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Comparative Morphology of the Male Reproductive Tract in the Rodent Genus *Peromyscus* (Muridae)

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The genus *Peromyscus* is a large, widespread, and ecologically diverse group of cricetine rodents. The earliest comprehensive review of the genus was that of Osgood (1909), who recognized six subgenera and arranged the many species of the subgenus *Peromyscus* into eight species groups. Except for the elevation of the subgenus *Baiomys* to full generic status, Osgood's classification has not been seriously challenged until fairly recently. Hooper (1957) pointed out that some of the dental characters used by Osgood to differentiate certain subgenera were more variable than previously suspected. Later, comparative study of the male phallus (Hooper, 1958) indicated that the subgenus *Ochrotomys* warranted separate generic rank and revealed other patterns of variation within the genus that were difficult to reconcile with Osgood's scheme. Hooper and Musser (1964) subsequently proposed a new classification of the genus in which seven subgenera were recognized. Four of these (*Peromyscus*, *Podomys*, *Haplomylomys*, and *Megadontomys*) were retained from Osgood, whereas three (*Osgoodomys*, *Isthmomys*, and *Habromys*) were new. Some shifts of species between subgenera and modifications in the mem-

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bership of certain species groups within the subgenus *Peromyscus* were also made. Acknowledging the taxonomic complexity of the group, these authors emphasized that their classification constituted a "tentative framework . . . against which subsequent systematic data may be tried for fit."

The major objective of the present study is to provide a further basis for an understanding of the phyletic relationships of *Peromyscus* through a comparative survey of the male reproductive tract, with particular emphasis on the accessory glands. The potential value of the genital system in mammalian systematics has been stressed by Simpson (1945) and Mossman (1953). Although the baculum and glans penis of *Peromyscus* have been investigated in some detail (Blair, 1942; Burt, 1960; Hooper, 1958; and Hooper and Musser, 1964), the remainder of the reproductive tract has received relatively little attention. Jameson (1950) considered the vesicular and prostate glands in connection with determination of breeding condition, Hoffmeister (MS) noted certain features of the accessory glands, and Arata (1964) briefly described the gross anatomy of the tract of *P. gossypinus*.

METHODS AND MATERIALS

Reproductive tracts used for gross anatomical study were, for the most part, obtained from intact carcasses originally preserved in 10 per cent formalin and later transferred to 70 per cent alcohol for storage, although a few tracts were dissected from freshly killed mice and preserved directly in 10 per cent formalin. Observations were made on the condition of the cremaster as opportunity afforded, but the nature of the material available largely precluded obtaining systematic data on this and other features of the external genitalia.

Most of the genital organs used for histological study were removed immediately after death and fixed in Bouin's fluid or a solution of formalin, acetic acid, and alcohol. In the case of those species that could not be procured alive, material for sectioning was obtained from specimens that had been snap-trapped and injected with fixative.

Immature and non-breeding adult tracts were examined when available as an aid to interpretation of fully developed structures, but species descriptions and comparisons are based on adult specimens in full breeding condition wherever possible. Enlarged cauda epididymal tubules containing copious amounts of spermatozoa constituted the principal criterion of breeding condition. Substantial series of genital organs of breeding adults of *leucopus*, *maniculatus*, *gossypinus*, and *floridanus* were studied to determine the extent of size and morphological variation to

be expected within a given population, in order to provide a better basis for evaluating the significance of differences between species represented by a limited number of specimens.

The following measurements were made to the nearest 0.1 mm. on preserved tracts. In the case of paired structures, each was measured separately, and the values were averaged.

TESTIS: Greatest length and width, exclusive of epididymis.

DEFERENT DUCT: Length from a point between ampullary glands to juncture with cauda epididymis, with duct straightened but not stretched.

URETHRA: Length along midline from bladder stalk to ventral flexure of penis, thus including entire membranous urethra and portions of prostatic and penile divisions.

AMPULLARY GLAND: Greatest length along anteroposterior axis of gland and greatest width.

VESICULAR GLAND: Greatest length in a straight line from midline to farthest point on outer curvature and maximum width of proximal, uncurved segment of gland.

ANTERIOR PROSTATE GLAND: Greatest length from base to tip and width across widest part.

DORSAL PROSTATE GLAND: Length from anteriormost to posteriormost point and greatest width.

VENTRAL PROSTATE GLAND: Greatest length of both pairs (when present) regarded as a single unit and greatest width at right angles to axis of previous measurement.

BULBO-URETHRAL GLAND: Greatest length from distalmost point on margin of gland to point at which gland narrows abruptly to form duct, and greatest width at right angles to axis of previous measurement.

