MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 159

Comparative Gross Morphology of Male Accessory Glands among Neotropical Muridae (Mammalia: Rodentia) with Comments on Systematic Implications

by
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INTRODUCTION

The South American cricetines comprise an impressive array of predominantly neotropical murid genera that have been characterized by their common possession of a complex glans penis. Hershkovitz (1944, 1955, 1962) divided these rats and mice into eight major groups which he defined on the basis of craniodental and external characters. Detailed studies of the phalli of 16 South American cricetine genera, however, impelled Hooper (1962) and Hooper and Musser (1964a) to recommend substantial modifications of this arrangement, and to propose an hypothesis of South American cricetine phylogeny which differed considerably from that of Hershkovitz (1962). Hershkovitz (1966b) subsequently defended his original classification, and questioned the usefulness of the glans penis as the best indicator of murid geneological relationships. Yet a third phylogeny for these rodents, based largely on chromosomal data, has recently been proposed by Gardner and Patton (1976).

Although Hershkovitz (1962) spoke of the 'progressive' nature of certain craniodental and external characters, Hooper and Musser (1964a) of ancestral *versus* specialized conditions of the glans penis, and Gardner and Patton (1976) of broad trends of karyotypic rearrangement accompanying phyletic divergence, none of these authors consistently grouped taxa by shared, derived character states, and it is therefore unclear to what extent the disparity of their proposed phylogenies is due to real disagreement of characters (homoplasy) or, instead, simply to the use of different criteria for inferring relationships. While a critical reappraisal of previously-described characters is surely in order, new data from additional organ systems also seems desirable.

The male accessory reproductive glands of rodents have traditionally been accorded scant attention in the systematic literature despite the variation in this organ system revealed by the work of some anatomists (Tullberg, 1899; Grosz, 1905; Howell, 1926; Mossman *et al,* 1932; Taylor, 1963). A paper by Arata (1964), however, described the accessory glands of 24 species of murids and sparked active interest in this aspect of the male reproductive tract as a source of taxonomically useful data. Lawlor (1969), Linzey and Layne (1969) and Carleton *et al* (1975) subsequently extended knowledge of male accessory gland variation among New World cricetines, and used their data to test theories of murid interrelationships.

We dissected the male reproductive tracts of many South American cricetine species in an attempt to evaluate the relative merits of the three competing phylogenies for these rodents discussed above. We also examined the male tracts of members of other murid groups in order to obtain comparative data for inferring the morphology of the primitive murid male accessory gland complement. In this paper, we report the results of our dissections and discuss their implications for the classification of neotropical murids.

MATERIALS AND METHODS

Entire male reproductive tracts were dissected from fluid-preserved carcasses and stored in 70% ethanol. All specimens, except where noted, are of adult males with scrotal testes and enlarged epididymal tubules. Permanent slides of spermatozoa were prepared for all specimens, and animals judged to be sexually active by the above criteria were found to have abundant epididymal sperm without exception. The measurements provided in Table 1 were taken with dial calipers and recorded to the nearest 0.5 mm. Linzey and Layne (1969) define the anatomical limits of most of our measurements, but our definition of bulbo-urethral length differs from theirs by including the basal duct as well as the body of the gland. Lengths of hind feet were taken from the collector's label or field catalog, or were measured on the fluid-preserved specimen. Nomenclature of the accessory glands follows Arata (1964) and, for the rest of the male tract, Howell (1926), and Hooper (1958). The senior author prepared the illustrations.

The 205 male reproductive tracts examined in the course of this study sample 65 species in 43 genera and subgenera, and include representatives of every generic group of complex-penised neotropical murids recognized by recent students (Hershkovitz, 1966b; Hooper and Musser, 1964a; Gardner and Patton, 1976). Our concept of Muridae follows Ellerman (1941) and Hershkovitz (1966a), and therefore includes Simpson's (1945) families Muridae and Cricetidae. Names of murid subgroups (not here accorded formal taxonomic rank) are those employed by Hooper and Musser (1964a), but we also recognize the distinctiveness of *Mystromys* by placing it in a group of its own as recommended by Vorontsov (1966). Use of Latin binomials for the South and Central American species generally follows Cabrera (1961) and Hall and Kelson (1959); in some instances, however, we have accepted the taxonomic recommendations of later workers.

Localities and museum catalog numbers of the material we examined are provided in Appendix 1.

VARIATION AND HOMOLOGY

Secretory organs of the male reproductive tract are dependent on sustained levels of testosterone and other blood androgens for their maintenance (Mann, 1964, 1974; Price and Williams-Ashman, 1961; Brown, 1972). Consequently, the size and shape of mammalian accessory glands vary with age, and considerable seasonal fluctuation in size of murid male glands is a well-documented phenomenon (e.g., Rowlands, 1936; Prasad, 1956; Haines, 1961). Although we selected only reproductively active males for dissection and description (criteria defined above), the exact degree of sexual activity at the time of preservation is difficult to ascertain; this, therefore, unavoidably introduces some non-genetic variation in glandular

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF SELECTED SOUTH AMERICAN CRICETINE SPECIMENS; SEE LINZEY AND LAYNE (1969) AND MATERIALS AND METHODS (ABOVE) FOR DEFINITIONS AND EXPLANATIONS. GLANDULAR ABBREVIATIONS ARE THE SAME AS FOR FIGURES 1 AND 2.

Species	Museum number	hind foot	urethra	length lat PP	length med PP	length BU	width BU	length DP	width DP	length med VP	length lat VP	length AP	width AP	length V	width V	length A	width A
Abrothrix longipilis	MSU 7155	–	—	—	—	7.0	3.5	11.5	14.5	8.5	8.0	15.5	6.0	22.0	5.0	7.0	6.5
Akodon arenicola	UMMZ 110446	20	—	—	—	6.0	2.5	5.0	4.0	2.5	7.5	6.5	3.0	11.0	2.0	2.5	2.0
Akodon azarae	AMNH 206076	22	11.5	11.0	—	4.0	2.0	3.5	3.0	3.0	6.5	5.5	2.0	10.0	2.0	2.5	1.5
Akodon cursor	UMMZ 124283	27	17.5	10.0	—	5.5	3.0	5.0	4.5	2.5	9.0	8.5	1.5	11.0	3.0	2.5	2.0
Akodon obscurus	MSU 18460	24	27.5	16.0	—	8.0	3.5	7.0	6.0	5.5	16.0	10.5	4.0	17.0	4.5	4.5	3.0
Akodon varius	UMMZ 125281	23	17.0	11.5	—	4.5	3.0	3.0	4.0	3.5	7.0	7.5	2.0	10.0	2.0	2.0	1.5
Akodon jelskii	UMMZ 115713	24	16.0	10.5	4.0	4.0	3.0	5.5	3.0	7.0	3.5	8.0	2.0	10.5	2.0	3.5	2.0
Akodon bogotensis	FMNH 18679	19	8.5	10.0	—	3.5	1.5	3.5	3.0	—	5.0	5.5	2.0	8.5	2.0	2.0	1.5
Andalgalomys pearsoni	UMMZ 130037	24	18.5	10.5	3.5	7.0	3.0	8.5	5.5	9.5	4.5	8.5	2.5	12.5	4.5	3.0	2.0
Anotomys leander	AMNH 244607	36	15.0	10.0	—	6.5	4.0	5.5	5.5	—	12.0	7.5	2.0	11.0	3.0	3.0	3.5
Calomys callosus	UMMZ 124241	20	18.0	10.0	—	6.0	3.5	5.5	5.0	8.5	5.5	10.5	3.5	14.5	2.5	3.0	2.0
Chilomys instans	AMNH 63372	22	17.0	9.0	—	5.5	2.0	5.0	5.0	5.0	2.5	9.5	3.5	14.0	3.0	3.0	2.5
Eligmodontia typus	UMMZ 110396	22	11.5	9.5	2.5	4.5	2.0	3.0	3.0	6.0	3.0	6.0	1.5	9.0	2.0	1.5	2.5
Holochilus brasiliensis	UMMZ 125491	41	32.5	15.5	—	8.5	4.5	10.0	8.0	17.5	11.5	16.0	3.5	23.0	5.0	6.0	2.5
Irenomys tarsalis	MSU 7470	–	16.0	—	—	4.5	3.0	5.5	5.0	11.5	3.0	8.5	3.5	10.0	4.0	2.5	1.5
Neacomys spinosus	AMNH 202647	24	16.0	6.5	—	4.0	1.5	3.5	3.0	8.5	3.5	7.0	2.0	10.0	2.5	2.5	1.5
Nectomys squamipes	RSV 178	53	42.5	25.0	—	12.0	5.0	12.0	12.5	20.0	13.5	17.5	5.5	23.5	5.5	6.0	4.0
Neusticomys monticolus	UMMZ 126297	27	—	6.0	—	6.5	3.5	5.5	6.0	10.5	4.5	9.5	2.5	17.0	2.5	3.5	3.5
Notiomys valdivianus	MSU 6749	–	—	—	—	8.0	6.5	7.5	15.5	7.5	6.0	11.0	5.5	16.5	3.5	4.5	5.0
Oryzomys altissimus	RSV 175	23	11.0	6.0	—	4.0	1.5	2.5	3.0	2.5	2.0	4.5	2.0	8.5	1.5	2.0	1.5
Oryzomys fulvescens	UMMZ 117103	21	14.0	—	—	4.0	2.0	3.0	3.0	6.0	2.5	6.5	2.0	8.5	2.0	2.0	1.0
Oryzomys albigularis	UMMZ 116926	37	20.5	—	—	6.5	4.0	7.0	6.0	9.0	8.5	11.0	3.5	17.0	4.0	5.0	3.0
Oryzomys alfaroi	UMMZ 113094	26	15.5	8.0	—	3.5	2.0	3.0	3.5	11.0	7.0	6.5	1.5	11.5	2.0	1.5	1.5
Oryzomys capito	UMMZ 117187	30	21.5	13.0	—	5.5	3.5	5.5	5.0	13.0	6.0	8.5	4.0	16.0	3.5	4.0	2.0
Oryzomys melanotis	UMMZ 120671	31	17.0	9.5	—	4.5	2.0	6.0	5.5	10.0	8.0	8.5	3.0	11.5	2.5	2.0	2.0
Oryzomys ratticeps	UMMZ 124201	40	21.5	8.5	—	7.5	4.0	7.5	8.0	12.0	9.0	13.0	3.5	19.0	4.5	5.0	3.0

TABLE 1 (continued)

Species	Museum number	hind foot	urethra	length lat PP	length med PP	length BU	width BU	length DP	width DP	length med VP	length lat VP	length AP	width AP	length V	width V	length A	width A
Oxymycterus delator	UMMZ 126271	30	26.5	24.0	14.0	5.0	2.0	6.5	4.5	17.5	12.5	10.0	3.0	14.5	4.0	3.5	2.5
Oxymycterus rutilans	MSU 19316	29	24.5	20.0	14.0	6.0	3.0	4.5	4.0	15.0	11.0	8.0	2.0	13.5	2.5	2.0	2.5
Phyllotis micropus	MSU 7439	--	---	---	---	7.5	4.5	8.0	7.5	16.0	4.5	12.5	3.5	17.0	3.0	4.0	3.0
Phyllotis darwini	MSU 7428	--	---	---	---	6.5	3.5	6.0	5.5	16.5	5.5	12.0	4.5	17.5	3.0	3.0	2.5
Phyllotis osilae	AMNH 241401	29	16.0	8.5	3.0	6.5	2.5	6.5	6.0	9.0	3.0	10.0	2.5	14.5	2.5	3.5	2.5
Reithrodon physodes	MSU 18398	33	16.5	9.0	2.5	7.5	4.0	6.0	6.5	13.5	8.5	13.0	4.0	18.0	4.0	3.5	2.5
Rheomys hartmanni	UMMZ 111986	27	---	---	---	6.5	4.5	7.5	6.0	7.0	6.5	10.5	2.5	15.5	4.0	3.0	2.5
Rheomys underwoodi	UMMZ 115389	38	---	10.5	---	8.0	6.0	7.0	8.5	10.0	8.0	14.5	6.0	22.5	4.5	3.2	3.5
Scapteromys tumidus	UMMZ 126266	38	26.0	20.5	---	7.5	3.0	9.5	7.0	17.5	8.0	15.5	4.5	19.0	4.5	5.0	3.5
Sigmodon hispidus	UMMZ 120711	30	---	17.0	13.0	9.0	6.0	10.5	7.0	24.5	15.5	13.5	4.5	16.5	5.0	4.5	3.5
Sigmodon alstoni	USNM 496014	28	27.5	22.5	14.5	8.0	4.5	8.5	6.0	22.0	20.0	14.0	3.5	23.5	4.0	5.0	3.0
Thomasomys aureus	UMMZ 127114	40	24.5	9.5	---	5.5	2.0	10.0	6.0	7.0	5.0	12.0	6.0	21.0	4.0	4.5	4.0
Thomasomys baeops	AMNH 63382	25	19.0	12.0	---	5.0	2.5	5.5	4.0	4.0	3.0	9.0	2.5	14.0	2.5	2.0	2.5
Thomasomys laniger	USNM 495630	24	16.5	---	---	4.5	2.5	6.5	5.0	7.0	4.5	7.5	2.5	14.0	3.5	3.0	1.5
Thomasomys rhoadsi	AMNH 63361	28	16.0	---	---	5.0	3.5	7.0	4.5	4.0	4.0	10.0	2.5	12.0	2.5	3.0	2.5
Zygodontomys brevicauda	AMNH 202645	27	---	---	---	9.5	2.5	5.0	5.5	12.5	8.0	10.5	3.5	14.5	3.0	3.0	2.0
Zygodontomys brevicauda	AMNH 204805	29	22.5	12.0	---	7.0	3.0	6.0	6.5	12.5	8.5	9.0	3.0	13.0	3.5	2.5	2.0
Zygodontomys brevicauda	UMMZ 111957	24	---	14.0	---	6.5	2.5	6.0	5.0	15.0	5.5	12.0	4.0	15.0	3.5	2.5	2.5
Zygodontomys brevicauda	USNM 517628	--	---	---	---	---	---	4.0	5.5	10.0	5.0	12.0	4.5	17.0	4.0	2.0	2.0
Zygodontomys lasiurus	AMNH 202643	23	---	---	---	6.5	4.0	4.0	4.0	2.0	7.5	11.0	2.5	13.0	4.0	3.0	2.0
Zygodontomys lasiurus	AMNH 214762	26	24.5	17.5	---	7.5	3.5	4.5	4.0	3.0	9.0	10.5	4.5	15.5	4.0	2.5	3.0
Zygodontomys lasiurus	UMMZ 124259	25	---	12.0	---	5.0	2.5	4.0	4.0	2.0	5.0	7.5	1.5	10.5	2.5	2.0	1.5

