvenile of *N. guianae*. Additional material of *spinosus* is needed for satisfactory appraisal of its characters.

Nectomys

N. alfari.—In regard to both glans and baculum this species resembles *O. caliginosus* and, especially, *O. alfaroi*. It is unique among these and all other oryzomyines examined, however, in the nature of the spiny investiture of the glans.

Glans elongate (diameter 30 per cent of length) and lobate, with prominent parotoid lobes and comparatively deep dorsal and ventral longitudinal troughs; investiture composed of unusually long overlapping spines, these present only on the distal four-fifths of the glans leaving the basal one-fourth smooth and spineless; the conical dorsal papilla tipped with a large spine; urethral flap long (length about equal to that of a lateral digit), its two attenuate distal processes constituting about half of that length (Fig. 2).

Baculum markedly shorter than glans, its proportions much as in *O. alfaroi* and *O. caliginosus* (Table 2); the bone slim throughout with a narrow base (in ventral aspect resembling an elongate isosceles triangle, without a proximal notch) and a slender almost cylindrical shaft with a slight terminal head; distal digits similar to those of *O. alfaroi*, but the medial one even longer and more slender relative to the robust lateral pair (Fig. 2).

THOMASOMYINE GROUP

We have samples of the following thomasomyine rodents (Hershkovitz, 1962): *Nyctomys sumichrasti*, *Rhipidomys mastacalis*, and *Thomasomys aureus*, *cinereus*, and *laniger*. These are few of possibly many species of *Rhipidomys* and *Thomasomys* (Cabrera, 1961).

The specimens are a diverse lot. Those of *N. sumichrasti* are so unlike the remainder as to suggest that the species is misplaced in this group and belongs elsewhere. The example of *R. mastacalis* differs from the specimens of *Thomasomys* in exterior structure, bacular mounds, and baculum, but

though these differences are well marked they are scarcely if at all greater than the distinctions seen between *T. aureus* on the one hand and *T. cinereus* and *T. laniger* on the other. To judge from the few phallic data, then, *T. cinereus* and *T. laniger* are similar, *T. aureus* and *R. mastacalis* are well differentiated both from each other and from *cinereus* and *laniger*, and *N. sumichrasti* fits near none of these.

Features of the phallus of the species of *Thomasomys* and *Rhipidomys* include: a crenate crater rim bordered by an erect narrow band of non-spinous tissue, and a long baculum (longer than glans), the base of which is shallowly concave ventrally and roughly triangular in ventral view (an apex of the triangle directed proximad). In all except *T. aureus* there are numerous spines in the crater—on the dorsal walls and floor in *T. cinereus* and *T. laniger*, on the lateral mounds in *laniger* and *R. mastacalis*, and on the urethral flap and large dorsal papilla in all three species.

Rhipidomys

R. mastacalis.—The glans of the adult at hand resembles glandes of *T. cinereus* and *T. laniger* in dimensions (Table 1), but it (and the baculum as well) is larger relative to size of hind foot and is more sway-back in shape; the lateral mounds are more densely spinous and more complexly curved, the curvature reminiscent of, but certainly not identical with, the condition seen in *Phyllotis darwini*, and the baculum is dissimilar in details. The specimen is described below.

Glans stubby (Table 2), regularly spinous and sway-back in outline because of prominent parotoid lobes; its surface indented by middorsal and midventral troughs, each deeply notching the crenate crater rim; bacular mounds dissimilar, the medial one distally slightly bulbous and inclined ventrad, and each of the slightly shorter lateral pair triple-curved—distad, ventrad and (terminally) laterad—the distal face of the laterally projecting part spine-studded (Fig. 6); dorsal papilla a densely spinous cone; urethral flap (slightly longer than wide) cleft in its distal one-half, the two erect processes spinous apically and ventrally, their tips well short of the distal limits of the lateral mounds.

Baculum composed of a long slender bone and short cartilaginous digits (Tables 1, 2), the bone with a small, shield-shaped, emarginate base and a long cylindrical shaft which terminates in a round head (Fig. 6); medial digit wider than deep basally and deeper than wide (blade-like) in its distal two-thirds; each lateral segment a slightly shorter, tapered, multi-curved rod, the curve progressing from the digit's base laterad and distad, then mediad and ventrad, and finally again laterad at the digit's tip.

Thomasomys

The single specimen of *T. aureus* is so unlike the examples of *T. cinereus* and *T. laniger* as to suggest that it may be abnormal or misidentified, although its identity has been double-checked. If it is typical of the species, then *aureus* phallically is strongly differentiated from the other two species, more so perhaps than is *R. mastacalis*.

T. aureus.—There is some question as to the spiny investiture and the dorsal papilla in the specimen of *aureus*. Almost all of the epidermis has been sloughed, but to judge from that remaining and from the size of the pits the surface of the glans was studded with small tubercles and, thus, was smooth in comparison with other glandes examined. In regard to the papilla, the ridge is present in which it might be situated but we are unable to find a papilla. Further description of the specimen follows.

Glans robust (Tables 1, 2), much longer middorsally than midventrally and rather strongly sculptured—a pair of proximally situated parotoid lobes and numerous flutings in its distal one-half; the crater rim, thus, correspondingly scalloped; bacular mounds nonspinous but otherwise strikingly dissimilar, the medial one a long cone which curves slightly dorsad and each of the lateral pair comprised of a slight blade-like structure the diameter and length of which are no more than one-fifth those of the medial mound; urethral flap spineless, wider than deep and cleft in its distal one-third, the two short processes extending distad only to the limits of the bone (Fig. 5).

Baculum unusually long relative to length of both foot and glans, almost one-third of its length attributable to the large, ventrally keeled, tapered, medial digit; lateral segments (strongly contrasted with the medial one) slight, deeper than wide, and gently curved laterad and distad; the bone in lateral view gently bowed so that its expanded tip is directed slightly dorsad, while in ventral view the large triangular base merges with a long, cylindrical, double-headed shaft (Fig. 5).

T. cinereus.—Glans with moderate parotoid lobes and invested with moderately large spines; dorsal and dorsolateral walls of crater also spinous; bacular mounds nonspinous and inclined slightly ventrad, the medial one slightly higher but much smaller in diameter than the gently incurved lateral pair; dorsal papilla a large mound densely spinous on all surfaces; urethral flap longer than wide, spinous ventrally and apically, and cleft for its distal one-half; the two acute-tipped processes extending approximately to midlength of the lateral mounds.

Bone of baculum gently bowed (dorsoventrally), slightly deeper than wide in its distal one-fourth, and with a slight terminal head; in ventral aspect its ventrally flat base equipped with sharp lateral points resembles

an inverted triangle; distal segments relatively short (Table 2), the deeper-than-wide (but dumbbell-shaped in ventral view) medial one scarcely longer than the deeper-than-wide, curved (laterad and distad) lateral pair.

T. laniger.—Glans similar to that of *T. cinereus* in size, shape, distribution of spines on crater walls, morphology of urethral flap, and size of proximal segment of baculum. It differs from that of *cinereus* as follows: external spines slightly smaller; bacular mounds dissimilar, each of the lateral pair spine-tipped and no more than one-half the height and two-thirds the diameter of the medial one; the spinous dorsal papilla larger, almost the size of a lateral mound; the bone with a slightly larger head and a dorsoventrally thinner base; digits more stubby, the erect medial one with approximately twice the diameter of each shorter, out-curved, lateral one (Fig. 6).

Nyctomys

N. sumichrasti.—To judge from present samples *N. sumichrasti* doesn't fit phallically near our species of *Rhipidomys* and *Thomasomys*; rather, like *Scapteromys aquaticus* and *S. tumidus*, it is set well apart from those and other species sampled in this study. Among its diagnostic features are: an investiture of large sparsely distributed spines which resembles that in *Tylomys* or *Ototylomys* (Hooper, 1960); a tri-lobed urethral flap which is the ventral part of a ridge that, joined to the bacular mass, elevates the meatus urinarius above the floor of the surrounding crater somewhat as in *Baiomys musculus* or *Scotinomys teguina* (Hooper, 1959, 1960); and a long slender bone which is capped by a mound of cartilage but no lateral digits. The specimens are described below.

Glans exteriorly plain, sculptured only by shallow middorsal and lateral depressions, but strongly spinous, the large sharp spines spaced such that they scarcely overlap one another; no spines anywhere in the comparatively open and shallow terminal crater or on a narrow erect band of tissue bordering it; bacular mound a globular structure supported by the baculum as usual; two lateral papillae which are scarcely larger than the dorsal papilla and are recessed on the sides of the mound; these papillae apparently are counterparts of the lateral mounds in other species; dorsal papilla a slim cone (bearing a conule near its base in two specimens) also recessed on the flank of the medial mound; urethral flap a broad triple-peaked structure (Fig. 6), which is the ventral part of a comparatively high wall of tissue that completely surrounds the urethra and elevates its meatus from the crater floor.

Baculum comprised of a slim, narrow-based, large-headed bone capped by a mass of cartilage (Fig. 6). In the specimens there is considerable varia-

tion both in the head of the bone and in its cartilaginous cap. In size and shape the osseous head varies from a simple, slight, ball-like expansion to a large three-lobed affair which in either depth or width is approximately two-thirds the width of the base of the bone. The cartilaginous mass is globular in some specimens, a short or long cone in others, and in one example it possibly is trilobed (shamrock-shaped in ventral view), but even if so, all of these lobes are directed into the medial mound. In no specimen is there an indication of lateral digits; the lateral mounds contain vascular and other soft tissues only.

AKODONT GROUP

Akodon

We have examined phalli of eight forms currently included in *Akodon* (Cabrera, 1961), namely *Akodon (Akodon) arviculoides*, *azarae*, *boliviensis*, *obscurus*, *orophilus*, *surdus*, *urichi*, and *Akodon (Microxus) bogotensis*, but we are reasonably confident of the data for only five of those species. Our specimens of *obscurus*, *orophilus*, and *bogotensis* are variously young, diseased or fragmented and are unsuited to our purposes. This is particularly unfortunate because certain traits seen in those specimens suggest that *orophilus* and *bogotensis*, and possibly also *obscurus*, may be distinguishable from the other five species.

We comment further on the three species, but we exclude them from the following diagnosis of the phallus of *Akodon*; further, we should point out that this summary will not fit all eight species if the traits seen in the specimens of *orophilus*, *bogotensis*, and *obscurus* prove to be characters of those species: glans externally plain, with middorsal and midventral troughs but no more than traces of parotoid lobes, its spiny investiture as in *Oryzomys*; bacular mounds erect, the medial one longer, but no larger in diameter, than the lateral pair; that pair closely appressed to the medial and exposed to the exterior (incompletely covered by the narrow ring of nonspinous tissue bordering the crater rim), the dorsal faces of those lateral mounds spinous in *arviculoides* and *azarae*; dorsal papilla spinous, at least apically, and in most species also on other surfaces; urethral flap relatively long (extending to or beyond distal limits of lateral mounds) and divided in its distal one-half or three-fourths into two attenuate erect processes; ventral face of the flap spinous in most if not all species.

Baculum slightly shorter than glans (Table 2), the shaft of its bone usually wider than deep proximally and deeper than wide in the distal third or quarter of its length; distal segments cartilaginous (some osseous tissue in *urichi*, however) and robust, the medial one oval in cross section and truncate and each of the lateral pair generally erect and blade-like, in

ventral aspect appearing weak and slender in comparison with the medial rod.

In regard to the phallus, *Akodon* is recognizable by a combination of characters none of which is unique. In size and proportions it overlaps oryzo-myines and phyllotines and its other traits are separately approached or matched in species of *Calomys*, *Eligmodontia*, *Phyllotis*, or *Zygodontomys*.

A. boliviensis.—Glans longer in relation to foot length (Table 2) than in other akodont species sampled; dorsal papilla an elongate conical mound studded with numerous spines on its dorsal and lateral faces and one on its tip; lateral bacular mounds truncate and closely appressed against the equally truncate but longer medial mound; urethral flap relatively long (extending to or slightly beyond the limits of the lateral bacular mounds) and cleft distally for half its length, its ventrolateral faces bearing numerous spines (Fig. 3).

Baculum long with respect to foot length (Table 2); shaft of proximal segment slightly deeper than wide distally and with an indistinct head; base of bone broadly and shallowly concave ventrally and narrowly concave dorsally between prominent dorsolateral condyles, its proximal face strongly convex and medially emarginate in ventral aspect (Fig. 3); medial distal segment about as wide as deep and gradually tapered to a truncate tip; lateral segments shorter, but in ventral view robust proximally and abruptly compressed distally to one-half the thickness of the medial segment.