PREPUTIAL GLAND: Greatest length, including duct, and greatest width.

Complete tracts and individual organs used for histological study were embedded in paraffin, serially sectioned at 10 microns, and stained with hematoxylin and eosin.

A total of 155 tracts, representing 28, or approximately one-half, of the species currently included in the genus, was available for gross study. Histological observations were made on 11 species. The numbers and collecting localities of the specimens studied are listed below, following the classification of Hooper and Musser (1964). An asterisk indicates histological, as well as gross, study.

Subgenus *Peromyscus*

Maniculatus group

**polionotus*: Florida: Alachua County, four; St. Johns County, two.

**maniculatus*: Colorado: Boulder County, two. New York: Greene County, two; Jefferson County, 13. Tennessee: Cocke County, five.

oreas: Washington: Clallam County, one.

melanotis: Mexico: Distrito Federal, one.

Leucopus group

**leucopus*: New York: Tompkins County, two. Tennessee: Cocke County, 25.

**gossypinus*: Florida: Alachua County, four; Gilchrist County, one. Tennessee: Cocke County, six.

Crinitus group

crinitus: California: Kern County, one; Deep Springs, one. No data: one.

Boylei group

pectoralis: Texas: Brewster County, four.

boylei: Arizona: Cochise County, two. Guatemala: Department of Quezaltenango, two; Department of Sacatepequez, two.

**oaxacensis*: Mexico: Chiapas, three.

Truei group

**truei*: Mexico: Oaxaca, one. Arizona: Cochise County, one. Colorado: Boulder County, one.

difficilis: Mexico: Oaxaca, one.

Mexicanus group

mexicanus: Guatemala: Department of Baja Verapaz, two; Department of Sacatepequez, one. Mexico: Chiapas, one.

nudipes: Costa Rica: Cartago, three. Panama: Chiriquí, two.

furvus: Mexico: Puebla, two.

guatemalensis: Guatemala: Department of Huehuetenango, one; Department of Sololá, one.

**megalops*: Mexico: Guerrero, two.

zarhynchus: Mexico: Chiapas, one.

grandis: Guatemala: Department of Baja Verapaz, one.

Subgenus *Haplomylomys*

**eremicus*: Mexico: Sinaloa, one. Arizona: Cochise County, one. California: Riverside County, one. Texas: Brewster County, four.

californicus: California: Riverside County, one.

interparietalis: Mexico: Baja California (Salsipuedes Island), three.

Subgenus *Habromys*

**lepturus*: Mexico: Oaxaca, four.

Subgenus *Osgoodomys*

banderanus: Mexico: Guerrero, five.

Subgenus *Podomys*

**floridanus*: Florida: Levy County, eight; Alachua County, two.

Subgenus *Isthmomy*

flavidus: Panama: Los Santos, four.

pirrensis: Panama: Darién, three.

Subgenus *Megadontomys*

**thomasi*: Mexico: Guerrero, four.

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SPECIES DESCRIPTIONS

The terminology of genital structures employed in the following accounts for the most part agrees with that of Hummel, Richardson, and Fekete (1966) for the laboratory mouse, *Mus musculus*, except that we follow Arata (1964) in designating as "anterior prostates" the glands termed "coagulating glands" by Hummel and her co-authors and many other authors.

Absolute and proportional measurements of reproductive structures in the species examined are given in tables 1 and 2, respectively. The generally small samples available together with the considerable variability of soft tissues make it obvious that these data are useful for rather broad general comparisons only.

SUBGENUS *PEROMYSCUS*

Figure 1

The gross anatomy of 18 of the 32 species included in this subgenus was studied, and seven species were examined histologically. Material was available for representatives of six of the seven species groups. The tract of *P. leucopus* is described in greatest detail as a basis for comparisons among the remaining species in this subgenus and other subgenera. In the accounts of other species, if no mention is made of specific differences from *leucopus*, it can be assumed that the species in question agree with *leucopus* in the particular feature.

Leucopus GROUP

Peromyscus leucopus

Figure 1

The general morphology of the male genital tract of this species is basically similar to that of *Mus musculus* (Hummel, Richardson, and Fekete, 1966) with the major exception that macroscopic preputial glands are lacking.

The cremaster of breeding adults is prominent and tends to become sparsely haired and heavily pigmented posteriorly. The testes are of about average size compared with those of the genus as a whole. There were six efferent ducts present in two specimens. The epididymis consists of the usual three divisions (caput, corpus, and cauda), with the caput epididymis embedded in a mass of fatty tissue.