size and shape. Additional variation is provided by *in vivo* distortion, rendered permanent by fixation, of soft glandular tissues by pressure from adjacent organs, particularly the caecum and colon. Measurements provided in Table 1 were taken from tracts we judged to be minimally distorted and maximally developed, and are intended to provide a basis for objective comparison when our written descriptions include references to relative size.

In contrast to the kinds of variation discussed above, the presence or absence of glands and certain aspects of their gross morphology appear to be constant within species if specimens of only breeding adults are used. Variation has been noted in the presence of supernumerary vesiculars in inbred strains of *Mus musculus* (Price, 1963), but such variability has not been reported, to our knowledge, in wild-caught murids; we observed only one case of intra-specific variation in the presence of accessory glands during the course of this study.

We infer the homologies of glands on the basis of morphological similarity and on position within the male reproductive tract. Accessory glands of *Rattus* and *Mesocricetus,* judged to be homologous by the criteria we employ, are similar embryologically (Price, 1936; Ortiz, 1947) and, together with their morphologically-determined presumptive homologs in *Mus* and *Meriones,* secrete immunochemically similar tissue-specific antigens (Barnes, 1972). Thus, we feel that confidence may usually be placed in identifications of accessory glands at the taxonomic levels considered here. Morphological criteria are likely to be inadequate, however, where loss and/or gross modifications of glands have obliterated the anatomical relationships otherwise employed to infer homologies; below, we explicitly indicate those instances where we believe this to be true.

DESCRIPTIVE MORPHOLOGY

I. South American Cricetines

Most of the South American cricetine species we examined have very similar accessory gland complements and conform closely to a single pattern of glandular morphologies. This widespread condition, hereafter referred to as 'typical', 'usual', or 'conventional', is described below; subsequent descriptions of individual taxa will emphasize only deviations from this pattern. Anatomical terms are illustrated in Figures 1 and 2.

The glandular complement of South American cricetines usually includes one pair each of preputial, bulbo-urethral, dorsal and anterior prostate, vesicular and ampullary, and two pairs of ventral prostate glands.

The preputials are conspicuous, modified sebaceous glands that lie lateral to the glans penis and are embedded in the connective tissue of the prepuce. Each gland is drained by a single large duct that emerges at the free margin of the prepuce and usually encircles the base of a long, stiff hair. Pre-

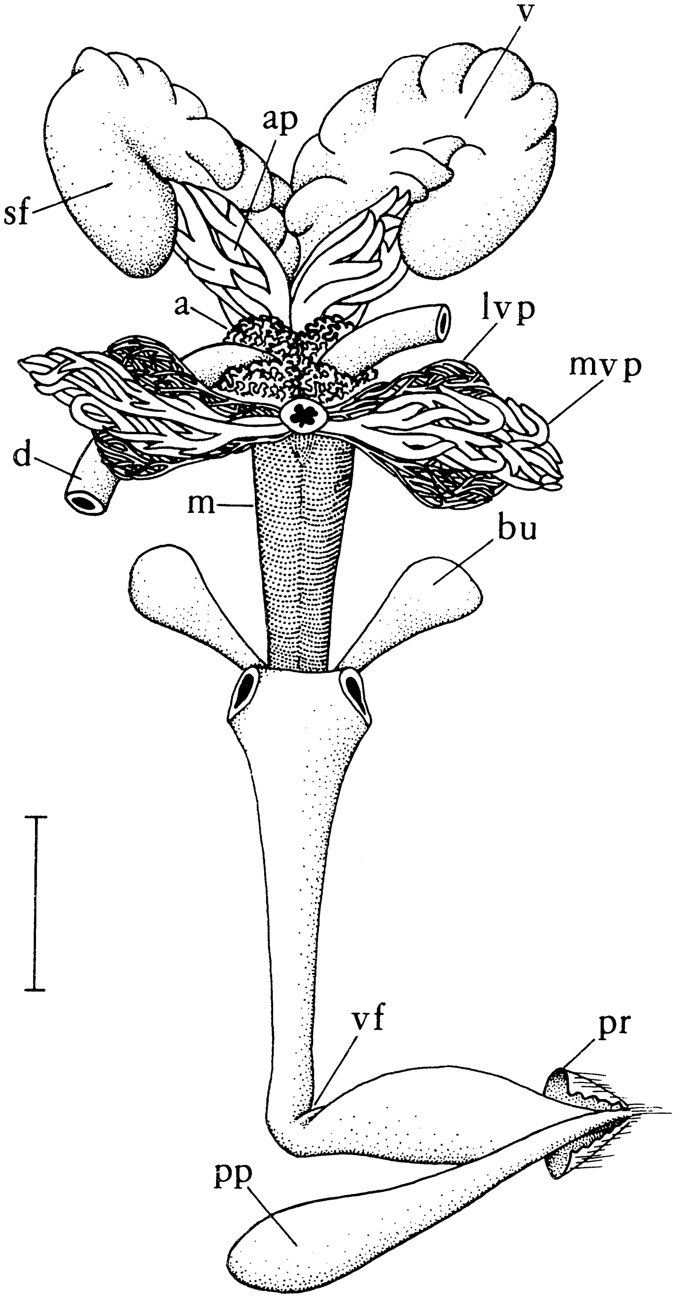

Fig. 1. Ventral view of the male reproductive tract of *Nectomys squamipes* (RSV 178); bladder and testes have been removed. Abbreviations: a, ampullary gland; ap, anterior prostate; bu, bulbo-urethral gland; d, deferent duct; lvp, lateral ventral prostate; m, *M. compressor urethrae* (enclosing the membranous urethra); mvp, medial ventral prostate; pp, preputial gland; pr, prepuce; sf, subterminal flexure of vesicular gland; v, vesicular gland; vf, ventral flexure of penis. Scale = 10mm.

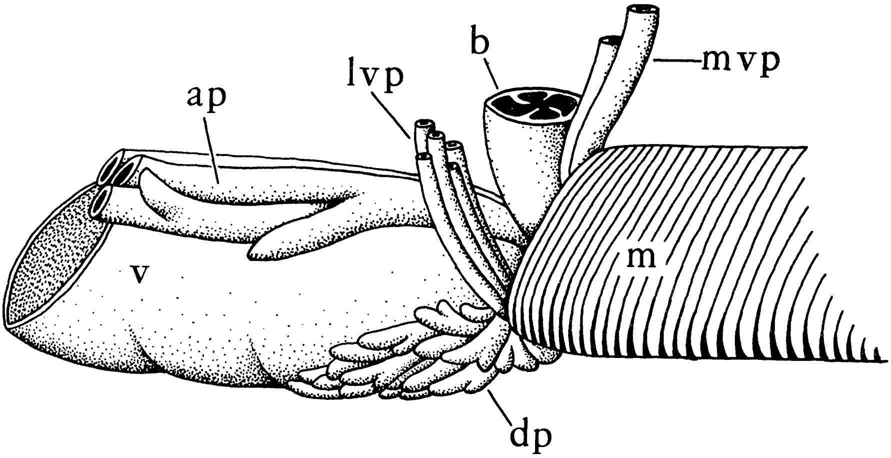

Fig. 2. Right lateral view of an idealized South American cricetine male reproductive tract to show the arrangement of prostatic ducts (deferent ducts and ampullary glands are not shown). Abbreviations: b, severed stalk of bladder; dp, dorsal prostate; other abbreviations are the same as for Fig. 1.

putials are flat and teardrop or strap-shaped depending on the degree of constriction of secretory tissue about the central duct proximal to the prepuce edge. In many species, the preputial glands exceed the prepuce in length and extend cranially for several millimeters or more beyond the ventral flexure of the penis to lie between the dermis and the superficial musculature of the abdomen. The secretory product is predominantly lipid in composition, and resembles a clear oil. Preputials are usually whitish or yellowish in color.

Bulbo-urethrals are present as a single pair of tubulo-alveolar glands situated cranial and dorsal to the bulb of the penis. The wedge-shaped body of each gland is drained by a single narrow duct that passes between *M. bulbocavernosus* and *M. ischiocavernosus* to enter the urethra just cranial to the juncture of the membranous and penile elements. A thin layer of muscle partially envelops the body of the gland distally. The descending colon passes between the bulbo-urethrals, and pressure from this organ as well as the state of contraction of *M. bulbocavernosus* and *M. ischiocavernosus* sometimes distorts these glands at the time of preservation. The color is usually white.

The dorsal prostates are two bilobed masses of branching tubules, divided middorsally, which surround the prostatic urethra dorsolaterally and embrace the descending colon. The basal ducts of these glands, usually five to nine on each side, enter the urethra under the cephalic margin of *M. compressor urethrae.* Usually, distinct dorsal and lateral lobes of this gland are evident on either side. Dorsal prostatic tubules are short and clumped together to form a compact mass invested by a common membrane. A medial tuft of tubules frequently projects cranially between the bases of the converging vesiculars, but this varies intraspecifically. The color of the dorsal prostate is an opaque or translucent white.

The medial ventral prostates enter the urethra by one to four basal ducts on each side under the anteroventral margin of *M. compressor urethrae* caudal and slightly lateral to the adjacent bladder stalk. The tubules are about twice the diameter of those of the dorsal and lateral ventral prostates, long, seldom-branching, only loosely bound by a common membrane and whitish in color. The medial ventral prostatic lobes are usually longer than those of the lateral ventral prostates.

The lateral ventral prostates are usually shorter and broader than the medial pair of glands, their tubules are narrower, more abundantly branched, and enter the urethra lateral and dorsal to those of the medial pair by two to eight, but usually three to six, basal ducts. Lateral ventral prostatic tubules are often rendered brittle and reddish in color by their contents, but this varies intraspecifically with breeding condition and with the nature of the preservative solution; when unpigmented, the tubules of this gland may resemble those of the dorsal prostate.

The anterior prostates are paired, elongate masses of branching tubules, each of which is closely applied to the lesser curvature of a corresponding vesicular. The distal portion of each gland is clasped by the subterminal flexure of its vesicular; vesiculars and anterior prostates are enveloped as a unit by a common membrane. Two (rarely one or three) basal ducts enter the urethra from each side adjacent to those of the vesiculars and to the openings of the deferent ducts. The tubules of the anterior prostate are larger in basal diameter than are those of any other gland of the prostate series. Anterior prostates are unpigmented.

The vesiculars are usually the largest glands in the male tract, and are the most conspicuous upon opening the body cavity. They resemble stout, J-shaped sacs that diverge as they course cranially from the prostatic urethra into which they drain by a single duct each. The distalmost 1/3 or so of each gland is abruptly reflexed ventrally and caudally to form the subterminal flextures that clasp the anterior prostates. The thick tunica of connective tissue is variously sculpted to lend the gland its species-typical form. As the vesiculars are among the most sensitive of the accessory glands to fluctuating levels of blood androgens, however, the degree and extent of such sculpturing exhibits considerable ontogenetic variation. Thus, the vesiculars of subadults or sexually inactive individuals are sometimes entirely smooth and unadorned with the lobes or papillate processes that may characterize the glands of conspecific adults in full breeding condition. Vesiculars are usually reddish or pinkish.