A. arviculoides.—The two adult specimens of *A. arviculoides* at hand do not match in morphology, age, or geography. One example (CM 44792), from Argentina, resembles specimens of *boliviensis* in most features of both glans and baculum. The other example (CM 44788), from Brazil, is older and larger and although similar to the Argentine specimen in proportions it differs from it as follows: lateral mounds relatively larger and spinous dorsally (nonspinous and smaller in diameter than medial mound in the Argentine specimen); urethral flap relatively longer; baculum slightly larger in all aspects, its shaft deeper than wide, its base entire (without medial notch proximally), and its lateral segments more robust and shorter, their tips incurved instead of erect. We doubt that these distinctions are related entirely to the age difference between the two examples. Measurements of the specimen from Brazil are listed in Table 1.

A. azarae.—The specimens of *A. azarae* differ from those of *boliviensis* as follows: glans smaller in most dimensions (Table 1) and barrel-shaped (instead of straight-sided) with a trace of parotoid lobes; dorsal papilla, urethral flap, and dorsal faces of lateral bacular mounds studded with numerous spines; these also scattered on the apical margins of the mounds and on the dorsolateral walls of the crater in one specimen.

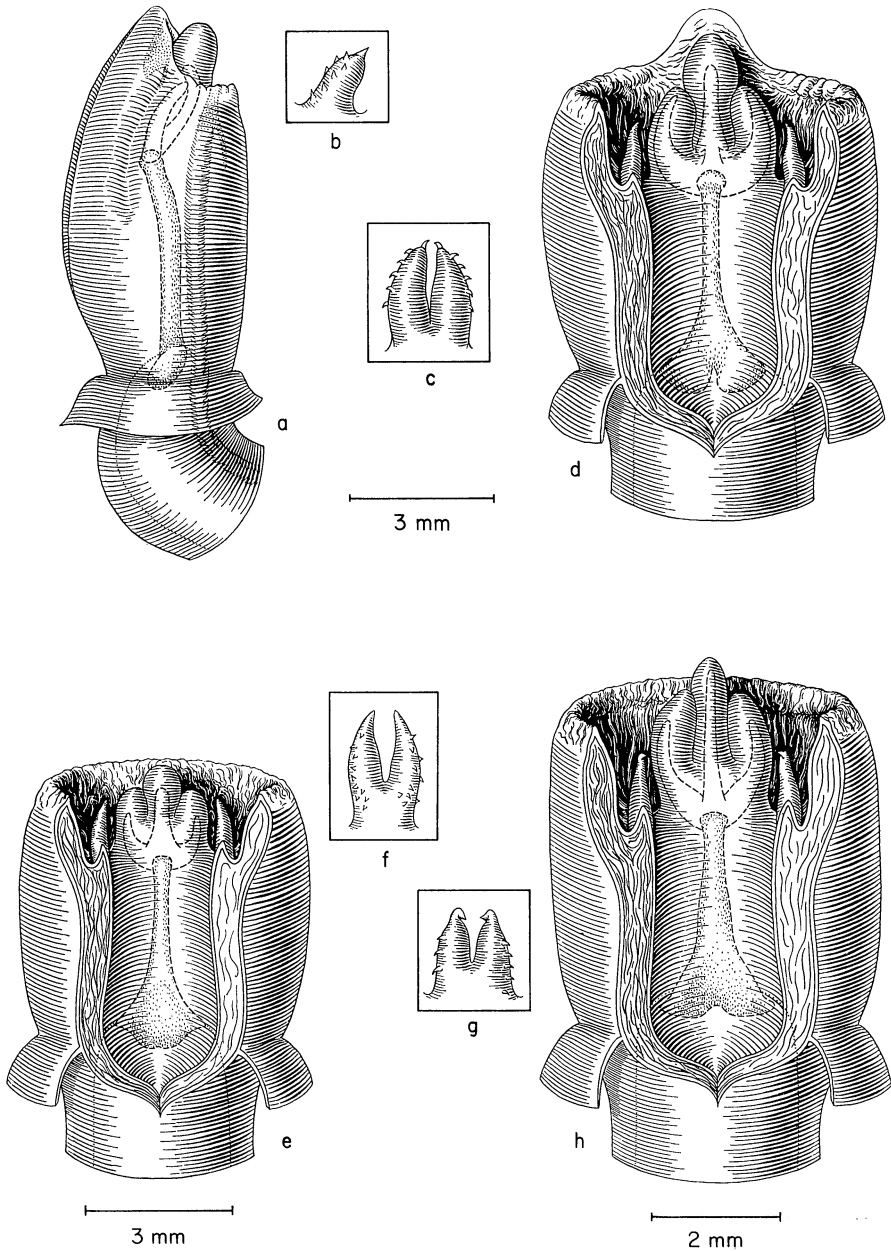


FIG. 3. Views of glans penis (lateral and ventral aspects, the glans incised midventrally in *d*, *e*, *h*) and of urethral flap (enlarged, ventral aspect) in three species: *a-d*, *Notiomys valdivianus* (MSU 6757), Chile; *e*, *f*, *Akodon boliviensis* (US 195007), Peru; *g*, *h*, *Calomys callosus* (CM 44795), Brazil.

Baculum slightly shorter with respect to both foot and glans lengths than in *boliviensis* (Table 2); proximal segment in ventral view wider throughout most of its length (tapered more gradually from base to distal half), the proximal face of its base markedly less convex (and more deeply emarginate medially in two of the three specimens at hand) between comparatively slight dorsolateral condyles; lateral digits relatively shorter (markedly shorter than the medial one).

A. surdus.—Glans and baculum similar to those of *boliviensis* except for the following distinctive features: glans stubby (diameter/length ratio .75, compared with .59 in *boliviensis*) and with greater flare distally in contrast to the cylindrical shape seen in *boliviensis*; bacular mounds relatively shorter, the medial one much larger than the lateral pair in both diameter and height; dorsal papilla and urethral flap spinous as in *boliviensis*, the flap, however, slightly broader and its two processes less attenuate.

Baculum actually shorter (Table 1) and less robust, the proximal face of the bone entire (without a medial cleft), and the head of the bone more prominent and directed more sharply dorsad; distal segments less robust and shorter relative to the main bone.

A. urichi.—Glans comparable to that of *boliviensis* in shape and dimensions (Tables 1, 2) but differing from it as follows: flared distally much as in *surdus* (basal and distal diameters more nearly equal in *boliviensis*); dorsal papilla much broader than deep, and spineless except for a single large spine at its tip; lateral bacular mounds less appressed to the medial mound, their tips pointed rather than truncate; urethral flap shorter than lateral mounds and more densely spinous ventrally and ventrolaterally than in *boliviensis*.

Baculum shorter, resembling *arviculoides* and *azarae* (Table 1), the bone wider than deep for the basal four-fifths of its length; lateral digits markedly more robust (each almost equalling the medial one in width), the three apparently lightly impregnated with osseous tissue.

A. orophilus.—The single specimen at hand, possibly young, is diseased and unsatisfactory for study. Its soft tissues bear numerous nodules and the spinous epidermis apparently is missing. The few uncontroverted parts appear to fit well enough in *Akodon*.

A. obscurus.—Three of the four available specimens of this species are young and, thus, provide no more than clues to fully adult characters. The fourth phallus also appears to be juvenile, but its matching skull indicates maturity though not senility. Its characters follow: glans resembles *surdus* in external configuration (small in diameter proximally and expanded distally), but unusually small (Table 1) and invested with tubercles instead of spines; all bacular mounds exposed, extending beyond the limits of the

terminal crater; dorsal papilla an elongate spineless finger; urethral flap shaped as in other *Akodon*, but spineless.

Baculum shorter than glans; bone (as seen ventrally) medially emarginate between weak dorsolateral condyles, this moderately wide base tapered evenly distad leaving only the terminal one-fourth of the bone deeper than wide; distal segments shaped as in *boliviensis* but disproportionately longer.

The distinctive qualities seen in this specimen may be attributable to age of the specimen. If they are indeed adult and, further, if they typify *obscurus*, then *obscurus* is morphologically set apart from our other species of *Akodon*.

A. bogotensis.—Although the single specimen at hand is young and misshapen and therefore is of limited use, we can see in it that *bogotensis* fits better in *Akodon* than in any other sampled genus. Slightly larger than that of *obscurus*, it resembles glanses of other *Akodon* examined except that the dorsal papilla appears spineless and the relatively long bone has a prominent head and a more angular, deeply emarginate base.

Notiomys

In keeping with their subfossorial habits mole mice of the genus *Notiomys* are, among cricetines, well differentiated cranially and externally (Osgood, 1925, 1943); and to judge from our samples of *N. valdivianus*, one of possibly six species of the genus (Cabrera, 1961), their phalli are also distinctive. In comparing the glanses we should estimate that *N. valdivianus* fits near or with our phyllotine and akodont species, approximately as close to them as are our species of *Oxymycterus*.

Diagnostic features of the glans of *valdivianus* are a prominent dorsal hood which extends well beyond and somewhat overhangs the deep terminal crater; proximally situated parotoid lobes; a spinous dorsal papilla; and a comparatively gross urethral flap, its lateral margins studded with long, curved, proximally directed spines. The baculum clearly is shorter than the glans, its bone is unusually short and delicate and the cartilaginous distal segments are dissimilar in size and shape. Details are given in the following description of three adult specimens, one fluid-preserved and two refurbished from dry study skins.

N. valdivianus.—Glans stubby (Table 2), its densely spinous surface (the spines slightly larger than in *Akodon*) indented by several troughs—three in the proximal two-thirds of the dorsal sector (a deep one middorsally and a dorsolateral pair) and shorter, shallower ones indenting the crater rim midventrally and ventrolaterally; a spinous triangular hood overhangs the dorsal sector of the terminal crater and directs the opening of the deep nonspinous crater somewhat ventrad instead of entirely distad; crater rim-

med only ventrally and ventrolaterally by soft nonspinous tissue, the dorsal border comprised of the spinous dorsal hood (Fig. 3); dorsal papilla a spinous conical mound (as in *Akodon*), the spines absent only ventrally; the long smooth bacular mounds inclined slightly ventrad, their curvatures corresponding with that of the dorsal hood; lateral mounds smaller in diameter and no more than three-fourths the length of the medial one; urethral flap erect, slightly longer than wide and cleft distally for approximately four-fifths its length, each of its two distal processes (these terminating at about midheight of the lateral bacular mounds) bearing a medially directed spine at its tip and numerous proximally directed spines on its lateral border (Fig. 3).

Baculum shorter than glans (Table 2), but unusually long relative to foot length (exceeded only by *Thomasomys aureus*); bone deeper than wide (blade-like, keeled ventrally) in its distal one-half, with a prominent dorsally directed head; as viewed ventrally (Fig. 3) base of bone shaped like an equilateral triangle with a medial notch on its proximal face, its ventral surface essentially flat except for a slight midventral keel, and its dorsal face broadly and deeply concave; digits cartilaginous and somewhat rod-like, but tapered distad from a rather large base, the erect medial one bowed slightly ventrad and the shorter lateral pair curved gently mediad and ventrad.

OXYMYCTERINE GROUP

Oxymycterus

Of eight species of *Oxymycterus* recognized by Cabrera (1961) we have seen samples of two, *paramensis* and *rufus*.

The samples suggest that *paramensis* and *rufus* are phallically well differentiated from the other cricetines studied. They approach species of *Thomasomys* and *Rhipidomys* in some respects (e.g., shape of bone and external appearance) and their relatively small lateral bacular mounds and segments are reminiscent of *Akodon*, but they do not match any of those.

Diagnostic features of the glans include: the crenate crater rim with essentially no bordering band of spineless tissue; dissimilar bacular mounds, the short, erect, peaked, lateral pair contrasting with the laterally compressed medial one; and the robust, spinous urethral flap. The distal segments of the baculum are short relative to the bone, the lateral pair particularly slight although partly osseous. Each erect lateral digit is approximately one-half the length of the bent medial one.