TABLE 1
AVERAGE MEASUREMENTS (IN MILLIMETERS) OF MALE GENITAL STRUCTURES IN *Peromyscus*
(Where two measurements are given, the first represents length; and the second, width.)

Species	N	Testis	Deferent Duct	Urethra	Ampullary	Vesicular	Anterior Prostate	Dorsal Prostate	Ventral Prostate	Bulbo- urethral
<i>polionotus</i>	6	6.0 × 4.0	10.9	8.9	1.7 × 1.7	7.1 × 2.6	4.9 × 1.6	3.3 × 1.9	5.0 × 1.9	3.0 × 2.3
<i>maniculatus</i>	22	8.5 × 5.1	13.8	20.0	2.0 × 2.0	8.3 × 2.8	4.3 × 1.8	3.4 × 1.9	5.1 × 1.8	1.9 × 1.8
<i>oreas</i>	1	5.0 × 3.0	^a	^a	1.0 × 1.0	2.0 × 1.0	1.0 × 1.0	1.5 × 1.0	1.5 × 1.5	2.0 × 1.0
<i>melanotis</i>	1	8.0 × 5.7	12.0	21.0	2.5 × 3.0	9.7 × 3.3	5.5 × 2.0	4.0 × 2.3	2.5 × 2.5	3.0 × 4.3
<i>leucopus</i>	19	8.8 × 5.2	11.7	17.8	1.9 × 2.2	7.1 × 2.6	3.8 × 1.6	2.8 × 2.1	3.3 × 1.9	1.7 × 1.7
<i>gossypinus</i>	9	13.3 × 7.0	17.4	29.1	2.8 × 2.7	10.9 × 3.8	6.3 × 2.3	5.5 × 2.4	5.2 × 3.8	1.9 × 2.0
<i>crinitus</i>	3	7.0 × 4.0	10.4	8.5	1.9 × 2.5	5.1 × 2.3	3.2 × 1.2	3.7 × 1.9	2.2 × 1.3	1.8 × 1.8
<i>pectoralis</i>	3	6.5 × 3.8	10.8	19.0	1.0 × 1.6	3.6 × 1.4	0.8 × 0.1	1.9 × 1.4	1.8 × 1.8	1.9 × 1.7
<i>boylei</i>	6	9.8 × 5.4	12.8	22.8	2.2 × 3.6	6.1 × 2.0	3.1 × 1.5	3.8 × 2.1	4.4 × 2.7	2.2 × 2.1
<i>oaxacensis</i>	3	9.4 × 4.9	12.6	18.1	1.4 × 2.1	5.1 × 1.5	2.6 × 1.3	3.4 × 2.2	3.0 × 1.2	2.0 × 1.8
<i>truei</i>	2	10.9 × 6.4	18.5	27.0	2.6 × 3.0	10.0 × 3.0	5.6 × 2.1	4.3 × 2.0	6.5 × 4.5	3.6 × 2.7
<i>difficilis</i>	1	10.0 × 6.0	15.0	26.5	2.7 × 3.0	7.0 × 2.0	3.5 × 1.7	5.0 × 3.0	3.0 × 2.5	2.5 × 2.7
<i>mexicanus</i>	4	10.6 × 6.2	16.3	23.5	1.9 × 2.3	7.8 × 2.3	4.2 × 1.8	4.0 × 2.3	4.9 × 3.7	2.8 × 2.9

TABLE 1—(Continued)