The ampullary glands are compact bunches of short, branched, pinkish tubules that empty separately into the ampulla of each deferent duct. Each clump of tubules is tightly bound by a common membrane and superficially resembles a finely-lobed but solid mass. Ampullary tissue is usually distributed unequally around the bases of the deferent ducts, and is often concentrated medially and cranially; the extent to which ampullary tubules completely encircle the ducts varies intraspecifically.

Below are described those aspects of accessory gland morphology in which South American cricetine species and genera depart from the generalized condition detailed above. For convenience and economy of description, genera are clustered into groups whose names and compositions generally follow Hershkovitz (1944, 1955, 1962, 1966b). *Chilomys* and *Irenomys*, genera not assigned to groups by Hershkovitz, are here provisionally regarded as an oryzomyine and as a phyllotine, respectively. The presence/absence of different glands among South American cricetines is summarized in Table 2.

Akodonts
(Figure 3)

Species examined: *Akodon (Akodon) arenicola* (2), *A. (A.) azarae* (1), *A. (A.) cursor* (6), *A. (A.) obscurus* (6), *A. (A.) varius* (4), *A. (Chroeomys) jelskii* (4), A. (*Microxus*) *bogotensis* (1), *A.* (*Thaptomys*) *nigrita* (1), *Notiomys valdivianus* (4).

In species of the subgenera *Akodon, Microxus,* and *Thaptomys,* a single

TABLE 2
MALE ACCESSORY GLAND COMPLEMENTS OF SOUTH AMERICAN CRICETINE SPECIES DESCRIBED IN THIS REPORT. GLANDULAR ABBREVIATIONS ARE THE SAME AS FOR FIGURE 1 AND 2. OTHER ABBREVIATIONS: X = GLAND PRESENT; XX = TWO GLANDS PRESENT; O = GLAND ABSENT; X_s = GLAND MUCH SMALLER THAN TYPICAL CONDITION; X_l = GLAND MUCH LARGER THAN TYPICAL CONDITION; (X) = GLAND MUCH MODIFIED FROM TYPICAL CONDITION; ? = REFER TO TEXT FOR EXPLANATION OR DESCRIPTION.

	PP	BU	DP	VP	AP	V	A
Akodonts							
Akodon arenicola	X	X	X	X_sX	X	X	X
A. azarae	X	X	X	X_sX	X	X	X
A. cursor	X	X	X	X_sX	X	X	X
A. obscurus	X	X	X	X_sX	X	X	X
A. varius	X	X	X	X_sX	X	X	X
A. jelskii	XX	X	X	XX	X	X	X
A. bogotensis	X	X	X	X	X	X	X
A. nigrita	X	X	X	X	X	X	X
Notiomys valdivianus	X	X_l	X	XX	X	X	X
Ichthyomyines							
Anotomys leander	X	X	X	XX	X	X	X
Daptomys venezuelae	X	X	X	XX	X	X	X
Neusticomys monticolus	X	X	X	XX	X	X	X
Rheomys hartmanni	X	X	X	XX	X	X	X
R. thomasi	X	X	X	XX	X	X	X
R. underwoodi	X	X	X	XX	X	X	X

(continued)

TABLE 2 (continued)

MALE ACCESSORY GLAND COMPLEMENTS OF SOUTH AMERICAN CRICETINE SPECIES DESCRIBED IN THIS REPORT. GLANDULAR ABBREVIATIONS ARE THE SAME AS FOR FIGURE 1 AND 2. OTHER ABBREVIATIONS: X = GLAND PRESENT; XX = TWO GLANDS PRESENT; O = GLAND ABSENT; X_s = GLAND MUCH SMALLER THAN TYPICAL CONDITION; X_l = GLAND MUCH LARGER THAN TYPICAL CONDITION; (X) = GLAND MUCH MODIFIED FROM TYPICAL CONDITION; ? = REFER TO TEXT FOR EXPLANATION OR DESCRIPTION.

Oryzomyines							
Chilomys instans	X	X	X	XX	X	X	X
Neacomys spinosus	X	X	X	XX	X	X	X
Nectomys squamipes	X	X	X	XX	X	X	X
Oryzomys caliginosus	X	X	X	XX	X	X	X
O. altissimus	X	X	X	XX	X	X	X
O. concolor	X	X	X	XX	X	X	X
O. fulvescens	O	X	X	XX	X	X	X
O. albigularis	O	X	X	XX	X	X	X
O. alfaroi	X	X	X	XX	X	X	X
O. capito	X	X	X	XX	X	X	X
O. melanotis	X	X	X	XX	X	X	X
O. palustris	X	X	X	XX	X	X	X
O. ratticeps	X	X	X	XX	X	X	X
Oxymycterines							
Abrothrix longipilis	XX	X	X	XX	X	X	X_l
Oxymycterus delator	XX	X	X	XX	X	X	X
O. rutilans	XX	X	X	XX	X	X	X
Phyllotines							
Andalgalomys pearsoni	XX	X	X	XX	X	X	X
Calomys callosus	X	X	X	XX	X	X	X
C. laucha	X	X	X	XX	X	X	X
Eligmodontia typus	XX	X	X	XX	X	X	X
Graomys griseoflavus	XX	X	X	XX	X	X	X
Irenomys tarsalis	?	X	X	XX	X	X	X
Phyllotis micropus	?	X	X	XX	X	X	X
P. darwini	XX	X	X	XX	X	X	X
P. osilae	XX	X	X	XX	X	X	X
Zygodontomys brevicauda	X	X	X	XX	X	X	X
Z. lasiurus	X	X	X	X_sX	X	X	X
Scapteromyines							
Scapteromys tumidus	X	X	X	XX	X	X	X
Sigmodonts							
Holochilus brasiliensis	X	X	X	XX	X	X	X
Neotomys ebriosus	XX	X	X	XX	X	X	X
Reithrodon physodes	XX	X	X	XX	X	X	X
Sigmodon hispidus	XX	X	X	XX	X	X	X
S. alstoni	XX	X	X	XX	X	X	X
Thomasomyines							
Nyctomys sumichrasti	XX	X	(X)	?	O	O	(X)
Thomasomys aureus	?	X	X	XX	X	X	X
T. baeops	X	X	X	XX	X	X	X
T. laniger	O	X	X	XX	X	X	X
T. rhoadsi	O	X	X	XX	X	X	X

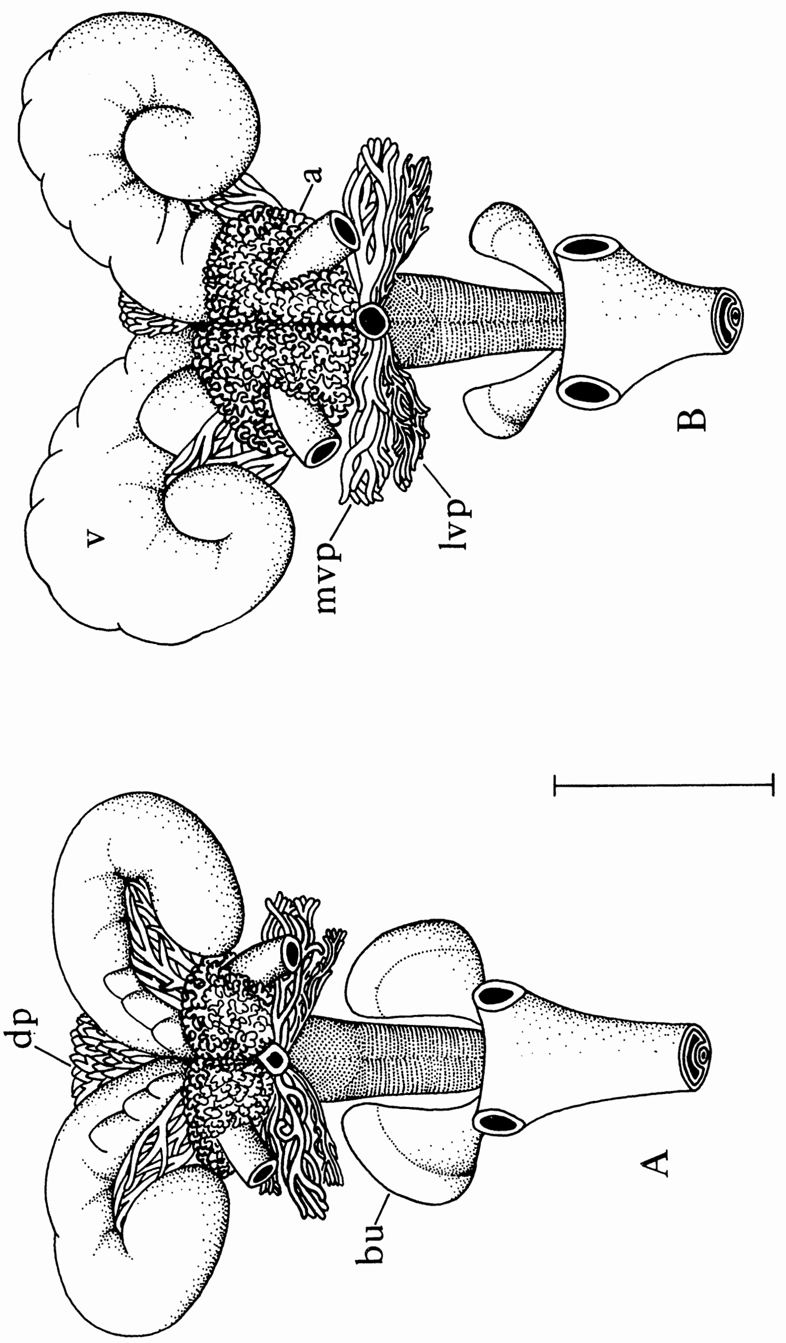

Fig. 3. Ventral view of the male reproductive tracts of two South American cricetines (bladders, testes and distal tracts have been removed). A, *Notiomys valdivianus* (MSU 6749); B, *Abrothrix longipilis* (MSU 7155). Abbreviations are the same as for Figs. 1 and 2. Scale = 10mm.

pair of preputials is present; these glands are large and usually extend cranially well beyond the ventral flexure of the penis. Two pairs of preputial glands are present in *A.* (*Chroeomys*) *jelskii* and in *Notiomys valdivianus*: a large pair of glands lying lateral to the glans penis, and a much smaller pair near the midventral margin of the prepuce. Except for the greater size of the lateral glands, the two pairs are very similar in gross morphology. In *A. jelskii* the lateral preputial glands extend beyond the ventral flexure of the penis as described above for *Akodon* (*Akodon*) species, but in *Notiomys* the lateral preputials are small and slender and do not exceed the prepuce in length. Bulbo-urethral, dorsal and anterior prostate, and ampullary glands are of conventional aspect in all species except *N. valdivianus.* In *Notiomys* all of these glands are unusually large and well-developed; the bulbo-urethrals of this species are particularly massive and nearly equal the vesiculars in size. In all five members of the subgenus *Akodon* that we dissected, the medial ventral prostates are between one-half and one-third the size of the lateral ventral prostates, in sharp contrast to the larger size of the medial glands in *A. jelskii* and *N. valdivianus* (Table 1). The diminutive stature of the medial ventral prostates of *Akodon* (*Akodon*) species is quite evident in both immature and fully adult tracts. Only a single pair of ventral prostates could be discerned in *A. bogotensis* and *A. nigrita;* these glands we tentatively homologize with the lateral ventral prostates of other species of *Akodon* because they occupy approximately the same anatomical position as do the lateral glands when both ventral prostatic pairs are present. Vesicular glands are lobed medially and along their greater curvatures; subterminal flexures are round and smooth except in *A. jelskii* where they are rough and irregular in appearance.

Arata (1964) reported two preputial pairs and only one pair of ventral prostates for a single specimen of an unidentified species of *Akodon.*

Ichthyomyines

Species examined: *Anotomys leander* (2), *Daptomys venezuelae* (1), *Neusticomys monticolus* (4), *Rheomys hartmanni* (3), *R. thomasi* (1), *R. underwoodi* (2).

Among all ichthyomyine species, we observed a single pair of small preputial glands that do not exceed the prepuce in length. In *Daptomys* and *Neusticomys* the medial pair of ventral prostates is substantially larger than the lateral pair, but in *Rheomys* species the two pairs are of nearly equal size. In *Anotomys leander* there is but a single discrete mass of ventral prostatic tubules, the basal ducts of which emerge from beneath *M. compressor urethrae* in a continuous series from ventral midline to the lateral limits of the dorsal prostate. This mass can be teased apart into subequal medial and lateral lobes, but as the tubules of each are identical in size and color we are not certain that both of the ventral prostates glands observed among other South American cricetines are really represented in *Anotomys.* The vesicular glands of *Daptomys, Neusticomys* and *Rheomys* are only weakly recurved, lack well-defined subterminal flexures, and often appear irregularly twisted; however, as none of the male tracts we examined for these genera appeared maximally developed by other criteria, it is possible that these peculiar features only reflect sexual quiescence of the animals at the time of preservation. The well-developed vesiculars of *Anotomys* are lobed on all surfaces including the subterminal flexures.