O. paramensis.—Glans oblong (Tables 1, 2), spinous, and without parotoid lobes but with six slight distal lobes, the pairs of three separated mid-dorsally and midventrally by deep longitudinal troughs; the correspond-

ingly hexalobate crater rim with essentially no ring of nonspinous tissue; bacular mounds dissimilar, the slight, peaked, lateral pair appressed tightly against the longer, deeper-than-wide medial one, its tip bent ventrad; dorsal papilla a low mound with at least two spines, one apically and one subapically; urethral flap robust (length and width about equal) and deeply cleft (Fig. 5), the two erect attenuate processes spinous apically and ventrally (the spines concentrated in two rows).

Bone of baculum slim in ventral view (Fig. 5) with a narrow proximally projecting base (its ventral face almost flat and its dorsal face narrowly concave between lateral condyles) and a long terminally enlarged shaft; bone in lateral view more robust and gently curved dorsad, its configuration similar to that in *Rhipidomys* and *Thomasomys*; medial digit a slightly deeper-than-wide, slim, cartilaginous rod, its tip inclined ventrad; each lateral digit also rod-like and erect, but smaller in diameter and height and with osseous tissue basally.

O. rufus.—The specimens of *rufus* are much like the example of *paramensis* except that they are larger (Table 1), the lateral mounds appear to be slightly smaller relative to the medial one, the dorsal papilla more spinous (as many as three dorsal spines), the urethral flap also more densely spinous and longer (extending to distal limits of lateral mounds), the proximal face of bone slightly different, and the medial digit flexed more strongly ventrad, which partly accounts for the small medial/proximal segments ratio in Table 2.

The specimen from Uruguay differs from the Argentine examples in that the glans is more strongly lobate, dorsal papilla and urethral flap more densely spinous (eight spines on the papilla and the entire ventral face of the flap tuberculate), and the bone emarginate proximally and with an angular terminal head.

SCAPTEROMYINE GROUP

Scapteromys

Of the five species provisionally recognized in *Scapteromys* by Cabrera (1961) we have specimens of two, namely *aquaticus* and *tumidus*. These specimens are set well apart in morphology of glans from all other South American examples at our disposal. Several of their unique traits are reminiscent of structures seen in the North American *Xenomys nelsoni* and *Neotoma alleni*.

Features of the glans of *aquaticus* and *tumidus* include the peculiar, compound dorsal papilla; essentially single, but triple-peaked, bacular mound; usually four-lobed urethral flap, and gross scoop-shaped bone capped by a large bifurcate or trifurcate cartilaginous mass.

S. aquaticus.—Glans appearing as an elongate laterally compressed bud (Table 1) furrowed by shallow grooves and densely studded with narrow spines. The terminal crater, which is rimmed by a relatively wide, erect fence of non-spinous tissue, contains a single large mound bearing three small conical eminences which possibly are distal counterparts of the three bacular mounds in other species. The dorsal papilla is peculiar in position and probably in shape. It consists of a finger-like dorsally spinous mound situated in a ridge on the dorsal flank of the bacular mound. Lobules adjacent to the finger (these spine-tipped in some specimens) may also be vascularly protractile parts of the papilla; if so, the structure is compound (multilobulate). The robust urethral flap, its length and width about equal, is cleft in its distal one-fourth and each of the two processes is also lightly divided in all but one of three specimens; this serrate (four-lobed) flap bears a row of spines on each lateral face and a single spine at the tip of each lateral process (Fig. 7).

Baculum composed of a short (Table 1) scoop-like bone, with deeply concave base and a short, robust, slightly deeper-than-wide, terminally expanded shaft capped by a mass of cartilage (Fig. 7). The cartilaginous mass and the bone as well varies considerably in the specimens. In one example the mass appears to consist of two rod-like tapered masses of dense cartilage beside a central core of diffuse cartilage. In the other examples the mass apparently is undivided basally, but distally it consists of three interconnected segments of various sizes, the lateral pair usually larger in diameter but not always in height. Vascular cores, but apparently no parts of the baculum proper, extend into the three conical eminences in the crater mound.

S. tumidus.—To judge from our specimens *tumidus* is similar to *aquaticus*. The two samples may differ in regard to dorsal papilla and shape of bone (a midventral keel and larger, laterally expanded head in the examples of *tumidus*).

PHYLLOTINE GROUP

Of the many phyllotine species (Pearson, 1958; Hershkovitz, 1962), we have examined only eight as follows: *Calomys callosus* and *laucha*; *Eligmodontia typus*; *Phyllotis (Phyllotis) darwini*, *P. (Graomys) griseoflavus*, and *P. (Auliscomys) pictus*; and *Zygodontomys brevicauda* and *lasiurus*.

In regard to morphology of glans these species are a diverse assemblage, one more varied than the oryzomyine group for example. They are well characterized at the generic level but some of them are no more similar to each other than some are to nonphyllotines. In all eight species the exterior spines are moderate in size and shape and there are no tubercles on the bacular mounds, the urethral flap is longer than wide and the robust

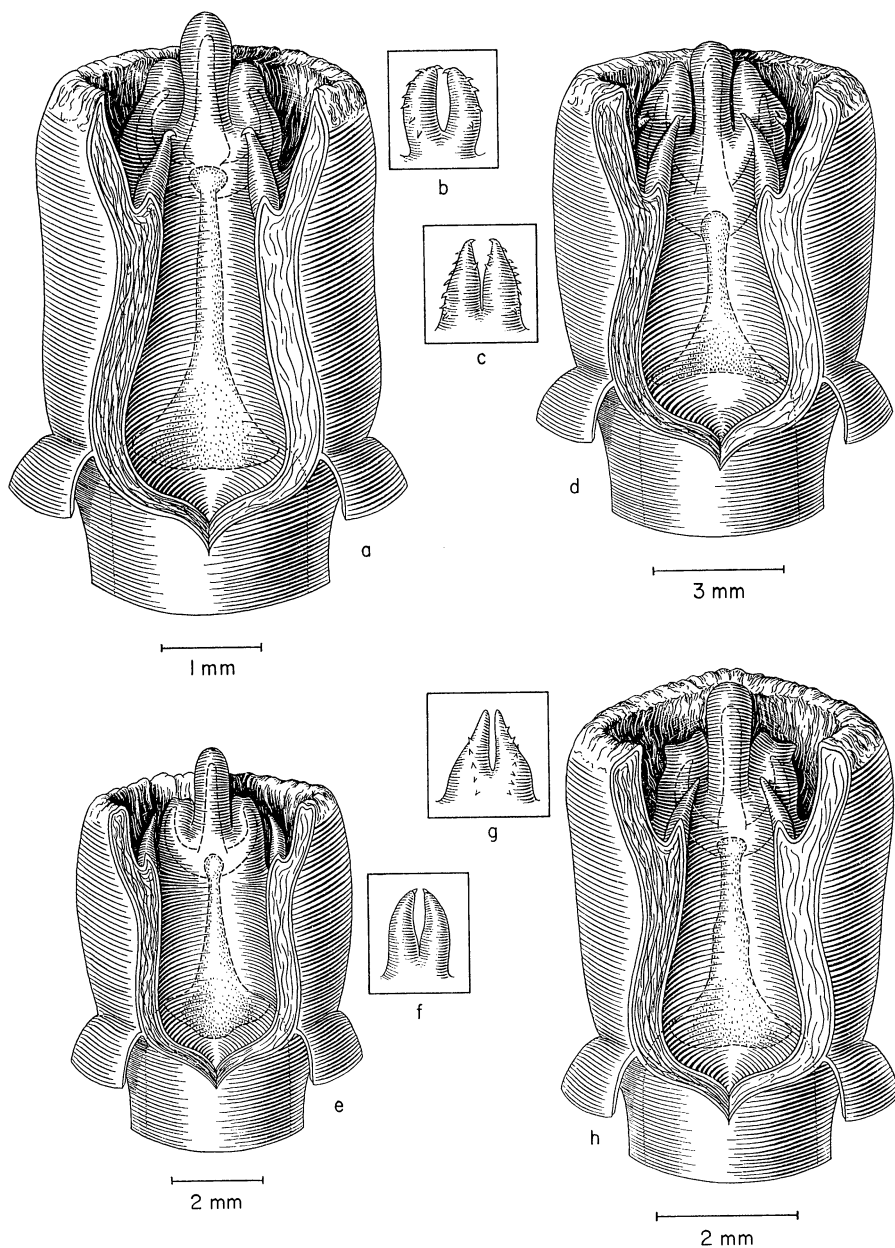


FIG. 4. Ventral views of glans penis (incised midventrally) and of urethral flap (enlarged, ventral aspect) in species of *Eligmodontia* and *Phyllotis*: *a, b*, *E. typus* (110397), Argentina; *c, d*, *P. darwini* (US 195099), Peru; *e, f*, *P. pictus* (US 194984), Peru; *g, h*, *P. griseoflavus* (109230) Argentina.

baculum has a wide, ventrally concave base and a laterally compressed shaft (distal part of it only), but none of these is peculiar to this group and neither is this set of characters unique. A synopsis of the specimens follows.

Calomys

Features of the specimens of *Calomys* include: exteriorly plain stubby glans; erect, blunt, smooth bacular mounds, the medial longer but much less robust than the lateral pair; deep crater rimmed by a narrow band of nonspinous tissue; small slim dorsal papilla, its tip bearing a large recurved spine; long urethral flap, a row of recurved spines on the side of each process and a similar spine at its tip; prominent subapical midventral keel on the bone; and long, erect, cartilaginous digits, the medial one much less robust than the lateral pair.

C. callosus.—Glans stubby (Table 2) and plain, with middorsal and midventral troughs but no parotoid lobes; spiny coat as in *Akodon* but the spines possibly slightly more robust; bacular mounds erect, long, and blunt, the medial about one-half each lateral one in diameter but taller (extending beyond the crater rim); dorsolateral wall of each side of crater with two spines; the slim dorsal papilla bears a few long spines dorsally and one apically; urethral flap (shorter than lateral mounds) cleft for one-half its length, each attenuate process armed with long curved spines—a ventrolateral row and a single medially directed one at its tip (Fig. 3).

Bone (about half as long as glans) wider than deep for its basal two-thirds and deeper than wide in the distal one-third; basal part concave and emarginate proximally (Fig. 3) and broadly concave ventrally; shaft with a high subapical ventral keel and a slight apical head; distal segments cartilaginous, the medial one a long (61 per cent in bone length), deeper-than-wide, slightly curved blade; lateral digits slightly shorter and much more robust in ventral view.

C. laucha.—The specimens of *laucha* differ slightly from the example of *callosus* in that there are no spines on the crater walls or on the dorsal papilla except at its tip, the urethral processes are less attenuate, the bone is erect instead of dorsoventrally bowed in lateral view, its subapical ventral keel is higher and the bacular digits are relatively longer (Table 2).

Eligmodontia

E. typus.—In structure of phallus *E. typus* is perhaps as close to species of *Akodon* as to phyllotines. From the phyllotines, among which it clearly is more similar to species of *Calomys* or *Phyllotis* than to *Zygodontomys brevicauda* or *Z. lasiurus*, it is distinguishable in size and proportions of

glans (especially see glans/foot ratio, Table 2), epidermal spines (much larger in basal than distal part of glans), and baculum (long, comparatively simple bone capped with short digits).

Glans short (relative to both its diameter and hind foot length), plain (without parotoid lobes), and armed with large spines (relatively largest of phyllotines examined), these particularly gross in the basal one-fourth of the glans; band of soft tissue bordering crater rim relatively wide and erect, not enveloping bacular mounds; the blunt medial mound perhaps one-third longer (extending well beyond crater rim) but smaller in diameter than the lateral ones, their blunt tips bent slightly laterad; dorsal papilla a minute finger tipped with several curved spines; ventrolateral margins of deeply bifurcate urethral process spinous, its two apices extending to midlength of lateral mounds and each tipped with a medially directed spine (Fig. 4).

Baculum equal to glans in length, the bone distinct among phyllotines in both length and shape (Table 2)—its basal part (as seen ventrally) quite wide, scooped ventrally and convex and slightly emarginate proximally, and its distal one-half or two-thirds deeper than wide, without a prominent keel but with a distinct terminal head; the comparatively short, erect, cone-shaped medial digit wider than deep basally and deeper than wide in its distal one-half; the shorter, less robust, deeper-than-wide, lateral pair horn-shaped in ventral aspect, each tapered and slightly incurved (Fig. 4).

Phyllotis

Our few phallic data support the conclusion of authors that *darwinii*, *griseoflavus*, and *pictus* are well differentiated from one another; Osgood (1947), Pearson (1958), and Cabrera (1961), but not Hershkovitz (1962), arrange the species in separate subgenera.

P. darwini.—The glans of the only adult example of *darwinii* at hand, the largest among the phyllotine species sampled (Table 1), resembles glandes of *Calomys* and *P. griseoflavus* in some proportions, in configuration of its urethral flap and in some details of its bacular digits. The species is markedly unlike those forms, however, in shape of the bacular mounds and bone and in other details as indicated below.

Glans much like that of *P. griseoflavus* and *Calomys* in regard to the spinous coat and external simplicity, but more stubby (Table 2) and with a deeper middorsal trough; bacular mounds subequal in length and in diameter, the medial one truncate and the slightly shorter lateral pair each double peaked, the short medial peak erect and the long lateral tip hooked laterad and ventrad (Fig. 4); dorsal papilla a slight spine-tipped finger; urethral flap similar to that of *C. callosus*, but more deeply cleft (for

about three-fourths the length) and possibly slightly shorter, each process terminating at midlength of the lateral mounds.

Baculum (longer than glans) comparatively gross, with a wide, angular, proximally concave base (its dorsal surface essentially flat) and a club-shaped, terminally expanded shaft; bacular digits cartilaginous, long and essentially erect; the slim medial one (almost as long as the bone) larger at each end than in its middle one-third, its tip bent slightly dorsad; the scarcely shorter but more robust lateral pair appearing as triple-curved (ventrad, mediad, and dorsad) tapered horns (Fig. 4).

P. griseoflavus.—Although this species resembles *darwini* and *pictus* in structure of the urethral flap and a few other details, it is distinguishable from those and other sampled species in a combination of characters as follows.

Glans exteriorly similar to that of *darwini* but slightly more elongate and with weaker spines and traces of parotoid lobes; bacular mounds approximately equal in diameter, the medial one truncate and the slightly shorter lateral pair lightly double-peaked (Fig. 4); dorsal papilla a small slim cone armed with tubercles both dorsally and apically; urethral flap much as in *callosus*, but more attenuate distally and bearing two ventral rows of tubercles instead of spines (a difference possibly related to unequal ages of the specimens).

Baculum, shorter than glans (Table 2), with a peculiar proximal segment; in ventral view (Fig. 4) its short basal part concave ventrally and slightly concave or convex proximally, and its shaft with lateral prominences (situated about midlength in the bone) and a round terminal head; medial digit a long (71 per cent of bone in length) tapered rod, its blunt tip directed dorsad; lateral digits (larger in diameter but shorter than the medial digit) cylindrical basally and blade-like (deeper than wide) distally, the blades gently curved ventrad and mediad.

P. pictus.—The structure of the phalli of our three specimens, none of which is old or otherwise entirely satisfactory for our purposes, suggests that *pictus* is morphologically set apart from the other species of *Phyllotis*, for example in shape of glans, nature of the dorsal papilla, and configuration of baculum, although the baculum in some respects resembles that of *E. typus*. Features of the best specimen at hand follow: glans faintly lobate, stubby (Table 2), and invested with low tubercles instead of spines; lateral bacular mounds truncate (not double peaked) and slightly smaller in diameter and about half the height of the conical medial one; dorsal papilla a short, broad-based, spine-tipped cone; urethral flap, shorter than the lateral bacular mounds, divided for approximately three-fourths its

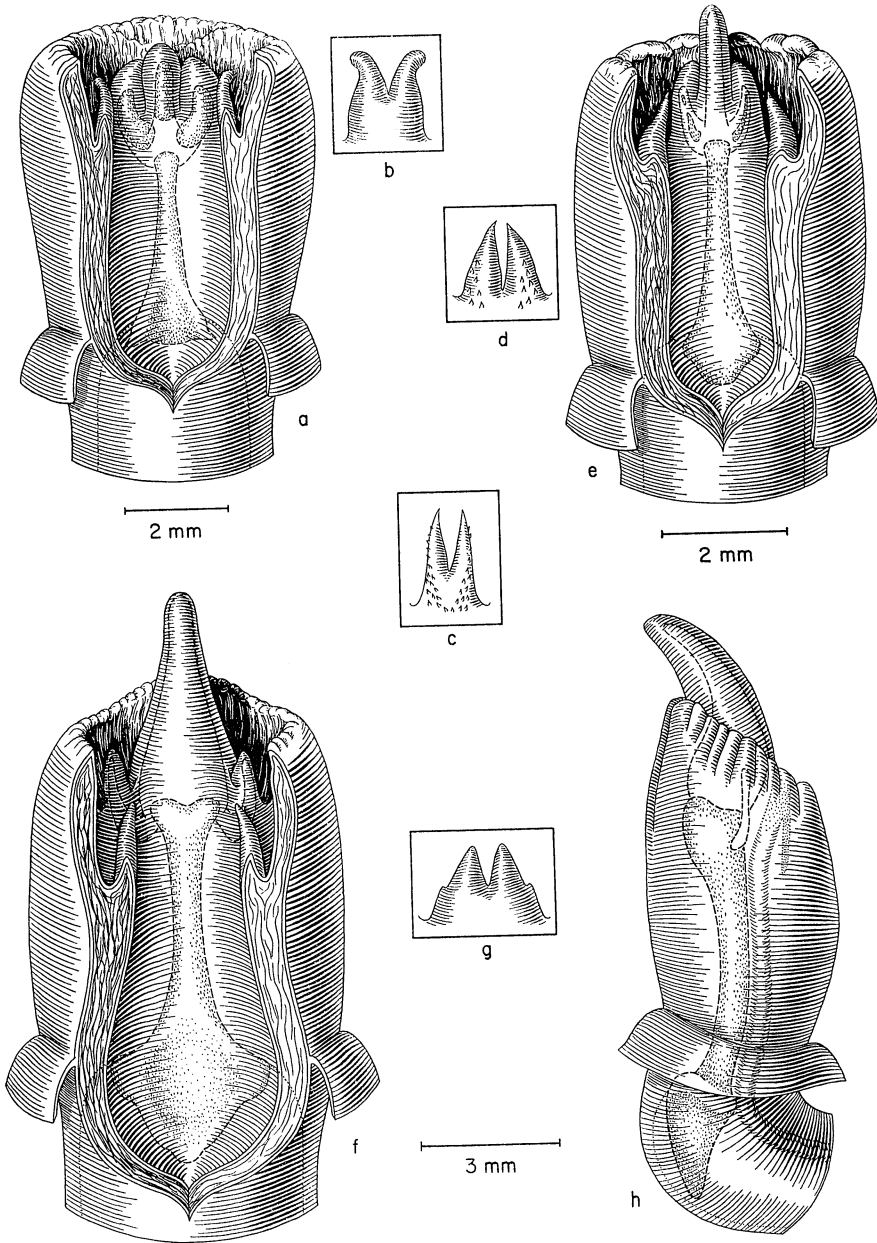


FIG. 5. Views of glans (lateral and ventral aspects, the glans incised midventrally in a, e, f) and of urethral flap (enlarged, ventral aspect) in four species: a, b, *Zygodontomys brevicauda* (111957), Costa Rica; c, *Z. lasiurus* (AM-CA 2643), Colombia; d, e, *Oxymycterus paramensis* (CM 53006), Brazil; f, g, h, *Thomasomys aureus* (CM 75588), Peru.

length, each attenuate process tipped with a tubercle but with no other spines (Fig. 4).

Baculum much longer than glans; the relatively long bone (Table 2) has a broad base (its proximal face strongly convex in ventral view) and a slender shaft which is slightly broader than deep distally and expanded terminally (Fig. 4); distal segments somewhat as in *E. typus*, the medial one, however, relatively wider basally and longer relative to length of bone (Table 2).

Zygodontomys

The combination of characters seen in the specimens of *Zygodontomys* set them apart from other phyllotines and, at the same time (and more than the examples of *Phyllotis*, *Eligmodontia*, or *Calomys*) connect the phyllotines with oryzomyines and akodonts. The prominent parotoid lobes, configuration of dorsal crater rim, and spineless outcurved urethral flap, as seen in *Z. brevicauda*, are features best developed in oryzomyines; the configurations of the bacular mounds, urethral process and baculum, as seen in *lasiurus*, approach conditions obtaining in *Akodon*; and finally, the shape of the bone in *brevicauda* is somewhat similar to but not identical with that in *Calomys*. The phallic data support other authors' conclusions (e.g., Ellerman, 1941; Hershkovitz, 1962) regarding relationships of *Zygodontomys*, *Akodon*, and phyllotine species.

Z. brevicauda.—Glans chunky and slightly sway-back because of the bulge dorsally of parotoid lobes which are much like those in *Oryzomys concolor*; spinous investiture as in *Calomys* or *Akodon*; dorsal sector of shelf of nonspinous tissue inset below the crater rim approximately on a level with the dorsal papilla (as seen in *Neacomys* and some *Oryzomys*); bacular mounds erect, blunt, and almost equal in diameter, the lateral pair (but not the slightly longer medial one) covered apically by the shelf of nonspinous tissue; dorsal papilla large, finger-like and tubercle-tipped; urethral flap spineless, longer than wide, and cleft for approximately one-half its length, the outcurved tips of its two processes situated at or slightly beyond the distal limits of the lateral mounds.

Baculum robust throughout, shorter than glans (Table 1); its main bone wider than deep in its basal three-fourths (the base concave both dorsally and ventrally) and deeper than wide in its distal one-fourth with scarcely any terminal enlargement (Fig. 5); digits blunt and relatively short (at most approximately one-half as long as bone); medial digit an evenly tapered rod, its tip bent slightly dorsad; lateral digits more robust, slightly shorter, and gently curved ventrad; all three digits osseous (except their tips) in the oldest specimen.

Z. lasiurus.—The single specimen of *Z. lasiurus* at hand (an adult) resembles those of *brevicauda* except that the glans is more stubby (diameter/length ratio .72 compared with .54); dorsal papilla smaller, with a spine dorsally and another apically; urethral flap more deeply cleft (Fig. 5), longer (extending slightly beyond distal limits of lateral mounds), and spinous ventrally but not apically; and baculum both relatively longer (Table 2) and different in shape; in lateral view the shaft deeper and slightly keeled midventrally, and in ventral aspect the base of the bone broader, the shaft narrower, and the terminal head more prominent; all distal digits cartilaginous, the laterals more blade-like and less robust than in *brevicauda*.

SIGMODONT GROUP

With specimens of *Holochilus brasiliensis* at hand for comparison with the already described examples of *Sigmodon*, *Sigmomys*, and *Reithrodon* (Hooper, 1962), we now have information on the phalli of all genera or subgenera of sigmodont rodents except *Neotomys* (Hershkovitz, 1955, 1962).

These specimens are a diverse lot, one which provides little support for the proposal that all species represented therein are closely related. Those of *Sigmodon* and *Sigmomys* are similar, although each form apparently is phallically distinctive. The specimens of *Reithrodon physodes*, however, fit morphologically nearer those of *Phyllotis* (e.g., *darwini*) than those of *Sigmodon*, *Sigmomys*, or *Holochilus*. Finally, the characters seen in the phalli of *Holochilus brasiliensis* are for the most part duplicated in and apparently typical of oryzomyine species.

Holochilus

H. brasiliensis.—The following description of *brasiliensis* is based on five specimens, two fluid-preserved and three refurbished from dry study skins.

The robust glans (Tables 1, 2) exteriorly plain (as in *O. albigularis*) with small spines, faint parotoid lobes, and a broad nonspinous ring of tissue which covers the lateral bacular mounds; configuration of bacular mounds similar to that in *Oryzomys palustris*, the erect, pointed, lateral pair larger in diameter and slightly shorter than the somewhat dorsally inclined medial one; dorsal papilla a finger-like cone tipped with a large spine; urethral flap nonspinous, longer than wide (slightly shorter than a lateral mound), and cleft for two-thirds its length, each acuminate process bearing a subapical lobule (Fig. 6) resembling that in *O. palustris*.