Oryzomyines
(Figure 1)

Species examined: *Chilomys instans* (1), *Neacomys spinosus* (2), *Nectomys squamipes* (5), *Oryzomys (Melanomys) caliginosus* (3), *O.* *(Microryzomys) altissimus* (1), *O.* *(Oecomys) concolor* (2), *O.* *(Oligoryzomys) fulvescens* (4), *O.* *(Oryzomys) albigularis* (4), *O.* *(O.) alfaroi* (6) *O.* *(O.) capito* (5), *O.* *(O.) melanotis* (4), *O.* *(O.) palustris* (7), *O.* *(O). ratticeps* (4).

A single pair of preputial glands is present in all species except *Oryzomys albigularis* and *O. fulvescens* which both lack preputials altogether. The preputials of *Neacomys spinosus* and *Chilomys instans* do not exceed the prepuce in length, but in other oryzomyines these glands extend to, or slightly beyond, the ventral flexure of the penis. Medial ventral prostates are conspicuously longer than the lateral ventral prostates except in *O. altissimus, O. albigularis* and *Nectomys squamipes,* in which the two pairs are of nearly equal size. Both ventral prostatic pairs are unusually small in *C. instans* and *O. altissimus.* The ampullary glands of *O. albigularis* and *O. capito* form pronounced tufts of tubules that thrust cranially from the bases of the deferent ducts. In *C. instans,* vesicular glands appear entirely smooth, but among all other oryzomyines these glands are scalloped along their greater curvatures and lobed medially; the vesiculars of *O. melanotis* and *O. alfaroi* are strongly compressed laterally. The subterminal flexures of the vesiculars are irregularly lobed and notched in *O. albigularis, O. alfaroi, O. capito* and *O. palustris* and are unusually small and finger-shaped in *O. melanotis;* in other species of oryzomyines this part of the vesicular is rounded and smooth.

Arata (1964) described the male tract of *Nectomys alfari,* for which he reported the presence of a second pair of dorsal prostate glands situated lateral and ventral to the mass of tubules which he believed to represent the conventional dorsal prostate of other murids. We were not able to discover such a second dorsal prostate in any of the South American cricetines we examined. Dorsal prostatic tissue, however, normally encroaches somewhat upon the lateral surface of the tract, and hypertrophy of this portion of the gland could result in a condition resembling that illustrated by Arata for *N. alfari.*

Oxymycterines
(Figure 3)

Species examined: *Abrothrix longipilis* (7), *Oxymycterus delator* (4), *O. rutilans* (6).

Two pairs of preputial glands are present; the large lateral glands extend well beyond the ventral flexure of the penis while the more medial and ventral glands are considerably smaller and do not exceed the prepuce in length. The dorsal prostates of *Abrothrix longipilis* are unusually large, but are partly covered by extensive lateral ventral prostatic tissue. In *Oxymycterus delator* and *O. rutilans,* the medial glands are the larger of the two ventral prostatic pairs, but the two pairs are subequal in *A. longipilis.* The ampullary glands of *Abrothrix* are approximately twice their usual

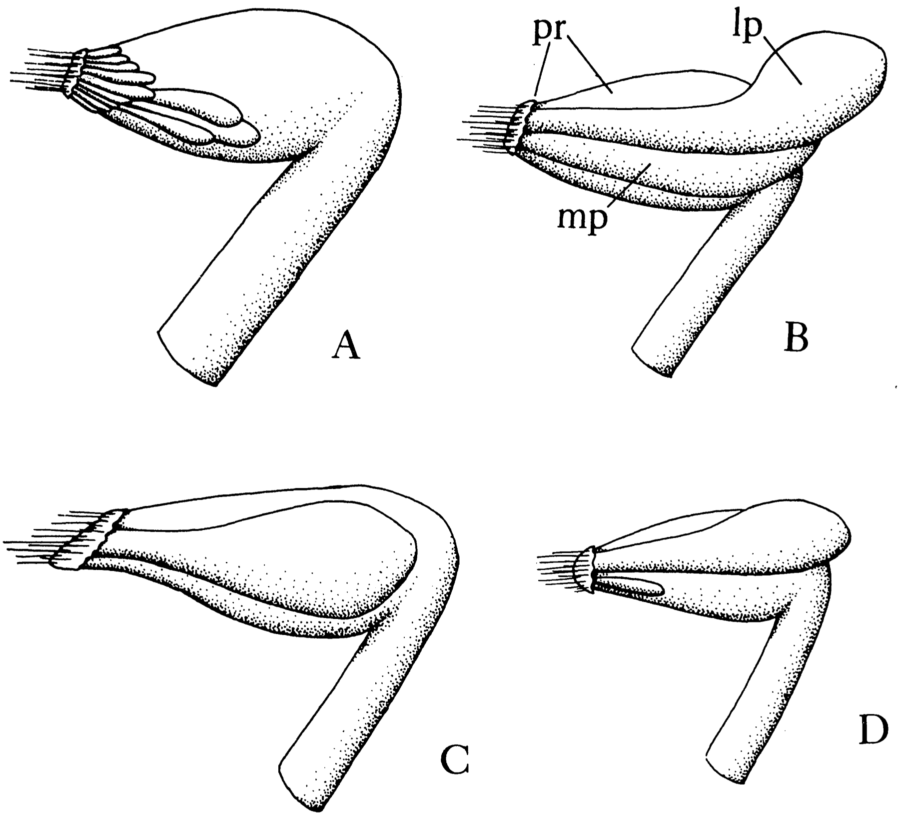

Fig. 4. Left lateral view of the distal tracts of four South American cricetine species (the hairy, outer layer of the prepuce has been removed from each). A, *Thomasomys aureus* (UMMZ 127114); B, *Sigmodon alstoni* (USNM 496018); C, *Scapteromys tumidus* (UMMZ 125954); D, *Andalgalomys pearsoni* (UMMZ 130037). Abbreviations: lp, lateral preputial gland; mp, medial preputial gland; other abbreviations are the same as for Fig. 1. Scale = 10mm.

size in relation to the male tract as a whole; the tubules are clustered thickly all around the bases of the deferent ducts, but tend to be concentrated cranially. Vesiculars in all three species are lobed medially and along their greater curvatures, but in some specimens of *A. longipilis* papilla-like processes rather than rounded lobes embellish the medial surfaces. The subterminal flexures of the vesiculars of *A. longipilis* and *O. delator* are rounded and smooth, but they are irregularly lobed in some examples of *O. rutilans.*

Phyllotines
(Figure 4)

Species examined: *Andalgalomys pearsoni* (1), *Calomys callosus* (4), *C. laucha* (1), *Eligmodontia typus* (1), *Graomys griseoflavus* (4), *Irenomys tarsalis (1), Phyllotis (Loxodontomys) micropus (1), P. (Phyllotis) darwini* (4), *P. (P.) osilae* (2), *Zygodontomys brevicauda* (9), *Z. lasiurus* (7).

In *Zygodontomys* and *Calomys,* preputials occur as a single pair and extend cranially beyond the ventral flexure of the penis. In all of the remaining species, except *Phyllotis micropus* and *Irenomys tarsalis* (for which we lack adequate material), there are two pairs of preputials. These consist of a larger, lateral pair of glands that extend to *(P. darwini, P. osilae)* or beyond *(Andalgalomys pearsoni, Eligmodontia typus, Graomys griseoflavus)* the ventral flexure of the penis, and a pair of smaller, ventral glands. In some specimens of *G. griseoflavus,* ventral preputials nearly equal the lateral preputials in length, but the ventral pair is substantially smaller than the lateral pair in the remaining two-preputialled phyllotine species. The medial ventral prostates are one-and-a-half to three times as long as the lateral ventral prostates except in *Z. lasiurus* where the medial pair is consistently much smaller than the lateral pair (Table 1). The lateral ventral prostates of *I. tarsalis* and of the *Phyllotis* species appear unusually small and are closely pressed against the lateral surfaces of the tract. Vesiculars are lobed medially and along their greater curvatures, but in *A. pearsoni* these glands are lobed laterally as well. Subterminal flexures appear lumpy and irregularly-formed in *A. pearsoni* and *C. callosus;* in the remaining species these portions of the vesiculars are rounded and smooth.

Scapteromyines
(Figure 4)

Species examined: *Scapteromys tumidus* (3).

A single pair of well-developed preputials extend to the ventral flexure of the penis. The lateral ventral prostates are less than half the length of the medial pair. The vesiculars, though well-developed, lack prominent sculpturing; they are only weakly lobed medially and dorsally, and the large subterminal flexures are smooth.

Hershkovitz (1966b: 133) noted the absence of preputials in two "half grown" specimens of *Scapteromys tumidus*. Since preputials are frequently inconspicuous and deeply embedded in connective tissue in inmature or sexually inactive animals, however, it is possible that these glands may have been overlooked in Hershkovitz's young examples; we have not observed preputials to vary with respect to their presence within species of South American cricetines.

Sigmodonts
(Figure 4)

Species examined: *Holochilus brasiliensis* (5), *Neotomys ebriosus* (1), *Reithrodon physodes* (5), *Sigmodon hispidus* (8), *S. alstoni* (3).

In *Holochilus brasiliensis* there is a single pair of preputial glands that reach cranially slightly beyond the ventral flexure of the penis. All of the remaining sigmodont species possess two pairs of preputials. The midventral pair of preputials in *Neotomys* and *Reithrodon* are small, inconspicuous, and lie very close to the free margin of the prepuce; the lateral preputials are large and extend to the ventral flexure of the penis. In *Sigmodon* the preputial pairs are more nearly equal in size; while both lateral and ventral glands extend fully to the ventral flexure, however, the lateral pair reaches considerably beyond to partly overlap the superficial musculature of the abdomen. The medial ventral prostates are longer than the lateral ventral prostates in *Sigmodon hispidus, Reithrodon* and *Holochilus,* but the two glands are of approximately equal length in *S. alstoni*. Vesiculars are lobed medially and along their greater curvatures, and the subterminal flexures are smooth. Papilla-like processes are produced on the medial surfaces of the vesiculars in some specimens of *Reithrodon.*

Thomasomyines
(Figure 4)

Specimens examined: *Thomasomys aureus* (2), *T. baeops* (2), *T. laniger* (2), *T. rhoadsi* (1).

No preputial glands were found in our specimens of *Thomasomys laniger* and *T. rhoadsi,* but a single pair of well-developed preputials is present in *T. baeops*. The single distal tract of *T. aureus* which we examined is distinctive; twelve elongated sebaceous glands are present on the left side of the prepuce, six on the right. Each gland drains by a single duct that surrounds a single stiff hair. These glands vary considerably in size, from 2mm on the dorso-lateral surface of the prepuce to almost 12mm ventro-laterally,

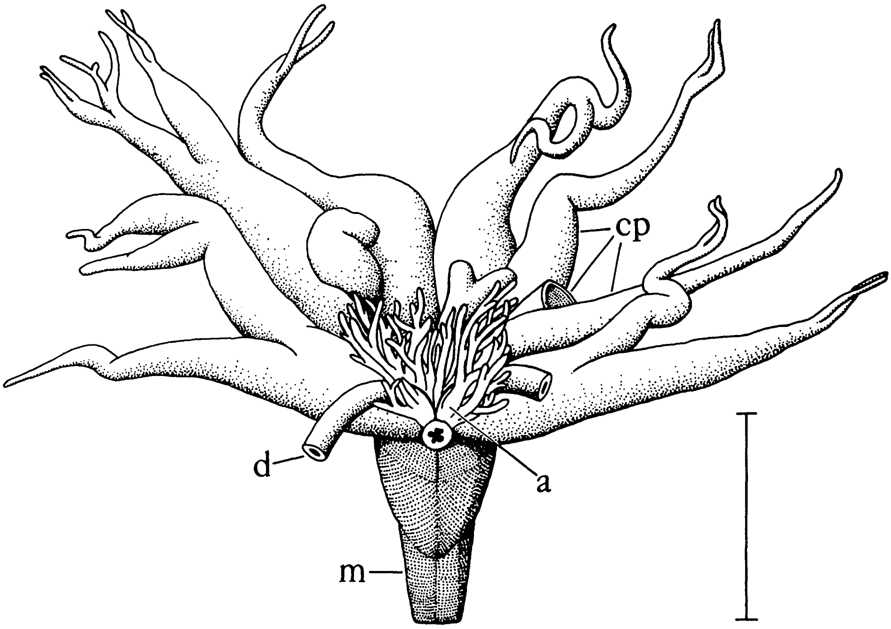

Fig. 5. Ventral view of the male reproductive tract of *Nyctomys sumichrasti* (UMMZ 113522); testes, bladder and distal tract have been removed. Abbreviations: cp, tubules of the 'cephalic prostate' gland (see text); other abbreviations as in Fig. 1. Scale = 10mm.

and lack the sharp definition of outline that characterizes the preputials of other South American cricetines; they are deeply embedded in the connective tissue of the prepuce and are whitish in color. The two pairs of ventral prostates are of nearly equal size in *T. aureus, T. baeops* and *T. rhoadsi,* but the medial pair is much the larger in *T. laniger*. Both ventral prostatic pairs are unusually small with respect to the male tract as a whole in *T. aureus* and *T. rhoadsi.* In all four species, the vesiculars are lobed medially and along the greater curvatures; the subterminal flexures are rounded and smooth.