Baculum slightly shorter than glans (Table 1), the broad base of the bone deeply scooped ventrally and proximally (Fig. 6) and the shaft deeper

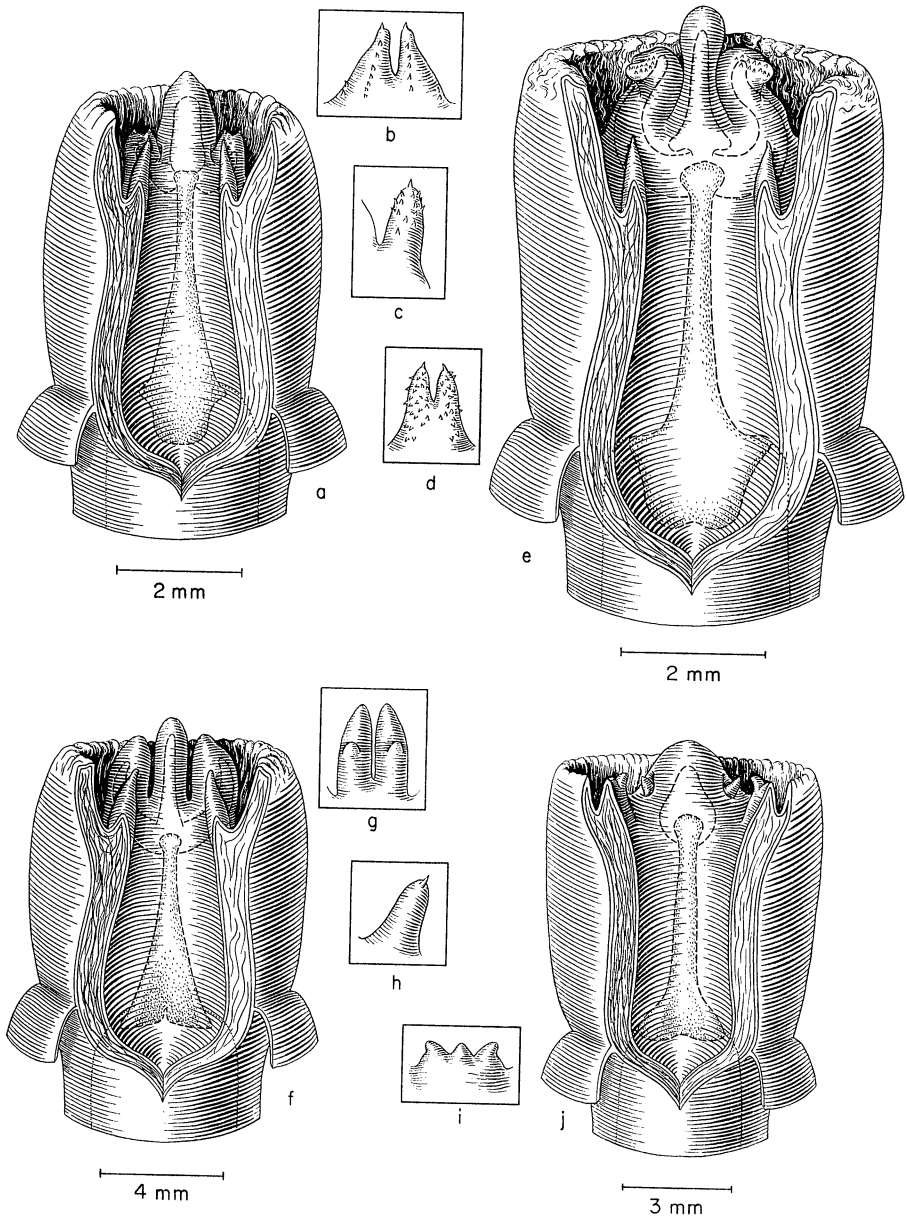


FIG. 6. Views of glans (incised midventrally), urethral flap (enlarged, ventral aspect), and dorsal papilla (enlarged, lateral aspect) in four species: a, b, *Thomasomys laniger* (CM 92555), Colombia; c, d, e, *Rhipidomys mastacalis* (AM-CA 2655), Brazil; f, g, h, *Holochilus brasiliensis* (MNHN 1166), Uruguay; i, j, *Nyctomys sumichrasti* (112378), laboratory-reared.

than wide (angular in lateral view); the entirely cartilaginous digits similar to those in several other species, the medial one (its length about half that of the main bone) a slim, slightly deeper-than-wide blade, its tip bent dorsad; each lateral one a more robust, deeper-than-wide arm extended gently laterad and distad from its attachment on the bone.

ICHTHYOMYINE GROUP

Rheomys

A sample of three well prepared specimens of *Rheomys hartmanni* provides information on one of the ichthyomyine rodents (Anthony, 1929; Tate, 1932*b*; and Hershkovitz, 1962).

These specimens are readily distinguished from all other examples on the basis of the exteriorly plain glans; highly dissimilar bacular mounds, the lateral pair papilliform and spinous; presence of three large spinous papillae on the crater walls; long nonspinous urethral processes; and a comparatively wide bone capped by three peculiarly shaped mostly osseous digits. This is a unique assemblage of traits, but as appears usual among South American cricetines each single character is approached or matched in other species. A plain exterior is seen in several kinds, e.g., *Akodon*, *Calomys*, or *Phyllotis*, the long urethral processes are similar to those in *Sigmodon* or *Calomys*; the dorsal and lateral papillae essentially match those in *Sigmodon*; the large, distally bent medial digit which is offset ventrally from the lateral pair also is reminiscent of *Sigmodon*; and aspects of the bone resemble those in various species—e.g., the midlength lateral expansion is as in *Phyllotis griseoflavus* and the lateral and proximal outline of its base is somewhat as in *Thomasomys laniger* or *T. cinereus*. A more detailed description of the specimens follows.

R. hartmanni.—Glans a stubby cylinder slightly compressed dorso-ventrally, its exterior comparatively plain—studded with small spines but with only traces of middorsal, dorsolateral, and lateral troughs; crater rimmed by a narrow medially inclined band of nonspinous tissue; medial bacular mound nonspinous, large, and globular, its distal part extending dorsad well beyond the small dorsolaterally situated lateral mounds; each lateral mound densely spinous and papilliform, its size approximately that of the dorsal papilla; dorsal papilla a comparatively large spinous cone (spines on dorsal and lateral faces and a large one apically) situated on the crater wall (as in *Sigmodon*) not on the flank of the medial mound; a lateral pair similar in appearance to the dorsal papilla is also present, each recessed in a spinous pocket in the crater wall adjacent to a lateral bacular mound (Fig. 7); urethral flap nonspinous, unusually long (its length greater than its width and more than the height of a lateral mound), and deeply

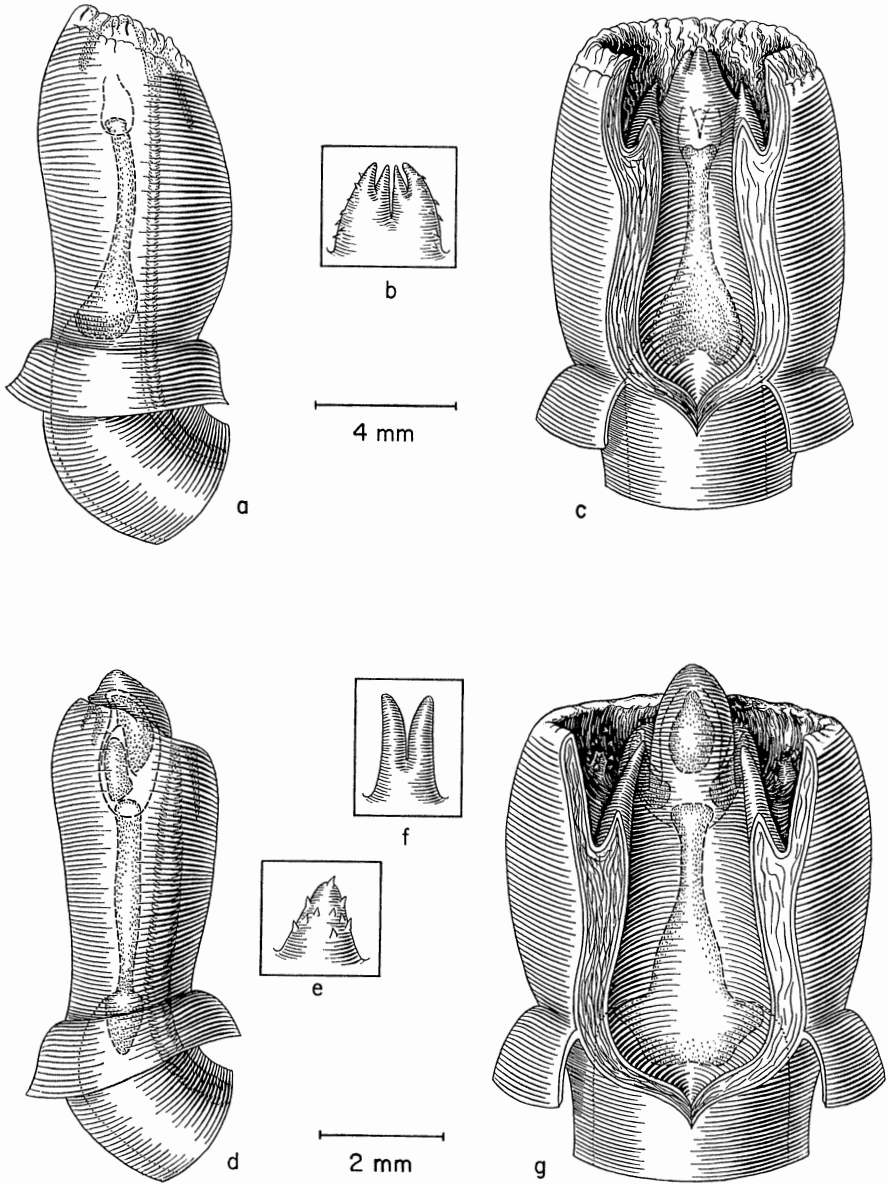


FIG. 7. Views of glans penis (lateral and ventral aspects, the glans incised midventrally in c, g), of urethral flap (enlarged, ventral aspect), and of dorsal papilla (enlarged, lateral aspect) in two species: a-c, *Scapteromys aquaticus* (110441), Argentina; d-g, *Rheomys hartmanni* (112301), Costa Rica.

cleft for approximately four-fifths its length, each attenuate process gently outcurved.

Proximal segment of baculum wider than deep throughout its length and with lateral prominences at three levels (Fig. 7)—at the terminal head, just short of midlength, and as sharp lateral points of the comparatively narrow, ventrally flat, proximally emarginate base; the three distal segments appear as a W in ventral view (Fig. 7); medial digit keeled mid-ventrally at its attachment with the main bone, but otherwise essentially a short gently tapered rod, its truncate tip abruptly bent dorsad; a robust ossicle present in the median digit of each specimen; each slight lateral digit a deeper-than-wide blade extending in a straight line distad and laterad from its wider base; the blade portion of the digit apparently mostly osseous in all specimens.

DISCUSSION

AFFINITIES OF THE SPECIES AS INDICATED BY THE PHALLUS

Most of the 43 species cluster in regard to morphology of phallus. A few are outliers, species set well apart from the others morphologically and possibly phylogenetically. *Nyctomys sumichrasti* is one of those. Features of its glans include its nonlobate but massively spinous exterior; spineless terminal crater; peculiar bacular mounds—a large globular medial one and recessed on the sides of it a pair of papilliform laterals; an elevated meatus urinarius; and a tripartite urethral flap which is joined by partitions to the medial mound. The baculum consists of a long, slender, straight bone capped by an entire or lobate mound of cartilage, which may or may not be a homologue of the medial digit. There are no lateral digits, although vascular cores alongside the mound of cartilage extend into the papillae. Paired vascular lobes below the crater floor are present as in other species.

Affinities of *N. sumichrasti* are somewhat obscure. In some of its characters it appears to be annectent between the neotomyines-peromyscines and the clusters of South American forms. In shape of glans and nature of spinous investiture it recalls *Ochrotomys*, *Ototylomys*, and *Tylomys*; the papilliform lateral mounds resemble similarly located papillae in *Tylomys*; the elevated meatus urinarius approaches the condition seen in *Scotinomys* and *Baiomys*; and the slender long bone with its distal cap of cartilage is not unlike the configuration of baculum seen in neotomyines and peromyscines. Burt (1960:63) saw resemblances in the bacula of *Neotoma* and *Nyctomys*.

On the other hand, the vascular lobes, three bacular mounds, multi-lobed urethral flap and some other characters appear to relate *Nyctomys* to the mass of South American species. We tentatively view it as a highly

differentiated outlier of that group, though we cannot readily overlook its several similarities with neotomyines-peromyscines. Clearly, as judged from our samples, *Nyctomys* is unlike *Rhipidomys* with which it has been aligned (Tate, 1932a; Hershkovitz, 1962); it does not belong closely with either *Rhipidomys* or *Thomasomys* as we know them.

Two other species which in morphology of phallus are set apart from the mass of forms are *Scapteromys aquaticus* and *S. tumidus*; these two comprise one of the strongly differentiated groups of South American cricetines. Features of its glans include its laterally compressed budlike shape, single three-peaked bacular mound, compound dorsal papilla and four-pronged urethral flap. The peculiar baculum consists of a robust bone with a deeply scooped, spoon-shaped base and a lobate terminal mass of cartilage which apparently represents three compressed cartilaginous digits. Three vascular cores course into the tips of the bacular mound; cartilage is restricted to the base of the mound.

In *Scapteromys* as in *Nyctomys* there are characters which resemble those of neotomyines. For example, the single bacular mound together with the peculiar shapes of urethral flap and baculum are reminiscent of features seen in the North American *Xenomys nelsoni* and *Neotoma alleni* (Hooper, 1960). That there are resemblances with neotomyines is apparent, and the possibility that *Scapteromys* as well as *Nyctomys* is related to those forms deserves consideration. Certainly the two are annectent forms in the sense that their characters bridge much of the morphological gap between the neotomyines and South American cricetines.

But the possibility that the resemblances with neotomyines were independently acquired is also apparent. The vascular system appears to be like that of the mass of South American species, not of neotomyines; the trilobed bacular mound and underlying cartilaginous mass appear to be strictly comparable to the three mounds and digits of the compound baculum, not to the simple baculum of neotomyines; and the multilobed dorsal papilla and four-pronged urethral flap are features that are typical of microtines and other forms with a compound baculum. On the whole, our specimens of *S. aquaticus* and *S. tumidus* fit morphologically nearer those of other South American species than those of neotomyines or other forms studied to date. Total evidence from glans and baculum suggests that *aquaticus* and *tumidus* are strongly differentiated relatives of the other 41 sampled species.

The remaining 40 species, together with previously discussed species of *Sigmodon*, *Sigmomys*, and *Reithrodon* (Hooper, 1962), cluster in regard to morphology of phallus, the large cluster comprised of several lesser groups and subgroups. In all of these forms the glans is a stubby structure which both externally and internally is much like that in microtines. Spines of

the exterior coat are moderate in size and densely spaced. The crater rim, either smooth or crenate but not papillose as in many microtines (Hooper and Hart, 1962), typically is bordered by a nonspinous collar. Contents of the crater include in various sizes and shapes: three bacular mounds, a bifurcate urethral flap, single dorsal papilla and, in some species, additional papillae; spines may invest any of these. There is no ventral shield as seen in microtines; however, possibly a shelf within the crater in *Neacomys* is its homologue. Large paired vascular lobes, two pairs or one which roughly parallel the main bone, are present in all species. The baculum consists typically of four parts. The proximal segment always is well developed and osseous in adults, while the digits vary in size, shape, and amount of ossification. Typically the digits are cartilaginous but in a few forms they contain a slight amount of osseous tissue, and in old *Sigmodon*, *Rheomys*, and *Zygodontomys* all digits bear ossicles; lateral digits are relatively small in *Oxymycterus* and in *Thomasomys aureus*. Morphological affinities of the 40 species as indicated by the glans and baculum are mentioned below.

Rheomys hartmanni is strongly differentiated from the other species. Among its features are the exteriorly plain glans, dissimilar bacular mounds, three spinous crater papillae, exceptionally long nonspinous urethral processes, and peculiarly shaped baculum. To be sure, most of its characters individually appear in similar or identical form in other species, but as a set they are unique and impressive. In viewing them we should consider *R. hartmanni* peripheral in the cluster of South American species. The data are in harmony with the suggestion that *Rheomys* like *Sigmodon* and *Sigmomys* which it resembles in some characters is an early offshoot from the ancestral South American muroid stock. Hershkovitz (1962) suggests that ichthyomyines (*Ichthyomys* and *Rheomys*) were in the vanguard of the cricetine invasion of South America.

The sampled species of *Sigmodon* and *Sigmomys* comprise a tight assemblage which also is well differentiated from the other 40 species, the amount of difference being about that between *Rheomys* and the rest of the species. Features of the phallus of *Sigmodon* and *Sigmomys* include the pronounced exterior lobation, numerous large spinous papillae in the crater—both characters being extremes among our species—and distinctive baculum with large digits which in old animals are mostly osseous, at least in *Sigmodon*; the condition in old *Sigmomys* is unknown. These and other characters suggest that *Sigmodon* and *Sigmomys* be arranged as a group apart from the other species. If they are closely related to *Holochilus* and *Reithrodon*, forms with which they are currently associated (Hershkovitz, 1955, 1962), evidence of that close relationship is not apparent in our samples.

Thomasomys aureus also must be listed as one of the strongly differentiated species if the characters seen in our lone specimen are typical of *aureus*. The large peculiarly sculptured glans with its crenate crater rim and highly dissimilar bacular mounds, but apparently with no dorsal papilla, together with the robust baculum with its long medial and tiny lateral digits are some of the features which may set *aureus* well apart from the other species; it is about as far removed from them morphologically as are *Sigmodon* and *Sigmomys*. Certainly the phallus differs greatly from the samples of the other species of *Thomasomys* and of *Rhipidomys*, so that while the phallic data may support the grouping of *T. cinereus*, *T. laniger*, and *R. mastacalis* as part of the *Rhipidomys-Thomasomys* group (Hershkovitz, 1962), they do not argue for the inclusion of *T. aureus* in that group. Assuming that the characters seen are typical of the species we view *aureus* as a well differentiated form which belongs within the main cluster of species, and possibly was derived from stock that gave rise to *T. laniger*, but which now fits closely with none of these.

When *Nyctomys sumichrasti* and *Thomasomys aureus* are excluded we are left with representatives of only three of the many species of the thomasomyine group, namely *T. cinereus*, *T. laniger*, and *Rhipidomys mastacalis*. These form an assemblage the phallic characters of which grade into those of other groups. For example, in regard to the closely similar *cinereus* and *laniger* the exterior configuration resembles that in some oryzomyines (e.g., *O. palustris* and *O. concolor*), the narrow nonspinous crater collar is like that in *Oxymycterus* and some *Akodon*, spininess of crater and contents as in some *Akodon* and *Calomys*, characters of dorsal papilla and urethral flap approaching conditions in *Akodon*, and shape of bone somewhat resembling that in *Sigmodon* and *Rheomys*. *R. mastacalis* differs more from *cinereus* and *laniger* than those two do from each other, but clearly it is morphologically closest to them in our samples.

Notiomys valdivianus fits near our akodonts or phyllotines but no more closely to them than, say, *Oxymycterus* does with akodonts. It is well differentiated phallically, set somewhat apart from the other species in a combination of traits including prominent dorsal hood, proximally situated parotoid lobes, spinous dorsal papilla and urethral flap, delicate bone, and robust dissimilar digits. The external shape is unique, but the dorsal papilla and urethral flap with their robust recurved spines are rather like those in *Akodon*, *Eligmodontia*, *Calomys*, and *Oxymycterus*, and the delicate bone is suggestive of that in *Reithrodon* or *Eligmodontia*. In regard to morphology of phallus, *Notiomys* is about as far removed from *Akodon*, *Eligmodontia*, *Calomys*, and possibly *Phyllotis* as *Oxymycterus* is; it clearly belongs with those assemblages.

Data from the phallus support the recognition of an oxymycterine group which fits near the thomasomyine or the akodont clusters, perhaps closer to akodonts. In present samples of *Oxymycterus paramensis* and *O. rufus* characters of the crater rim and of the bone are reminiscent of features in *Rhipidomys* and *Thomasomys*, while shape and spininess of dorsal papilla and urethral flap and configuration of bacular digits approach conditions in *Akodon*. *O. paramensis* and *O. rufus* appear to be similar; the observed difference between the two is slight, scarcely more than that between *Calomys callosus* and *C. laucha* for example.

Phallic data also support the recognition of an oryzomyine cluster and, within it, of subgroups which mostly but not entirely conform with current genera and subgenera. The samples of *Oryzomys* and *Nectomys* form a comparatively homogeneous assemblage which corresponds in part to Hershkovitz' (1944, 1962) oryzomyine group, but which, present data suggest, also should include *Holochilus* from his sigmodont group. Phallic subgroupings, some of which cut across current subgeneric boundaries, are indicated in the following synopsis of the oryzomyine species.

The specimens of *Holochilus brasiliensis* are unlike examples of *Sigmodon*, the genus with which *Holochilus* has been associated (Ellerman, 1941; Hershkovitz, 1955). They closely resemble oryzomyines in almost all respects except absolute size. In exterior configuration, characters of crater rim and walls, shapes of bacular mounds, nature of urethral flap, and morphology of baculum they fit with oryzomyines, with the samples of *O. palustris*, *O. albigularis* and *O. concolor* in particular. This striking and apparently fundamental resemblance of *Holochilus* and *Oryzomys* suggests that the position of *Holochilus* be reexamined with the thought in mind that it may be a well differentiated oryzomyine rather than a sigmodont.

In characters of phallus, *Oryzomys palustris* fits near *O. albigularis* and allies and, except in absolute size, near *Holochilus brasiliensis*. Nevertheless, because it stands slightly apart from those and other oryzomyines, we view it as our sole representative of a minor subgroup of oryzomyines.

Oryzomys albigularis, *O. devius*, *O. capito* and *O. concolor* comprise a comparatively compact morphological unit. *O. albigularis* and *O. devius* are closely similar, an observation which is in harmony with the suggestion that *devius* is the Central American counterpart of *albigularis* (Hershkovitz, 1944:72). *O. capito* and *O. concolor* are approximately equally differentiated from each other and from *albigularis-devius*, although in regard to exterior configuration and shape of urethral flap *capito* is similar to *albigularis*. The data do not support the subgeneric separation of *concolor* and *capito* (Hershkovitz, 1960).

Oryzomys flavescens, *O. fulvescens* and *O. nigripes* are phallically simi-

lar if not identical. Although larger and somewhat differently proportioned, *O. longicaudatus* also fits with those forms. Together they form a minor morphological unit characterized by small size of glans, rather prominent exterior lobes, peculiar crater rim collar, and subequal bacular digits which may contain osseous tissue. They bear a few resemblances to *Neacomys guianae*, to *O. albigularis*, and (through *longicaudatus*) to *capito*. This unit is distinctive, but it is close to other oryzomyines; for example, the gap in morphology between these forms and *capito* is scarcely more than that between *concolor* and *capito* and it definitely is less than between *palustris* and either *capito* or *albigularis*. There is good support in the phallic data for abandoning the subgenus *Oligoryzomys*, as most contemporary authors have done.

Oryzomys caliginosus, *O. alfaroi*, *O. melanotis*, and *Nectomys alfari* comprise another compact morphological assemblage, features of which are slender shape of glans, narrow crater collar, long slender bone, and relatively short digits, the slim medial one contrasting with the robust, horn-shaped lateral pair. Of these four species *alfaroi* and *melanotis* are the most similar, the two differing but slightly if at all. *O. caliginosus* and *N. alfari* are more strongly differentiated both from each other and from *alfaroi-melanotis*; but clearly the four belong in the same morphological subgroup, for *N. alfari* differs no more from *O. alfaroi* than *O. albigularis* does from *O. concolor*, for example. Data from glans and baculum support the inclusion of *N. alfari* in *Oryzomys*, but they do not emphasize the need for its subgeneric segregation (*Sigmodontomys*) therein (Hershkovitz, 1948:54).

Neacomys guianae is a well differentiated species which is distinguishable from other forms in a combination of characters including prominent parotoid lobes and dorsal hood, complete collar of nonspinous tissue which is inset below the crater rim, relatively large dorsal papilla, delicate bone with a diamond-shaped base, and slight digits which apparently tend to contain osseous tissue. It resembles *Oryzomys flavescens* and allies to some extent and a few of its traits suggest conditions in *Zygodontomys brevicauda*. All characters considered, however, it (and probably *N. spinosus* also) fits within the oryzomyine group and because of amount of differentiation probably should be listed separately therein, excluded from the other subgroups.

The systematic position of species of *Zygodontomys* has long been obscure. One or the other of the two species *brevicauda* and *lasiurus* at various times has been considered an *Oryzomys* (Allen and Chapman, 1893), an *Akodon* (Thomas, 1916; Ellerman, 1941), and a phyllotine (Hershkovitz, 1962), and one may infer from those reports that most cranial

and external characters of those species are seen separately also in *Oryzomys*, *Akodon*, or some phyllotines (e.g., *Calomys*). Hershkovitz (1962:202) considered *Zygodontomys* "an annectant [*sic*] form between phyllotine and akodont rodents," but at the same time he pointed out that clarification of its status must await a thorough systematic review of akodonts.