Nyctomys
(Figure 5)

Species examined: *N. sumichrasti* (5).

Two pairs of preputials are present; the lateral glands are large and extend well beyond the ventral flexure of the penis, but the more medial and ventral glands are smaller and do not exceed the prepuce in length. Conventional dorsal and anterior prostates and vesiculars are absent. Four of our specimens lack ventral prostates entirely, but in one example from Panama (USNM 460165) there is a single, small pair of these glands. Ampullaries occur as loose clusters of long, seldom-branching tubules that arise from the caudal, medial and cephalic surfaces of the deferent ducts. The largest and most conspicuous gland in our male tracts of *Nyctomys,* however, consists of six to twelve large prostatic tubules that emerge from the urethra dorsal to the deferent ducts and diverge like the arms of an octopus as they course cranially from thickened bases to long, branched-filiform tips. Arata (1964) identified this gland as a modified anterior prostate, but we believe it as likely to be of dorsal prostatic origin for two reasons: (1) anterior prostates and vesiculars are known to be closely interdependent in function (Walker, 1910; Greenstein and Hart, 1964), and it seems to us unlikely that one should be so elaborated in the absence of the other; (2) the number of basal ducts (as many as six on a side) more closely resembles the number of ducts normally observed for the dorsal prostates of other species (five to nine) than for the anterior prostates which usually have only two ducts per side (rarely one or three). Immuno-chemical methods (Barnes, 1972) will probably be required to convincingly establish the homology of *Nyctomys'* cephalic prostate, but whatever its identity, the morphology of this gland together with the absence of vesiculars sets this genus well apart from all of the other South American cricetines we have examined.

II: Other Murid Groups

Microtines

Descriptions of the male tracts of 19 microtine species of six genera are provided by Rowlands (1936), Raynaud (1951), Delost (1955), Arata (1964), Indyk (1968) and Aksenova (1973). All microtine species described by these authors possess a single pair each of preputials, bulbo-urethrals, dorsal and anterior prostates, vesiculars and ampullaries. Two pairs of ventral prostates occur in all forms except *Neofiber alleni* for which Arata (1964) reports only one pair. The male accessory glands of microtines closely resemble their presumed homologs among South American cricetines. The vesicular glands of *Synaptomys, Ondatra* and *Neofiber,* as described and figured by Arata (1964), are tubular in appearance, not tightly recurved, and lack well-defined subterminal flexures, but the vesicular morphology of the remaining microtine species appears indistinguishable from the typical South American cricetine condition.

Gerbillines

Species examined: *Meriones shawi* (2), *M. tristrami* (3), *M. unguiculatus* (2), *Pachyuromys duprasi* (4), *Tatera brantsi* (1), *T. indica* (3).

No preputial glands were found in our specimens of *Meriones, Pachyuromys,* and *Tatera indica,* but a single pair of small preputials was discovered in *T. brantsi.* Bulbo-urethrals, dorsal and anterior prostates and ampullaries closely resemble their homologs in South American cricetines. In *P. duprasi* and both species of *Tatera*, there is a single pair of ventral prostate glands. In the three species of *Meriones*, however, the ventral prostatic mass is distinctly bilobed, and both of the ventral prostate pairs characteristic of South American cricetines may therefore be represented in this genus. The ventral prostates of *Meriones, Pachyuromys* and *Tatera brantsi* are unusually small by South American standards. Vesiculars of all species are lobed medially and along their acutely-edged greater curvatures. Gross, finger-like processes are sometimes produced on the medial vesicular surfaces of *Tatera* species. The subterminal flexures of the vesiculars are rounded and smooth in *Meriones* and *Pachyuromys,* but are rough and irregularly-lobed in species of *Tatera.*

Allanson (1958) describes the accessory glands of *Tatera afra* and *T. brantsi* and illustrates the male reproductive tract of the former species. Brown (1972) reports the absence of preputial glands in *Gerbillus.*

Old World Cricetines

Species examined: *Cricetulus barabensis* (3).

A single pair each of preputials, bulbo-urethrals, dorsal, ventral and anterior prostates, vesiculars and ampullaries are present. The preputials are small and narrow, and do not extend to the ventral flexure of the penis. Large masses of prostatic tubules that emerge from beneath the anterolateral margins of *M. compressor urethrae* are difficult to separate from the dorsal prostate, and may represent ventrolateral expansions of that gland. Bulbo-urethrals, dorsal, ventral and anterior prostates, and ampullaries closely resemble the usual South American cricetine condition. The vesiculars are lobed medially and along their acutely-edged greater curvatures; the subterminal flexures are rounded and smooth.

Arata (1964) and Ortiz (1947) describe the accessory glands of *Mesocricetus auratus.* A single pair each of conventional bulbo-urethrals, dorsal, ventral and anterior prostates, and ampullaries are present. Preputials are absent, and the vesicular glands are finely lobed along their greater curvatures. Illustrations of the male reproductive tract of *M. auratus* are provided by Arata (1964) and by Price and Williams-Ashman (1961). Brown (1972) and Grosz (1905) report the presence of preputial glands in hamsters of the genus *Cricetus.*

Mystromyines

Species examined: *Mystromys albicaudatus* (2).

Four to seven separate preputial glands occur on each side of the prepuce; in both specimens we examined, the number of glands on right and left sides are unequal. These glands lack the sharp definition of outline characteristic of South American cricetine preputials, but are instead compressed irregularly into a variety of oblong shapes. Large and small glands alternate in a haphazard array along the free margin of the prepuce. The largest preputials, one or two per side, extend cranially to the subterminal flexure of the penis. Only one pair of large ventral prostates can be confidently distinguished, but the ease with which the mass of tubules on either side can be divided into medial and lateral lobes suggests that this gland may be compound. Anterior prostates arise from two to three large basal ducts on each side and form elongate clusters of white tubules applied loosely along the lesser curvatures of the vesiculars; these tubules taper gradually from the urethra and branch distally into many long, filiform tips. The vesiculars are laterally compressed, and a series of stout papillae are produced along the greater curvatures. The subterminal flexures are rounded and smooth. Ampullaries, bulbo-urethrals and dorsal prostates resemble the typical South American cricetine condition.

Murines

Species examined: *Acomys dimidiatus* (2), *Apodemus flavicollis* (3), *Beamys hindei* (1).

A single pair of small preputial glands is present in *Beamys hindei* and *Apodemus flavicollis;* these glands are narrow, deeply embedded in the connective tissue of the prepuce, and do not extend to the ventral flexure of the penis. *Acomys dimidiatus* lacks preputials entirely. Two pairs of small ventral prostates are present in *A. dimidiatus,* but only a single pair could be distinguished in *A. flavicollis* and *B. hindei.* In the latter two species, however, masses of prostatic tubules extend over the lateral surfaces of the urethra and may represent a coalescence of the lateral ventral prostate with the dorsal prostate; these clumps of tubules correspond to the 'lateral prostate' of Kowalska-Dyrcz and Pawlowska-Indyk (1969). A single pair each of bulbo-urethrals, anterior prostates and vesicular glands, each closely resembling its South American cricetine counterpart, are present in all three species.

The male accessory glands of *Mus musculus* and *Rattus norvegicus* closely resemble those of South American cricetines (Arata, 1964), except that *R. norvegicus,* like *A. flavicollis* and *B. hindei,* also exhibits lateral prostates of uncertain homology.

Neotomine-Peromyscines

Members of this murid assemblage exhibit a wide array of glandular morphologies (Howell, 1926; Taylor, 1963; Arata, 1964; Lawlor, 1969; Linzey and Layne, 1969; Carleton *et al,* 1975). *Peromyscus (Peromyscus* and *Haplomylomys), Scotinomys, Baiomys* and *Reithrodontomys* display acces-

TABLE 3
MALE ACCESSORY GLAND COMPLEMENTS OF MURID SPECIES DESCRIBED IN THIS REPORT AND/OR BY PREVIOUS AUTHORS. ALL ABBREVIATIONS ARE THE SAME AS FOR FIGURES 1 AND 2 AND TABLE 2. SOURCES: (1) AKSENOVA, 1973; (2) ALLANSON, 1958; (3) ARATA, 1964; (4) CARLETON *ET AL.*, 1975; (5) DELOST, 1955; (6) INDYK, 1968; (7) KOWALSKA-DYRCZ AND PAWLOWSKA-INDYK, 1969; (8) LAWLOR, 1969; (9) LINZEY AND LAYNE, 1969; (10) RAYNAUD, 1951; (11) ROWLANDS, 1936; (12) TAYLOR, 1963; (13) THIS STUDY.

	PP	BU	DP	VP	AP	V	A	Source
Microtines								
Clethrionomys (2 sp)	X	X	X	XX	X	X	X	3, 6, 11
Microtus (12 sp)	X	X	X	XX	X	X	X	1, 3, 5, 6, 10
Neofiber alleni	X	X	X	X	X	X	X	3
Ondatra zibethicus	X	X	X	XX	X	X	X	3
Pitymys (2 sp)	X	X	X	XX	X	X	X	3, 6
Synaptomys cooperi	X	X	X	XX	X	X	X	3
Gerbillines								
Meriones (3 sp)	O	X	X	X_SX_S	X	X	X	13
Pachyuromys duprasi	O	X	X	X_S	X	X	X	13
Tatera afra	X	X	X	X	X	X	X	2
T. brantsi	X	X	X	X_S	X	X	X	2, 13
T. indica	O	X	X	X	X	X	X	13
Old World Cricetines								
Cricetulus barabensis	X	X	X	X	X	X	X	13
Mesocricetus auratus	O	X	X	X	X	X	X	3
Mystromyines								
Mystromys albicaudatus	?	X	X	X	X	X	X	13
Murines								
Acomys dimidiatus	O	X	X	XX	X	X	X	13
Apodemus agrarius	?	X	X	X	X	X	X	7
A. flavicollis	X	X	X	X	X	X	X	13
Beamys hindei	X	X	X	X	X	X	X	13
Mus musculus	X	X	X	XX	X	X	X	3
Rattus norvegicus	X	X	X	XX	X	X	X	3
Neotomine-Peromyscines								
Baiomys taylori	X	X	X	X	X	X	X_S	3, 4
Neotoma floridana	O	X	O	X	(X)	O	(X)	3
Ochrotomys nuttalli	X	X	X	XX	X_S	X_S	O	3
Onychomys (2 sp)	X	X	X	X	O	O	O	3, 12
Ototylomys phyllotis	X	X	O	X	O	(X)	X	8
Peromyscus (Peromyscus)	O	X	X	XX	X	X	X	9
Peromyscus (Haplomylomys)	X	X	X	XX	X	X	X	9
Peromyscus (Habromys)	O	X	X	X_l	X_S	X_S	X	9
Peromyscus (Osgoodomys)	X	X	X_S	X	O	O	X_l	9
Peromyscus (Podomys)	O	X	X_S	X_SX_S	X_S	X_S	X_l	9
Peromyscus (Isthmomys)	O	X	X	X	(X)	(X)	X	9
Peromyscus (Megadontomys)	O	X_l	X	XX	X	X	X_l	9
Reithrodontomys humulis	O	X	X	XX	X	X	X	3
Scotinomys (2 sp)	X	X	X	X	X	X	X	4

sory gland complements that resemble those of South American cricetines save for the absence of preputials in *Peromyscus (Peromyscus)* and *Reithrodontomys*, and the presence of only a single pair of ventral prostates in *Baiomys* and *Scotinomys*. Other genera (and some subgenera of *Peromyscus)*, however, depart conspicuously from the typical South American cricetine morphology (Table 3). Differences most frequently involve relative size or presence/absence of anterior prostates and vesiculars, but pronounced variation is sometimes evident in bulbo-urethrals and ampullaries as well. The glandular variation summarized in Table 3 for the 14 genera and subgenera of neotomine-peromyscines for which published data are available far exceeds that which we have observed for the 35 genera and subgenera of South American cricetines described in this report (Table 2); indeed, the variability of neotomine-peromyscine accessory gland complements is greater than that currently reported for all other members of the family Muridae.

SYSTEMATIC IMPLICATIONS OF ACCESSORY GLAND MORPHOLOGY

One pair each of bulbo-urethrals, dorsal and anterior prostates and vesiculars, and at least one pair of ventral prostates occur together in most South American cricetines, many neotomine-peromyscines, and all microtines, gerbillines, murines, Old World cricetines and mystromyines whose male reproductive anatomy is known. That these glands are so widespread within the family Muridae and occur also in zapodid and dipodid rodents (Tullberg, 1899; Grosz, 1905; Wrigley, 1972; Kowalska-Dyrcz, 1973) strongly suggests their ancient presence in the male tract of the ancestral murid. Ampullaries have not been reported for dipodoid rodents, but small glandular swellings on the bases of the deferent ducts of heteromyids (Midgely, 1938; M. S. Hafner, pers. comm.; R. S. Voss, unpublished data) might be homologous with murid ampullary glands. The resemblance between murid and heteromyid ampullary adornments is not particularly close, however, and we prefer to support our hypothesis that the presence of ampullaries is primitive for Muridae only by observing that this constitutes the simplest explanation for the occurrence of these glands in all murids whose male tracts have been described with the exception of the monotypic genus *Ochrotomys* and two species of *Onychomys* (Tables 2 and 3). Preputials occur in every murid group thus far examined, usually as a single pair. The presence of preputials could thus reasonably be regarded as primitive, but their absence is almost as widespread, and we are not, therefore, entirely confident of polarity for this gland.

That the possession of one pair each of bulbo-urethrals, dorsal and anterior prostates, vesiculars and ampullaries is primitive for South American cricetines seems likely because these glands are so widespread among other murid groups and because all but two known South American cricetines have at least this complement of glands. Two pairs of ventral prostates occur in most South American cricetines (as well as in all but one known microtine, some neotomine-peromyscines, some murines and perhaps some gerbils) and also appear probably to be primitive for this group. We hypothesize that the presence of only one pair of ventral prostates in a few genera is the result of loss of one pair (*Akodon,* subgenera *Microxus* and *Thaptomys)* or, perhaps, fusion of both pairs *(Anotomys); Nesoryzomys narboroughi* is the only South American cricetine known to lack ventral prostates altogether (Patton and Hafner, in press). A single pair of preputials is the commonest state for this gland among South American cricetines, and is represented in every generic group which we have sampled (Table 2). By contrast, the presence of two preputial pairs is a much less common condition that appears largely restricted to tetralophodont (*sensu* Hershkovitz, 1962) groups: phyllotines, akodonts, sigmodonts and oxymycterines. Because of its more widespread distribution, we cautiously suggest that a single pair of preputials is primitive for South American cricetines.

If the foregoing arguments about glandular polarities are accepted and the distribution of glands among New World cricetines is considered (Tables 2 and 3), then the conclusion must be drawn that accessory gland morphology provides no support for, although it similarly does not deny, the dichotomy among hesperomyine rodents suggested by anatomy of the glans penis (Hooper, 1959, 1960; Hershkovitz, 1962). By this we mean only to say that we are not aware of any condition of the male accessory glands which would enable one to identify *Peromyscus interparietalis,* say, as a peromyscine or *Akodon cursor* as a South American cricetine. Arata (1964: 28) implied that his glandular data supported the simple/complex penis dichotomy, but an inspection of his Table 2 reveals no glandular attribute peculiar to either group and the most that may be concluded is that greater variation in glands exists among simple-penised murids than among murids with a complex penis.

Nyctomys sumichrasti differs markedly in accessory gland anatomy from all of the other South American cricetines we have examined. Hershkovitz (1944, 1962) placed this arboreal rat in his 'thomasomyine' group on the basis of craniodental character states shared with *Thomasomys, Rhipidomys* and a few other neotropical genera. Hooper and Musser (1964a), however, found the baculum of *Nyctomys* to lack lateral digits, removed the genus from the thomasomyine group, and observed that "in some of its characters it appears to be annectant between the neotomine-peromyscines and the clusters of South American forms" (Hooper and Musser, 1964a: 41). Arata's (1964) dissection of a single male tract of *Nyctomys* also led him to regard this genus as an intermediate form. Hershkovitz (1966b) concurred with this view, but also cautioned that Arata's survey of murid accessory glands was limited in taxonomic scope. Our considerably broader sampling of South American cricetine genera confirms Arata's (1964) perception of *Nyctomys* as a phenetic outlier, but phylogenetic interpretation of this datum is rendered difficult by our inability to diagnose either neotomine-peromyscines or South American cricetines on the basis of accessory gland morphology.

No certainly derived state of any character has yet been discovered to define South American cricetines as a group. Instead, these rodents seem usually to display phenotypic attributes believed by murid anatomists to be primitive (e.g., Cockerell *et al,* 1914; Hooper and Musser, 1964a; Carleton, 1973; Reig, 1977; this study). Nevertheless, their marked phallic uniformity and zoogeographic cohesiveness does suggest that these mice and rats may comprise a closely-interrelated assemblage. To this assemblage we believe *Nyctomys* may be only distantly related for the following reasons: (1) *Nyctomys* does not have a tri-partite baculum; (2) those character states shared between *Nyctomys* and thomasomyines (as complex cheek teeth, short-wide palates and weakly developed zygomatic plates) occur also among some peromyscines (Hershkovitz, 1944) and could easily be regarded as primitive; (3) derived aspects of *Nyctomys*' proximal tract are shared by no other South American cricetine that we have examined, but are duplicated among some simple-penised North American genera as both Arata (1964) and Hershkovitz (1966b) observed; (4) characters of the postcranial skeleton also argue that *Nyctomys*' affinities lie without the South American cricetines (Carleton, 1980). In light of these observations, it seems best to regard *Nyctomys* as Muridae *incerta sedis,* and our use of the term 'South American cricetines' hereafter explicitly excludes *Nyctomys* from consideration therein.

Another neotropical murid with an unusual accessory gland complement is the Galapagoan rat, *Nesoryzomys narboroughi.* As described by Patton and Hafner (in press) this species lacks ventral and anterior prostates and has very small vesicular glands; a single pair each of preputials, bulbo-urethrals, dorsal prostates and ampullaries are present. Patton and Hafner also observe that *Nesoryzomys* departs chromosomally, biochemically, and in characters of the skull and penis from other oryzomyines, but they believe it to have descended from a mainland species of *Oryzomys (Oryzomys)* that subsequently evolved many derived attributes in isolation. We have not ourselves examined material of this genus.

The remaining 34 genera and subgenera of South American cricetines described in this report exhibit a singular uniformity of accessory gland anatomy that provides little in the way of critical data for evaluating alternative phylogenetic arrangements. *Abrothrix longipilis* and *Notiomys valdivianus* depart in morphology of their ampullaries and bulbo-urethrals, respectively, from the mass of South American cricetines, but the glandular peculiarities of these mice are unique and therefore shed no light on their affinities. Neither bulbo-urethrals and ampullaries nor anterior and dorsal prostates exhibit appreciable variation among the remaining species of South American cricetines. Vesicular glands vary with respect to the amount and distribution of surface sculpturing, but this appears sufficiently variable within some species and among congeners to make us hesitant about applying the character at higher levels until sample sizes are augmented considerably. Certain morphological aspects of preputial and ventral prostate glands, by contrast, vary between species and genera but appear constant within species and so merit further discussion.

Thomasomys aureus exhibits a preputial array that is unique among the 52 South American cricetine species we examined. Previous anatomists have also remarked the aberrant nature of this rat in the morphology of its penis (Hooper and Musser, 1964a) and stomach (Carleton, 1973), but their material consisted of only a single specimen from Peru (FMNH 75588). Our characterization of the preputial morphology of *T. aureus* is, unfortunately, likewise based on a single example (UMMZ 127114), one of a small series collected by the senior author in eastern Ecuador. Stomachs and a single penis from these Ecuadorean specimens confirm some of the gastric and penile features reported by Carleton and by Hooper and Musser, but more material of this species, as well as broader sampling of its supposed congeners is necessary before taxonomic recommendations can be adequately supported.

The derived presence of two preputial pairs in *Eligmodontia* supports recent chromosomal data that led Pearson and Patton (1976) to place this genus in a monophyletic group that includes *Phyllotis* and *Graomys,* but not *Calomys* or *Zygodontomys (contra* Hershkovitz, 1962); our subjective appreciation of dental characters, however, leaves us skeptical of Pearson and Patton's hypothesis that *Eligmodontia* is descended from a *Phyllotis*-like ancester. *Andalgalomys pearsoni,* another phyllotine, would also seem, on the basis of its preputial complement, nearer *Eligmodontia, Graomys* and *Phyllotis* and less close to *Calomys* than Williams and Mares (1978) have argued. The presence of only one pair of preputials in *Holochilus* is consistent with penile data (Hooper and Musser, 1964a) which suggests that this genus may not be so closely allied to *Sigmodon* as Hershkovitz (1955) believed, but provides no direct support (by synapomorphy) for the former authors' proposal that *Holochilus* is an oryzomyine. Osvaldo Reig's recommendation (cited in Bianchi *et al,* 1971) that *Chroeomys* and *Abrothrix* be raised to full generic rank is at least consonant with our observation that specimens of these taxa have two preputial pairs while members of *Akodon (Akodon)* have only one pair. Other relationships suggested by preputial morphology appear highly improbable; for example, the affinity among *Oryzomys albigularis, O. fulvescens, Thomasomys laniger* and *T. rhoadsi* implied by the derived absence of preputials in these species. The distribution of preputial glands among murids is incompatible with many

TABLE 4

TWO-WAY CONTINGENCY TESTS (AFTER SNEATH AND SOKAL, 1973: 349) FOR COMPATIBILITY OF PREPUTIAL GLAND OCCURENCE WITH FOUR OTHER MORPHOLOGICAL CHARACTERS. MORPHOLOGICAL DATA DERIVED FROM THIS STUDY, ARATA (1964), COCKERELL *ET AL* (1914), HOOPER (1958, 1962), HOOPER AND MUSSER (1964a), KESNER (1977), KLINGENER (1968), LINZEY AND LAYNE (1969), RINKER (1954) AND VOSS (UNPUBLISHED).

a)

PREPUTIALS	LATERAL BACULAR DIGITS absent	LATERAL BACULAR DIGITS present
one pair	*Peromyscus eremicus*	*Zygodontomys brevicauda*
two pairs	*Nyctomys sumichrasti*	*Sigmodon hispidus*

b)

PREPUTIALS	STYLOHYAL CARTILAGE absent	STYLOHYAL CARTILAGE present
absent	*Mesocricetus auratus*	*Neotoma floridana*
present	*Oryzomys palustris*	*Synaptomys cooperi*

c)

PREPUTIALS	POSTERIOR PALATINE PITS present	POSTERIOR PALATINE PITS absent
present	*Oryzomys capito*	*Thomasomys baeops*
absent	*Oryzomys albigularis*	*Thomasomys laniger*

d)

PREPUTIALS	ORBICULAR APOPHYSIS OF MALLEUS present	ORBICULAR APOPHYSIS OF MALLEUS absent
absent	*Oryzomys fulvescens*	*Mesocricetus auratus*
present	*Sigmodon hispidus*	*Ondatra zibethicus*

other taxonomic characters (Table 4), and we feel that independent loss and/or evolution of preputial pairs must be hypothesized in order to explain such patterns. Nevertheless, preputials may be no worse in this regard than most characters used in rodent classification (Wood, 1974) and it therefore seems defensible to have cited instances in which data from these glands support or contradict hypotheses of kinship suggested by other workers.

Medial and lateral ventral prostate glands vary in relative size among South American cricetines. Figure 6 is a bivariate plot of lengths of the two ventral prostate pairs for specimens whose measurements are listed in Table 1. The diagonal line that runs from lower left to upper right maps ordered pairs of equal glandular measurements; above this line fall species in which medial ventral prostates exceed the lateral glands in length, below