Information from the glans and baculum does little in clarifying the situation other than to indicate that phallically, as well as cranially and externally, *Zygodontomys* is an annectent form. To judge from present samples, *brevicauda* and *lasiurus* are similar, the two differing in details. Together they form a minor assemblage the characters of which are variously duplicated in *Oryzomys* (e.g., in external configuration, characters of crater collar, and shape of dorsal papilla in *flavescens* and allies), *Akodon* (e.g., in nature of urethral flap and some aspects of the baculum in *urichi*), *Calomys* (shape of bone in *callosus*), or, even, *Sigmodon* or *Sigmomys* (inflexion and ossification of bacular digits). But on the whole there is more resemblance to *Oryzomys* or *Akodon* than to *Calomys*. Conceivably, *brevicauda* and *lasiurus* more than most others retain traits of a stem stock from which evolved *Oryzomys*, *Akodon*, *Sigmodon*, and *Sigmomys*.

All of our species of *Akodon* apparently belong together, each probably distinguishable in glans and baculum but none highly differentiated. For example, *surdus* differs from the other *Akodon* about as much as *Oryzomys albigularis* does from *O. capito*. *A. urichi*, the most distinct, contrasts slightly more; in that species the glans is more distinctly lobed, dorsal papilla spine-tipped, and digits subequal. In these characters *urichi* approaches some *Oryzomys*. *A. obscurus*, *orophilus*, and *bogotensis* appear to be smaller and otherwise somewhat unlike the other forms, but when measured against adequate specimens this observation may prove to be incorrect. In short, the eight species comprise an assemblage which morphologically is close to *Oryzomys* and at the same time is not far removed from *Calomys*.

Eligmodontia typus is distinguishable from other forms on the basis of small size of glans and baculum, rather gross spiny coat, shape of baculum, and other characters. Its robustly spinous dorsal papilla and urethral flap are like those in *Calomys*, the conformation of the baculum, particularly of the digits, is reminiscent of that in *Phyllotis pictus*, and there are several similarities with species of *Akodon*; the resemblance to some of the small species—*obscurus*, *orophilus*, or *bogotensis*—may be especially close. In considering all characters we should place *Eligmodontia* near *Calomys* and *Akodon*.

Five of the six species remaining to be discussed have been grouped as phyllotines on the basis of evidence from skin and skull (Osgood, 1947;

Hershkovitz, 1962). In regard to morphology of phallus, too, they form a cluster, but a loose one and one which also should include a sixth species, *Reithrodon physodes*. All but two apparently are well differentiated such that the difference between some of them (e.g., *P. darwini* and *P. griseoflavus*) exceeds that between some *Oryzomys* and *Akodon*. Notwithstanding this diversity the six of them appear as forms in one radiating network which impinges on that of *Eligmodontia* and *Akodon*.

The specimens of *Calomys callosus* and *C. laucha* are similar. Features seen in them include large recurved spines on both a small dorsal papilla and a long urethral flap, elongate bacular mounds, long erect digits, and ventrally keeled bone. A similarly spined dorsal papilla and urethral flap is also seen in *Eligmodontia*, but excepting those likenesses *Calomys* appears no closer to *Eligmodontia* than to *Akodon*. There is more resemblance to *Phyllotis*, specifically to *P. griseoflavus* which is similar to it in proportions, external configuration, and other details, but is rather unlike it in structure of baculum.

To judge from present specimens *Phyllotis griseoflavus*, *pictus*, and *darwini* are rather sharply set apart from one another. *P. darwini*, with its long bacular mounds (the laterals of which are sinuous and hooked) and short broad-based bone with long robust digits, is the most strongly differentiated. Externally and in some proportions of parts, however, it resembles *P. griseoflavus* and *Calomys*, and with respect to sizes and lateral flexures of the bacular mounds—to mention two characters—it approaches *Reithrodon physodes*. *P. darwini* is about equally differentiated from *griseoflavus* and *pictus* on the one hand and *Calomys* and *Reithrodon* on the other. *P. griseoflavus*, more than the other two species, ties them morphologically to *Calomys*.

In morphology of glans and baculum *Reithrodon physodes* appears to belong near *Phyllotis*, in our samples possibly closest to *P. darwini*. The specimens are unlike those of *Sigmodon* and *Holochilus*, forms with which *Reithrodon* tentatively has been associated on the basis primarily of cranial features (Hershkovitz, 1955). Tate's reference (1932b:2) to a *Reithrodon-Phyllotis* complex is more in harmony with the information from glans and baculum. Phallically *R. physodes* fits in the phyllotine cluster and therein is morphologically but slightly farther from *Phyllotis* than is *Calomys*.

In summary, the new information presented here points to the following conclusions regarding the 43 Neotropical cricetine species.

The phalli of most, possibly all, of these species are fundamentally alike in structure and may have been derived from a single ancestral stock. Differentiation in them has led to nothing major and new but rather has amounted mainly to the sorting among the species of modifications or

ornamentations in that basic plan. These species are much like microtines (Hooper and Hart, 1962) in regard to both morphology of glans and baculum and patterns of differentiation therein.

Three forms, *Nyctomys sumichrasti*, *Scapteromys aquaticus* and *S. tumidus*, stand apart from the mass of species. In characters they grade toward neotomyines, but the evidence does not convince us that they belong in that simple-glans group. Closer affinities appear to be with the mass of South American cricetines.

Groupings based on the glans and baculum do not entirely conform to current classifications which are founded principally on cranial and external characters. Important discrepancies between the two in regard to the species studied are mentioned below.

ORYZOMYINE GROUP.—*Holochilus* fits near *Oryzomys* rather than with *Sigmodon*. *Nectomys alfari* resembles *Oryzomys alfaroi* and together with *O. caliginosus* and *O. melanotis* they form a group apart from the other *Oryzomys* and from *Neacomys*.

THOMASOMYINE GROUP.—*Nyctomys* is excluded¹. *T. aureus* apparently also is well removed from the other species of *Thomasomys* and from *Rhipidomys*.

AKODONT GROUP.—*Notiomys* is no closer to *Akodon* than *Oxymycterus* is; the three forms are listed independently.

PHYLLOTINE GROUP.—*Zygodontomys* belongs near *Oryzomys* or *Akodon* and not with *Calomys* and some *Phyllotis*. *Eligmodontia* perhaps also should be arranged nearer *Akodon*.

¹ The monotypic genus *Otonyctomys* apparently is phallically well differentiated from *Nyctomys* and from other Neotropical forms examined. These remarks are based on a dried glans (now reconstituted in fluid) of *O. hatti* recently received through the courtesy of J. K. Jones of the University of Kansas Museum of Natural History. The stubby, tubercle-invested glans externally resembles other glandes of the complex type, its tubercles moderate in size in strong contrast to those in *Nyctomys*. In the spine-studded terminal crater there are three mounds, the lateral pair basally recessed in the flank of the larger medial one. The dorsal papilla and urethral flap are the most elaborate seen in Neotropical forms. The former isn't a cone, but instead is a papillose ridge extending from the dorsal wall of the crater to the medial mound; each papilla (9 counted) is capped with a spine. The urethral flap is basically three-lobed as in *Nyctomys*, but the large lateral lobes are papillose, each papilla spine-tipped. The main bone, of the four-part baculum, terminates in a broad, medially-cleft head somewhat as in *Thomasomys aureus* (Fig. 5), to which are attached three cartilaginous digits, an erect medial one and a smaller, outcurved, lateral pair. Features of this specimen suggest that *Otonyctomys* is a well differentiated form which may be more closely related to *Nyctomys* and *Thomasomys aureus* than to other Neotropical forms examined. In the diagram of possible relationships (Fig. 8b) it might fit as an independent offshoot between those two genera.

SIGMODONT GROUP.—*Holochilus* is an oryzomyine, and *Reithrodon* belongs near species of *Phyllotis*. *Sigmodon* and *Sigmomys* remain as sigmodonts.

TYPES OF GLANDES IN MUROID RODENTS

In earlier reports Hooper (1958, 1959, 1960; Hooper and Hart, 1962) pointed out that all of the muroid glandes examined to date appeared to be constructed according to one or the other of two basic schemes, one simple, the other complex. The simple type of glans contains a single bone, with or without a cartilaginous tip, and spongy vascularized layers which extend most of the length of the glans and occupy much of the cross-sectional diameter of that organ. In the complex type the baculum typically consists of four parts—a basal bone and three digits; the spongy layer is comparatively thin and functionally apparently partly replaced by pairs of sac-like sinuses that are situated alongside the baculum below the floor of the terminal crater; and in addition there usually is an array of processes and embellishments not seen in the simple glans. These two types are described in detail elsewhere (Hooper and Hart, 1962).

Other species in addition to those reported on to date (Hooper, 1958, 1959, 1960; Hooper and Hart, 1962) have since been examined and there is now firmer factual basis for comments regarding morphological types of glandes and their bacula in muroid rodents. The additional species include: nine Old World cricetines of seven genera (*Callomyscus*, *Cricetulus*, *Crice-tus*, *Mesocricetus*, *Myospalax*, *Mystromys*, and *Phodopus*); 15 murines of 12 genera or subgenera (*Acomys*, *Apodemus*, *Arvicanthis*, *Dasymys*, *Gunomys*, *Leggada*, *Lophuromys*, *Micromys*, *Mus*, *Nesokia*, *Pelomys*, and *Rattus*); one nesomyine (*Macrotarsomys*); 4 gerbillines of three genera (*Gerbillus*, *Meriones*, and *Rhombomys*); one otomyine (*Otomys*); one dendromurine (*Dendromus*); one rhizomyid (*Tachyoryctes*), and several non-muroid forms including *Aplodontia*, *Glaucomys*, *Muscardinus*, *Sciurus*, *Sicista*, *Thomomys*, and *Zapus*. Several New World caviomorphs have also been studied (Hooper, 1961).

Information obtained from the phalli of these species is in harmony with the premises that the Muridae and Cricetidae belong together morphologically and probably derive from one and the same ancestral stock, and secondly, that in this large assemblage there has been much differentiation at low taxonomic levels, but little or none which on morphologic grounds warrants familial recognition. The phalli fit as representatives of one major group of great variation.

In most of the sampled species the glans is of the complex type, and by its vascular system and other fundamentals it is recognizable as such even when the glans has no lateral digits, crater papillae, or some other features

which characterize the fully complex glans and baculum. It is clear that the complex phallus is the cosmopolitan type in murids and cricetids. Considering the sampled forms it is seen in all murines, gerbillines, otomyines, dendromurines and nesomyines, all Old World cricetines except one (*Myospalax*), all microtines except one (*Ellobius*), and all Neotropical cricetines described herein. Few of the species in these aforementioned groups have all of the complexities seen in the most elaborate of these phalli, but although some may be comparatively plain, all of them are of the complex type if we interpret them correctly. It is possible that in this array of forms, each similar appearing and comparable part—the three-digit baculum, urethral flap, dorsal papilla or vascular lobes, for example—is not homologous. In the absence of evidence to the contrary, however, we assume that they are homologous and we consider the occurrence of these parts in complex-type phalli as evidences of kinships.

By comparison, a phallus which we consider to be fundamentally simple is seen in few forms, all or almost all of which are restricted to the New World, mainly to North America. Possible exceptions are the Old World *Myospalax*, *Ellobius*, and perhaps *Tachyoryctes*, the phalli of which are inadequately known. Excluding these because of insufficient information, the kinds with fundamentally simple glandes are New World forms, namely *Baiomys*, *Neotoma*, *Neotomodon*, *Nelsonia*, *Ochrotomys*, *Onychomys*, *Otodylomys*, *Peromyscus*, *Reithrodontomys*, *Scotinomys*, *Tylomys* and *Xenomys*. On the basis of structure of the penis we view these as constituting a natural assemblage of muroids which, like groups with complex glandes, has adaptively radiated in structure and habits to fill various niches.