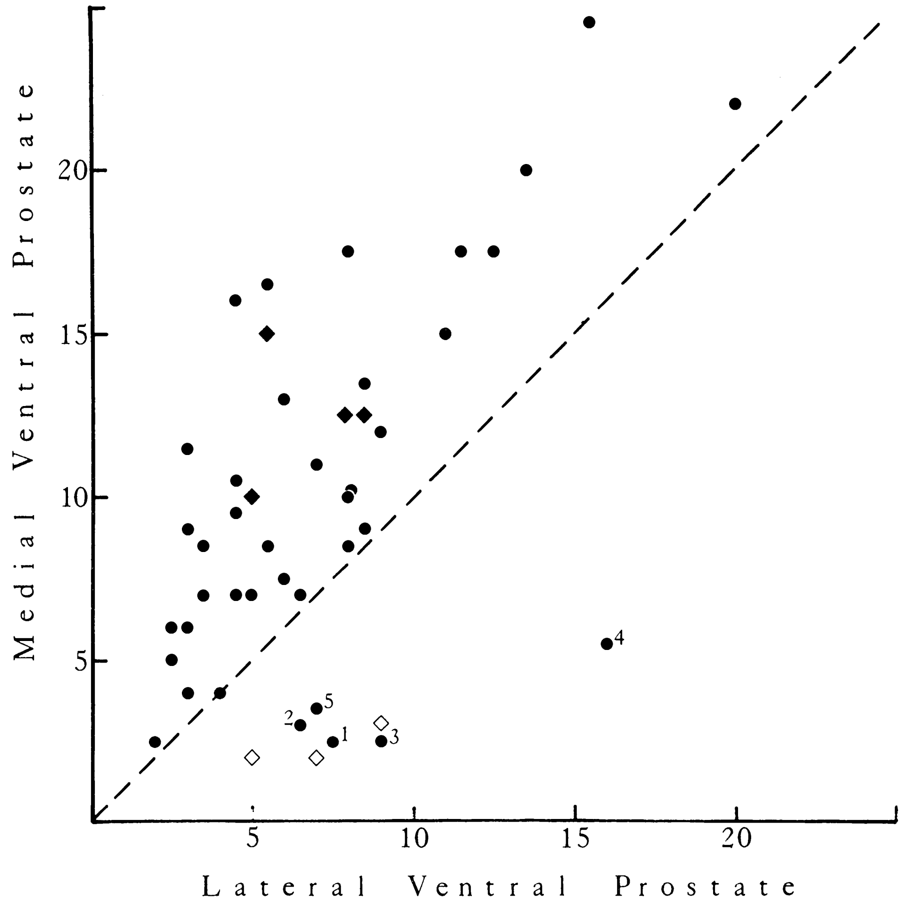

Fig. 6. Bivariate plot of lengths (mm) of medial and lateral ventral prostate glands for 41 South American cricetine species (see text for explanation). Open diamonds represent specimens of *Zygodontomys lasiurus*; closed diamonds represent specimens of *Z. brevicauda*. Numbered dots: (1) *Akodon arenicola;* (2) *A. azarae;* (3) *A. cursor;* (4) *A. obscurus;* (5) *A. varius.*

this line are species for which medial glands are the smaller. Of the 41 species whose glandular dimensions are available, only six are seen to have smaller medial than lateral ventral prostates; five of these are species of *Akodon (Akodon)* and the sixth is *Zygodontomys lasiurus* (represented by specimens from Brazilian, Bolivian, and Paraguayan populations). *Z. brevicauda* (represented by specimens from Costa Rica, Colombia, Venezuela

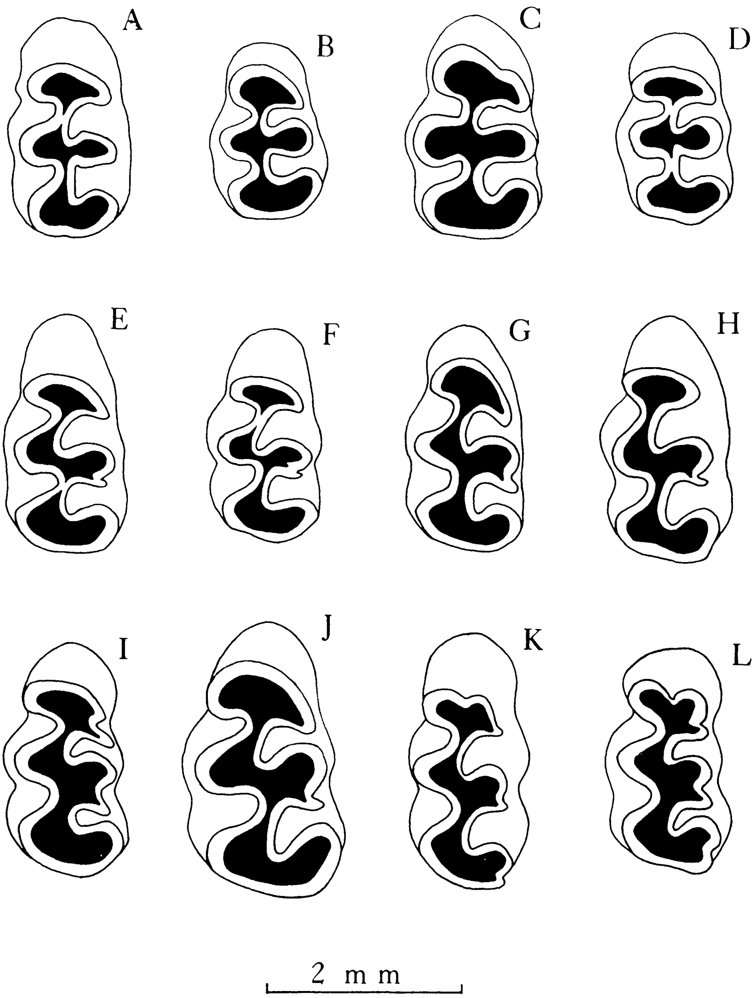

Fig. 7. Occlusal patterns of left upper first molars of *Zygodontomys brevicauda* (top row), *Z. lasiurus* (middle row) and several species of *Akodon* (bottom row). A, *Zygodontomys brevicauda tobagi* (AMNH 184779, topotype); B, *Z. b. griseus* (AMNH 34592, holotype); C, *Z. b. brevicauda* (AMNH 4708, holotype); D, *Z. b. ventriosus* (USNM 171098, holotype); E, *Z. lasiurus tapirapoanus* (AMNH 37518, holotype); F, *Z. lasiurus* subspecies indet. from Goias, Brasil (AMNH 134489); G, *Z. lasiurus* subspecies indet. from Beni, Bolivia (AMNH 210058); H, *Z l. lenguarum* (UMMZ 124263, near-topotype); I, *Akodon benefactus* (UMMZ 109223); J, *A. obscurus* (UMMZ 115507); K, *A. varius* (UMMZ 125500); L, *A. cursor* (UMMZ 125971).

and Trinidad), however, always exhibits larger medial than lateral ventral prostates, and in this respect resembles the majority of other South American cricetines. That mice referred by Hershkovitz (1962) to *Z. lasiurus* are really more similar to some species of *Akodon (Akodon)* than to *Z. brevicauda* is supported by other lines of evidence, and has been remarked by previous researchers. *Z. lasiurus* shares a predominantly acrocentric diploid karyotype of 34 chromosomes with *Akodon amoenus, A. arviculoides* and *A. obscurus* (Gardner and Patton, 1976; Pearson and Patton, 1976; Bianchi *et al,* 1971), while specimens of *Z. brevicauda* exhibit diploid counts of 84-88 chromosomes (Gardner and Patton, 1976; Kiblinski *et al,* 1970). Dental and cranial features vary similarly; Figure 7 illustrates first upper molars of *Z. brevicauda, Z. lasiurus, Akodon varius, A. cursor, A. obscurus* and *A. benefactus.* In *Z. brevicauda,* transverse lophs uniting opposite labial and lingual cusps are orthogonal to the long axis of the tooth and to the colinear anterior and median mures; usually, no trace of a mesoloph can be seen. In both *Z. lasiurus* and species of *Akodon (Akodon),* however, transverse lophs are oblique to the long axis of the tooth, anterior and median mures are never colinear, and a small mesoloph is almost always present. *Brevicauda*-like (northern) and *lasiurus*-like (southern) populations of *Zygodontomys* both have small ears, generalized body forms, grizzled-brownish pelages, short rostra, beaded, divergent interorbital regions and narrow braincases, but some species of *Akodon* are indistinguishable from either in these regards (Hershkovitz, 1962; our personal observations), and such a suite of character states is not uncommon among other small cursorial murids.

Because the possession of large medial ventral prostates is by far the more widespread state, considerations of parsimony argue that the diminutive medial ventral prostates of *Akodon (Akodon)* and *Zygodontomys lasiurus* represent a derived condition, and we suggest that the species displaying such small medial glands comprise a monophyletic group to which *Z. brevicauda* and the remaining South American cricetines we studied do not belong. This cladistic hypothesis is consistent with the phenetic patterns discussed in the preceding paragraph and with the observations of Thomas (1916) and Ellerman (1941), both of whom experienced difficulty in separating southern forms of *Zygodontomys (sensu* Hershkovitz, 1962) from species of *Akodon.* We would follow Gardner and Patton (1976), therefore, in referring *Z. lasiurus* to *Akodon,* and recommend that *Zygodontomys* be restricted in content to the northern, *brevicauda*-like mice for which the genus was originally erected (Allen, 1897).

LEVELS OF MORPHOLOGICAL VARIABILITY AMONG SOUTH AMERICAN CRICETINES

South American cricetines occupy a range of habitats that embraces dry coastal deserts, temperate grasslands, cold montane woodlands, lowland rainforests, palm swamps and tundra; included among these rodents are semiaquatic, scansorial, cursorial, arboreal and fossorial forms. Reflecting this ecological diversity is an array of craniodental and external morphologies that has inspired some glirologists to compare various South American cricetines with gerbils, voles, murines, hamsters, gophers, rabbits, shrews, moles, opossums, and small carnivores (Hershkovitz, 1955, 1962, 1966b; Hooper, 1968; Thomas 1893, 1896; Williams and Mares, 1978). With regard to their male reproductive anatomy, however, these same neotropical murids are astonishingly uniform. Among the 35 genera and subgenera of South American cricetines described in this report, there is less diversity of male accessory gland complements than exists within the single North American genus *Peromyscus* (Linzey and Layne, 1969). Nor is this uniformity restricted to the proximal portion of the male tract: Variation in glandes penes among the 18 genera of South American cricetines described by Hooper (1962) and by Hooper and Musser (1964a) is less than exists within *Peromyscus* (Hooper and Musser, 1964b), within *Neotoma* (Hooper, 1960), among microtines (Hooper and Hart, 1962) and among New Guinean murids (Lidicker, 1968). A similar constancy obtains for South American cricetine spermatozoan morphology (R. S. Voss, unpublished data). Why are South American cricetines, despite their craniodental and external morphological diversity, so uniform with respect to male reproductive structures?

Although more than one lineage of complex-penised cricetines may initially have invaded South America (Baskin, 1978), the many extant genera endemic to that continent, and the absence of cricetines in early and middle Pliocene neotropical fossil faunas (Patterson and Pascual, 1972; Reig, 1978) suggests that rapid phyletic proliferation of these rodents may have followed a relatively recent passage southward across either the Panamanian landbridge or a narrow water gap. Abundant Pleistocene and post-Pleistocene vicariance events (Vuilleumier, 1971; Simpson and Haffer, 1978) and accelerated rates of chromosomal rearrangement (Gardner and Patton, 1976) may have contributed to the swiftness of this radiation. Marshall (1979) suggested that such an explosive cladogenetic event may have occurred subsequent to a mid-Pliocene invasion of the continent by waif dispersal during a brief period of lowered sea levels. An hypothesis of much earlier (Miocene) entry of cricetines into South America, as yet unsupported by fossil evidence, was proposed by Hershkovitz (1966a) in order to reconcile his belief that all South American cricetines are descended from pentalophodont (complex-toothed) invaders with the fact that the earliest known South American fossil cricetines are tetralophodont (simple-toothed) forms from the late Pliocene of Argentina. If Baskin (1978) is correct, however, in arguing that several tetralophodont middle Pliocene North American genera are actually ancient and pre-invasive members of the South American cricetine assemblage, then *in situ* differentiation of the tetralophodont late Pliocene Argentine mice from pentalophodont invaders is not required. and an hypothesis of Miocene arrival to temporally accommodate such a morphological transition is rendered unnecessary.

Students of other vertebrate groups have observed that morphological changes accompanying adaptive radiations are often most evident in phenotypic attributes associated with feeding and with locomotory requirements of specific foraging modes and habitats (Amadon, 1947, 1950; Lack, 1961; Fryer and Iles, 1972; Keast, 1972; Greenwood, 1974). Resource competition among the radiating taxa is frequently advanced as a causal explanation for this phenomenon and, to the extent that competition-elicited changes in diet and habitat are accompanied by adaptive modification of the teeth, skull and integument, might account for the diversity of South American cricetine craniodental and external morphologies. That such an envisioned rapid episode of resource- and habitat-partioning could have left the male reproductive tract largely unaffected is less clear, however.

Current ignorance regarding the functional significance of observed differences in murid male reproductive anatomies is profound. Blandau (1945) demonstrated that the three bacular digits of *Rattus norvegicus* probably function to displace fleshy lappets that occlude the cervix of the female, but the biological roles of urethral flaps, papillae, terminal craters, spines and other phallic adornments of murids remain obscure. Conceivably, such structures could have evolved in the context of reproductive isolation, as was once proposed for the male genitalia of insects (Dufour, 1844); however, the fact that male *Microtus pennsylvanicus* are as successful as conspecific males in eliciting ovulation and luteal activation in *M. ochrogaster* females, (Gray *et al,* 1977) despite the substantial differences in penis morphology between the two species (Hooper and Hart, 1962), lends little support to this hypothesis. Broad correlations between penis shape and some aspects of murid copulatory behavior have been noted (Dewsbury, 1975), but convincing relationships between either penis morphology or copulatory behavior and diet or habitat have yet to be established. Voss (1979) reviewed the literature on male accessory gland variation among murids, and proposed that secretion of a chastity-enforcing copulatory plug may have been a major factor in the evolution of this organ system; the male accessory gland complements of murids which do not secrete copulatory plugs are reduced or modified from the presumed ancestral condition, and non-plug-secreting murids with reduced glandular complements include the two species for which best evidence of long-term pair-bonding and possible monogamy exists. The extent to which social phenomena might influence other aspects of the male tract has yet to be investigated. Even if it were true, however, that many of the selective pressures effecting morphological change in murid male reproductive structures are provided by the social environment of the species, it could not then be argued that such structures are therefore completely unrelated to spatio-temporal patterns of food abundance, food type, or habitat characteristics, since all of these factors appear to have been of importance in the evolution of mammalian social systems (Altmann, 1974; Jarman, 1974; Bradbury and Vehrencamp, 1977; Elliot, 1978). Nevertheless, the fact that no character of the murid male reproductive tract has yet been shown to be correlated with any observable ecological variable or dietary proclivity strongly suggests that functional relationships between this organ system and those environmental aspects which are usually thought to be of importance in competitive interactions among rodents (e.g., Brown, 1971; Cameron, 1964; Cameron, 1971; Grant, 1972; Price, 1978) are very tenuous or involve an as-yet-unappreciated complexity of adaptive compromises with other attributes of the whole organism. Either the existence of such complex trade-offs or a lack of ecological immediacy could have prevented the male reproductive tract from keeping pace with the changes in crania, dentitions and external characters as South American cricetines diversified in the late Pliocene or early Pleistocene; that groups such as *Peromyscus* or *Neotoma,* of appreciably less ecological amplitude than the South American cricetines, are nonetheless more variable in male reproductive anatomy might be attributable to a greater antiquity for these genera (as they are currently constituted) than has yet been recognized by paleontologists.

The hypothesis elaborated in the preceeding paragraphs, which we advance as a possible explanation only for the discrepancy between levels of variability of different organ systems, does *not* imply that the male reproductive tract provides more certain evidence of phylogenetic affinity than do craniodental or external characters. Some mammalian systematists (Burt, 1936; Mossman 1937, 1953), by contrast, once argued that because certain reproductive structures appear less proximal to environmental selective pressures than the dentition and integument, they therefore constitute more reliable indicators of geneological relationships. The value of a character for inferring phylogeny, however, seems to us more a function of how often the character has independently (i.e., in not-closely-related organisms) responded in the same way to similar selective pressures rather than a function of whether the relevant selective pressures are ecological or physiological in kind. Surely, various mammalian reproductive anatomies are adaptive responses to real biological problem-situations and if similar problem-situations arose more than once in the course of a group's evolution, convergent reproductive-anatomical responses would be expected. Thus, while the measure of functional independence from craniodental and external morphology that some reproductive characters may enjoy might be used to advantage in testing phylogenies based on features of teeth, skull and integument, we cannot defend those who would accord reproductive attributes exalted status in systematic studies because of a supposed lesser tendency to exhibit homoplasy.

SUMMARY

1. The male accessory gland complements of 54 species in 35 genera and subgenera of South American cricetines are described; included are representatives of all of the major generic groups recognized by recent workers. The male reproductive tracts of some murines, gerbillines, hamsters and mystromyines are also described, and literature on the gross morphology of murid accessory glands is reviewed.

2. From these data it is concluded that the primitive murid male accessory gland complement included one pair each of preputial, bulbo-urethral, dorsal and anterior prostate, vesicular, ampullary and at least one pair of ventral prostate glands. The same array of glands is believed to be primitive for South American cricetines except that two pairs of ventral prostates were likely present in the most recent common ancestor of this group.

3. South American cricetines comprise a homogeneous assemblage with respect to their accessory gland complements. *Nyctomys sumichrasti,* however, departs markedly from all other South American cricetines in characters of its male reproductive tract, and may not be closely related to any of these rodents. Implications of presence/absence of preputial pairs among South American cricetine genera are discussed. Based on ventral prostate morphology as well as dental and chromosomal data. *Zygodontomys lasiurus* is referred to *Akodon,* and the genus *Zygodontomys* is restricted in content to populations occurring north of the Amazon Basin.

4. Despite their craniodental and external morphological diversity, South American cricetines are remarkably uniform in male reproductive anatomy. This phenomenon is cautiously attributed to the rapid cladistic proliferation of these rodents, during which resource competition may have placed a selective premium on morphological changes that permitted exploitation of diverse kinds of food and habitats. Such an evolutionary episode is hypothesized to have more swiftly effected divergence in morphology of teeth, crania and integuments than in the (perhaps) less ecologically proximal male reproductive tract.

5. Despite arguments summarized in (4), reproductive anatomy provides no more certain evidence of phylogenetic affinity than does craniodental or external morphology, and cannot be weighted disproportionately in systematic studies. However, because male and female reproductive tracts may enjoy a substantial degree of functional independence from characters traditionally used in mammalian phylogenetics, characters drawn from them may provide valuable tests of preexisting hypotheses of phylogeny.

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Appendix 1

SPECIMENS EXAMINED

Below are provided localities (COUNTRY, state/province/department) and museum catalog numbers of the material we examined in the course of this study. Species are listed in alphabetic order. Institutional abbreviations are as follows: AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; MSU, Museum of Michigan State University; UMMZ, University of Michigan Museum of Zoology; USNM, National Museum of Natural History. Numbers prefixed with RSV are field catalog designations of material collected by the senior author; this material will eventually be deposited in the American Museum of Natural History.

Abrothrix longipilis—CHILE, Arauco (MSU 7184,86,89), Malleco (MSU 7155,72, 7323-24). *Acomys dimidiatus*—Laboratory stock (UMMZ 113374, 78). *Akodon arenicola*—ARGENTINA, Buenos Aires (UMMZ 110445-46). *Akodon azarae*—URUGUAY, Rocha (AMNH 206076). *Akodon bogotensis*—VENEZUELA, Táchira (FMNH 18679), *Akodon cursor* – PARAGUAY, Itapúa (UMMZ 124285-87), Misiones (UMMZ 124279,83,84). *Akodon jelskii*—BOLIVIA, La Paz (AMNH 241615,19), no additional locality data (UMMZ 115712-13). *Akodon nigrita*—PARAGUAY, Itapúa (UMMZ 126265). *Akodon obscurus*—ARGENTINA, Buenos Aires (MSU 17801,18284,18410, 58,60; UMMZ 122359). *Akodon varius*—PARAGUAY, Chaco (UMMZ 124268-70), Nueva Asunción (UMMZ 125281). *Andalgalomys pearsoni*—PARAGUAY, Nueva Asunción (UMMZ 130037). *Anotomys leander*—ECUADOR, Napo (AMNH 244607; UMMZ 126294). *Apodemus flavicollis*—IRAN, Khūzestān (UMMZ 122996,98,99). *Beamys hindei*—TANZANIA, no additional locality data (UMMZ 122360). *Calomys callosus*—PARAGUAY, Chaco (UMMZ 124235,41,47,125464). *Calomys laucha*—PARAGUAY, Nueva Asunción (UMMZ 125297). *Chilomys instans*—ECUADOR, Pinchincha (AMNH 63372). *Cricetulus barabensis*—laboratory stock (UMMZ 103734-35,37). *Daptomys venezuelae*—VENEZUELA, Sucre (AMNH 69907). *Eligmodontia typus*—ARGENTINA, Neuquén (UMMZ 110396). *Graomys griseoflavus*—ARGENTINA, La Pampa (UMMZ 109230,32); PARAGUAY, Chaco (UMMZ 124251,53). *Holochilus brasiliensis*—ARGENTINA, Buenos Aires (MSU 18692, 18797); GUYANA, Essequibo (AMNH 140464); PARAGUAY Central (UMMZ 124226), Chaco (UMMZ 125491). *Irenomys tarsalis*—CHILE, Malleco (MSU 7470). *Meriones shawi*—EGYPT, Matrûh (UMMZ 118894, 118930). *Meriones tristrami*—IRAN, Teheran (UMMZ 118272,75; FMNH 97388). *Meriones unguisulatus*—Laboratory stock (UMMZ 110997, 119480). *Mystromys albicoudatus* — Laboratory stock (UMMZ 111119, 122363). *Neacomys spinosus* — COLOMBIA, Meta (AMNH 202647); PERU Huánuco (FMNH 24767). *Nectomys squamipes*—ECUADOR, Napo (RSV 178); PARAGUAY, Cordillera (UMMZ 126275), Paraguarí (UMMZ 124189, 94); TRINIDAD, no additional locality data (AMNH 214456). *Neotomys ebriosus*—BOLIVIA, El Cumbre (AMNH 241678). *Neusticomys monticolus* —ECUADOR, Napo (AMNH 244608; UMMZ 126297), Pinchincha (AMNH 64632; UMMZ 126298). *Notiomys valdivianus*—CHILE, Malleco (MSU 6749,52,57,6745). *Nyctomys sumichrasti*—Laboratory stock (UMMZ 112378); GUATEMALA, Sololá (UMMZ 113520,22); PANAMA, Bocas del Toro (USNM 323880), Panamá (USNM 460165). *Oryzomys albigularis* COSTA RICA, Alajuela (UMMZ 123205); PANAMA, Chiriquí (UMMZ 116926-27; USNM 323906). *Oryzomys alfaroi*—GUATEMALA, Izabel (UMMZ 113145); MEXICO, Oaxaca (UMMZ 113094,113833,34), San Luis Potosí (UMMZ 113840); PANAMA, Chiriquí (UMMZ 116888). *Oryzomys caliginosus* — COSTA RICA, Cartago (UMMZ 111965), San José (UMMZ 111968); PANAMA, Darien (USNM 310521). *Oryzomys capito*—PANAMA, Canal Zone (UMMZ 117184,87-88), Los Santos (USNM 323913); TRINIDAD, no additional locality data (AMNH 204802). *Oryzomys concolor* — PARAGUAY, Chaco (UMMZ 125456); VENEZUELA, Aragua (USNM 517571). *Oryzomys fulvescens*—COSTA RICA, Cartago (UMMZ 111976), Puntarenas (UMMZ 117103), San José (UMMZ 111972-73). *Oryzomys melanotis* — MEXICO, Campeche (UMMZ 120670-71), Quintana Roo (UMMZ 120890), San Luis Potosí (UMMZ 113849). *Oryzomys altissimus*—ECUADOR, Napo (RSV 175). *Oryzomys palustris*—COSTA RICA, Guanacaste (UMMZ 115286-88); UNITED STATES, Alabama (4 uncataloged specimens). *Oryzomys ratticeps*—PARAGUAY, Misiones (UMMZ 124197), 124201,04,125617). *Oxymycterus delator*—PARAGUAY, Canendiyu (UMMZ 124291,94,98, 126271). *Oxymycterus rutilans*—ARGENTINA, Buenos Aires (MSU 18856,91, 19057, 19316; UMMZ 110442-43). *Pachyuromys duprasi* — EGYPT, Beheira (UMMZ 118569, 119420,24,29). *Phyllotis darwini*—CHILE, Malleco (MSU 7413,16. 24, 28). *Phyllotis micropus*—CHILE, Malleco (MSU 7439). *Phyllotis osilae*—BOLIVIA, La Paz (AMNH 241400-01). *Reithrodon physodes* — ARGENTINA, Buenos Aires (MSU 17891, 18398, 18668,89); URUGUAY, Treinta y Tres (AMNH 206361). *Rheomys hartmanni*—COSTA RICA, Puntarenas (UMMZ 116934), San José (UMMZ 111986-87). *Rheomys thomasi*—GUATEMALA, Huehuetenango (UMMZ 114711). *Rheomys underwoodi*—COSTA RICA, Alajuela (UMMZ 115389, 115460). *Scapteromys tumidus*—ARGENTINA, Buenos Aires (UMMZ 110441); PARAGUAY, Cordillera (UMMZ 125954, 126266). *Sigmodon hispidus*—MEXICO, Campeche (UMMZ 120711, 13-14, plus 3 uncataloged specimens), Michoacan (UMMZ 110728); UNIT-

ED STATES, Florida (UMMZ 111127). *Sigmodon alstoni*—VENEZUELA, Bolívar (USNM 496003), Monagas (USNM 496014,18). *Tatera brantsi* — SOUTH AFRICA Transvaal (UMMZ 111118). *Tatera indica*—IRAN Khūzestān (UMMZ 120195); PAKISTAN, Deh Amilano (UMMZ 118886, 119403). *Thomasomys aureus*—ECUADOR, Napo (UMMZ 127114); PERU, Cuzco (FMNH 75588). *Thomasomys baeops*—ECUADOR, Tunguragua (AMNH 63380, 82). *Thomasomys laniger*—VENEZUELA, Mérida, (USNM 495630, 33). *Thomasomys rhoadsi*—ECUADOR, Pinchincha (AMNH 63361). *Zygodontomys brevicauda*—COLOMBIA, Meta (AMNH 202645); COSTA RICA, Puntarenas (UMMZ 111956-57,60); TRINIDAD, Bush Bush (AMNH 203134,36,59, 204805); VENEZUELA, Aragua (USNM 517628). *Zygodontomys lasiurus* — BOLIVIA, Cochabamba (UMMZ 116400), Beni (AMNH 211826,37, 214762); BRAZIL, Goiás (AMNH 202643); PARAGUAY, Misiones (UMMZ 124259,61).

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