The question as to the nature of the ancestral muroid glans is one for which there is now no obvious and definitive answer. An elongate glans enclosing a single bone without terminal digits may be primitive in rodents, since a phallus of that simple type apparently is standard in most non-muroid rodents. It also may be the sort obtaining in early muroids. If it was, then peromyscines-neotomyines, *Myospalax*, *Ellobius*, *Tachyoryctes*, and perhaps *Mystromys* and *Macrotarsomys*—some or all of these—may be considered primitive in regard to structure of phallus, and conversely all other sampled muroids are more advanced. Supposedly, then, the evolutionary trend has been toward complexity of glans and baculum. If this was the trend in the mass of muroids, and assuming that murines, gerbillines, microtines, South American cricetines and western Asian cricetines are natural assemblages, which they seem to be, then a complex phallus with its characteristic vascular system, compound baculum, several bacular mounds, and other appurtenances must have evolved in a parallel fashion in each of those groups. This to us seems unlikely.

An alternative hypothesis is that while the primitive muroid phallus may or may not have been simple, the ancestral murid-cricetid glans was complex, something in the order of that seen in contemporary hamsters (*Cricetus* and *Mesocricetus* for example). The trend, then, in these groups has been toward simplification of glans and baculum. Accordingly, the comparatively simple penes (of the complex basic scheme) seen in some microtines, murines, Neotropical cricetines and Old World cricetines are, as suggested by Bittera (1918), evidences of secondary reduction or loss of parts, vestiges of which are commonplace among them.

In our view the latter hypothesis best fits the available information. The comparatively plain penes seen in some microtines, murines, South American cricetines and Old World cricetines are secondarily simple, derived from a complex-penis ancestral stock that gave rise to this mass of muroids. Similarly the glandes of peromyscines and neotomyines then should also be considered as results of secondary reduction and loss of parts.

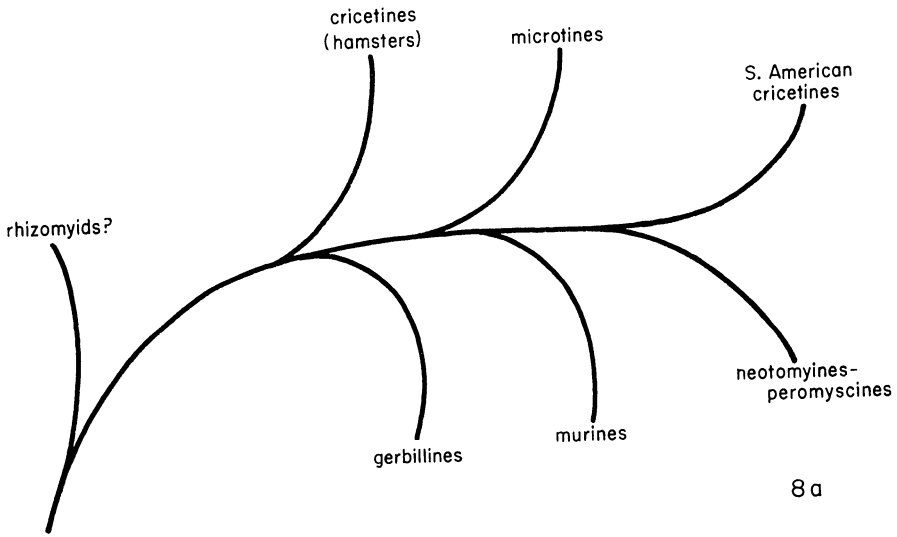
Thus, although the penes of the majority of muroid species remain to be studied, the information now available on a number of representatives of various families, subfamilies and tribes permits the following tentative statements regarding classification of muroids. For purpose of general orientation, the way in which the groups of muroids might fit on the basis of information from glans and baculum is suggested in Figures 8 and 9.

In regard to structure of the phallus, the sampled species represent one major assemblage which is composed of six large groups and possibly several smaller ones. The major assemblage corresponds to the current Muridae and Cricetidae combined (Simpson, 1945). As we interpret them the phallic data give no strong support to the recognition of either the Cricetidae or Cricetinae as currently constituted. Three of the groups within the major assemblage correspond to current subfamilies; three do not. Each is distinguishable from the others in characters of glans and baculum. The groups are mentioned below.

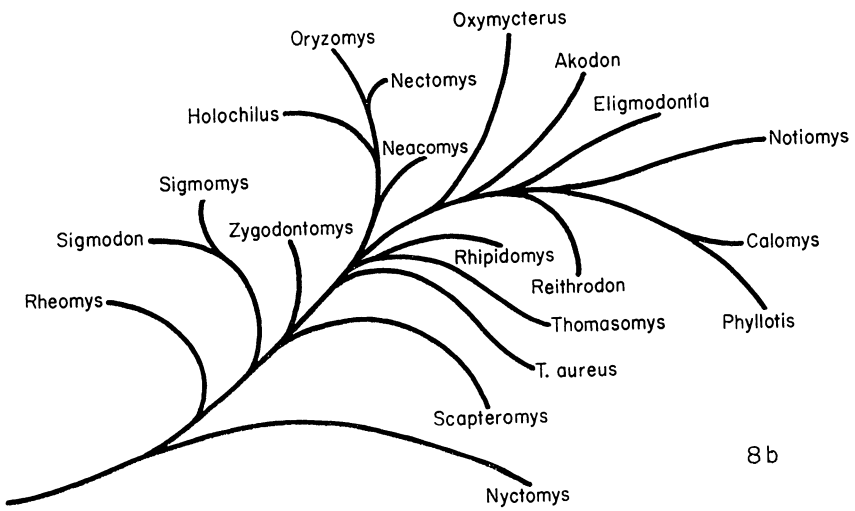
The Murinae fit together to the exclusion of other forms. *Lophuromys* may be aberrant; the single specimen differs strikingly from the others. In the murines examined the lateral bacular mounds, whether small or large, are supported below apparently mostly by vascular tissues, not by cartilage or bone, and the meatus urinarius lies in a second crater within the terminal crater.

The Gerbillinae also belong together in regard to structure of phallus. Although distinctive, they resemble microtines and Old World cricetines.

Microtines, discussed elsewhere (Hooper and Hart, 1962), constitute a third group characterized by ventral shield, crater rim papillae, and other features of glans and baculum. *Ellobius* likely is the most aberrant form; it may not belong in the group (*op. cit.*).



8 a



8 b

FIG. 8. Diagram of possible relationships of some rodents: *a*, groups of muroids; *b*, South American "cricetines." Based on information from the glans penis.

A fourth assemblage is comprised of the Old World cricetines, *Callomyscus*, *Cricetus*, *Cricetulus*, *Mesocricetus*, and *Phodopus*. Phallically, *Myospalax* clearly warrants tribal separation from those and possibly should be excluded from this group of hamsters. *Mystromys* also apparently does not fit well; its position should be reexamined.

The monotypic genus *Callomyscus* should remain with the hamsters, but it warrants special comment because of its close external and cranial resemblance to *Peromyscus* (Osgood, 1947; Vorontsov, 1959). Vorontsov arranged the two genera in a single tribe (*Reithrodontomyini*) along with *Reithrodontomys* and *Baiomys*, while Osgood (1947:166) thought that *Callomyscus* "is so similar to the American *Peromyscus* that it probably signifies a late Pleistocene invasion [of the Old World] from North America."

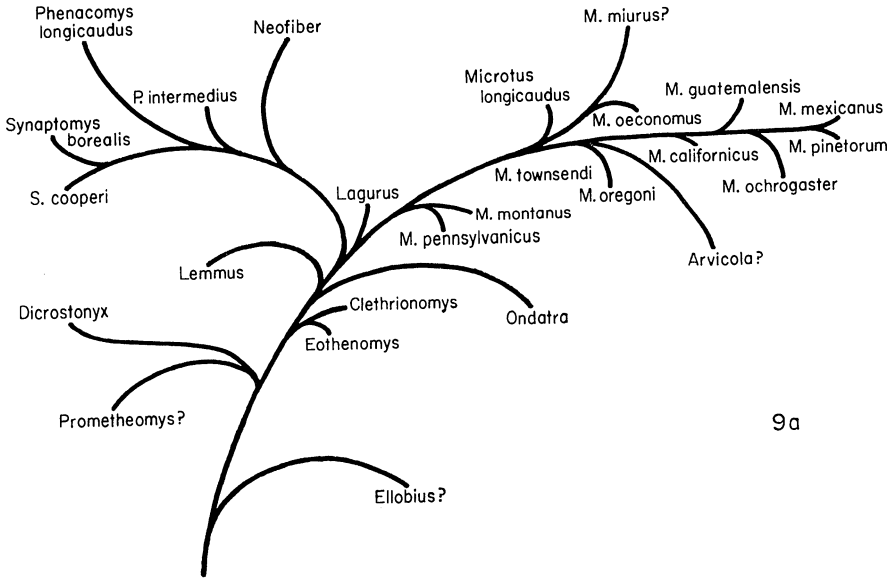
To judge from structure of phallus the resemblances which Osgood and Vorontsov saw are evidences of parallelism or convergence, not of close affinities between the two genera. The glans in *Callomyscus* is a normal complex type complete with three-digit baculum and mounds, urethral flap, dorsal papilla, and vascular lobes. It is no more similar to glans of *Peromyscus* than are those of *Mus*, *Gerbillus*, or *Cricetulus*. It clearly belongs with complex-glans forms, not with peromyscines or neotomyines. Of the hamsters examined, *Callomyscus bailwardi* is phallically closest to *Cricetulus migratorius*.

The South American cricetines, identities stated in the present report, constitute a fifth group of muroids. Their characters tie them to each of the preceding assemblages.

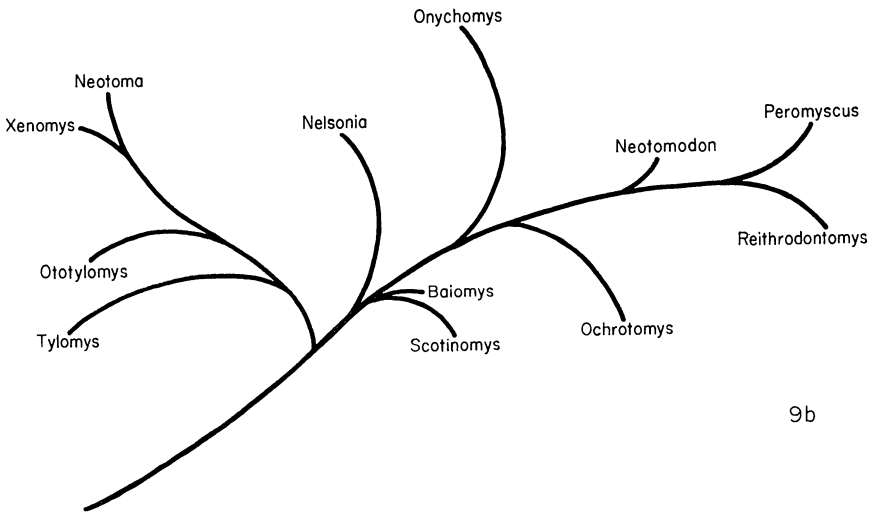
A final large assemblage is comprised of the North American simple-glans cricetines; these are discussed above and elsewhere (Hooper, 1959, 1960).

Among currently recognized muroids (Simpson, 1945) are the subfamilies Nesomyinae, Dendromurinae, and Otomyinae, and the family Rhizomyidae. Present samples of these groups are so small as to be essentially worthless. The specimen of *Tachyoryctes* (Rhizomyidae) is peculiar in many respects. So is the example of *Macrotarsomys* (Nesomyinae). The specimens of *Dendromus* (Dendromurinae) and particularly *Otomys* (Otomyinae) are similar to murines.

In regard to morphology of glans and baculum, the North American simple-glans group is comprised of two assemblages of tribal level which are termed the peromyscines and neotomyines. The peromyscines include *Baiomys*, *Scotinomys*, *Ochrotomys*, *Neotomodon*, *Peromyscus*, *Reithrodontomys* and *Onychomys*. *Baiomys* and *Scotinomys* are close and are connected through *Ochrotomys* to *Peromyscus* and *Reithrodontomys*. *Neotomodon* is near the latter two. *Onychomys* is set slightly apart from the others. The neotomyine group consists of *Nelsonia*, *Ototylomys*, *Tylomys*, *Neotoma*,



9a



9b

FIG. 9. Diagram of possible relationships of some rodents: *a*, microtines, principally North American, studied by Hooper and Hart (1962); *b*, neotomyines and peromyscines. Based on information from the glans penis.

and *Xenomys Nelsonia* appears to be removed somewhat toward the peromyscines. *Neotoma* and *Xenomys* are close; they connect morphologically with *Ototylomys* and *Tylomys*.

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