Species	N	Testis	Deferent Duct	Urethra	Ampullary	Vesicular	Anterior Prostate	Dorsal Prostate	Ventral Prostate	Bulbo-urethral
<i>nudipes</i>	5	12.2 × 7.5	18.5	29.3	2.7 × 3.4	9.7 × 3.3	4.8 × 2.1	5.1 × 2.5	5.2 × 3.5	4.7 × 4.6
<i>furnus</i>	5	13.0 × 6.9	18.8	30.0	2.4 × 3.2	7.1 × 2.4	4.2 × 1.8	6.0 × 3.2	4.3 × 2.0	3.7 × 4.1
<i>guatemalensis</i>	2	14.1 × 9.1	19.4	30.0	3.1 × 3.5	11.4 × 3.6	8.1 × 2.5	5.9 × 2.9	6.4 × 3.4	5.7 × 4.9
<i>megalois</i>	1	15.0 × 9.7	27.3	26.0	3.5 × 4.0	14.0 × 4.0	7.5 × 3.0	6.0 × 3.0	6.5 × 4.7	6.7 × 4.7
<i>zariynchus</i>	1	14.5 × 9.3	24.8	33.5	3.5 × 4.0	13.7 × 4.3	7.7 × 3.0	4.3 × 3.0	9.0 × 4.3	4.5 × 4.3
<i>grandis</i>	1	15.5 × 9.0	24.5	36.5	3.7 × 4.0	14.0 × 4.0	6.3 × 3.3	8.3 × 4.5	8.0 × 8.5	6.5 × 5.0
<i>eremicus</i>	5	8.2 × 5.2	14.5	21.7	3.0 × 2.8	10.1 × 4.2	6.5 × 2.6	4.0 × 2.3	4.6 × 3.4	2.5 × 2.7
<i>interparietalis</i>	3	9.0 × 5.4	12.1	21.0	2.0 × 3.3	8.8 × 3.6	5.5 × 2.8	4.3 × 2.9	4.3 × 3.4	3.8 × 3.1
<i>californicus</i>	1	7.5 × 5.0	11.5	20.5	3.0 × 3.0	9.0 × 4.0	6.7 × 1.5	4.7 × 2.7	5.3 × 3.0	2.0 × 2.0
<i>lepturus</i>	4	5.0 × 4.0	13.0	17.8	1.5 × 2.0	4.3 × 1.3	—	2.0 × 1.5	9.6 × 6.3	2.3 × 1.7
<i>banderanus</i>	5	13.5 × 7.1	20.4	19.0	5.5 × 10.7	—	—	—	3.6 × 2.9	5.3 × 4.8
<i>floridanus</i>	6	12.3 × 6.7	20.0	22.6	7.7 × 4.7	8.6 × 2.0	4.4 × 0.9	2.2 × 1.8	5.0 × 3.0	5.6 × 5.4
<i>flavidus</i>	4	15.0 × 5.4	25.6	^a	4.3 × 4.8	10.3 × 3.5	7.4 × 2.5	3.9 × 2.2	3.8 × 3.2	4.3 × 4.3
<i>pirrensis</i>	3	17.6 × 7.8	29.3	^a	9.1 × 6.1	15.1 × 5.4	10.8 × 4.3	3.6 × 2.1	7.1 × 3.9	6.3 × 5.5
<i>thomasi</i>	2	19.0 × 10.1	35.5	45.0	8.5 × 9.2	19.5 × 6.1	9.3 × 3.8	7.3 × 3.5	7.6 × 8.5	6.0 × 12.4
Mean of all species		10.5 × 6.2	17.7	23.4	3.2 × 3.5	8.6 × 3.0	5.3 × 2.1	4.2 × 2.4	4.9 × 3.4	3.6 × 3.5

^aNo data.

TABLE 2
 SIZE OF GENITAL STRUCTURES OF *Peromyscus* EXPRESSED AS PERCENTAGE OF LENGTH OF HIND FOOT
 (Measurements used are means given in table 1. In the case of the testis and accessory glands, the sums of mean length and width measurements are used in order to give a better indication of the total size of the structures.)

Species	Testis	Deferent Duct	Urethra	Ampullary	Vesicular	Anterior Prostate	Dorsal Prostate	Ventral Prostate	Bulbo-urethral
<i>polionotus</i>	58	63	52	20	56	38	30	40	31
<i>maniculatus</i>	63	64	93	18	52	28	25	32	17
<i>oreas</i>	35	^a	^a	9	13	9	11	13	13
<i>melanotis</i>	65	57	100	26	62	36	30	24	35
<i>leucopus</i>	67	56	86	20	47	26	23	25	16
<i>gossypinus</i>	88	76	126	24	64	37	34	39	17
<i>crinitus</i>	56	53	43	22	38	24	28	18	18
<i>pectoralis</i>	49	51	90	12	24	4	16	17	17
<i>boylei</i>	61	51	91	23	32	18	24	28	17
<i>oaxacensis</i>	58	51	79	14	27	16	23	17	15
<i>truei</i>	77	83	121	25	58	34	28	49	28
<i>difficilis</i>	61	58	102	22	35	20	31	21	20
<i>mexicanus</i>	67	65	94	17	40	24	25	34	23

TABLE 2—(Continued)

Species	Testis	Deferent Duct	Urethra	Ampullary	Vesicular	Anterior Prostate	Dorsal Prostate	Ventral Prostate	Bulbo-urethral
<i>nudipes</i>	71	67	106	22	47	25	27	31	34
<i>furvus</i>	67	64	102	19	32	20	31	21	26
<i>guatemalensis</i>	78	66	102	22	51	29	30	33	36
<i>megalops</i>	80	88	84	24	58	34	29	36	37
<i>zarlhynchus</i>	72	75	102	23	54	32	22	40	27
<i>grandis</i>	70	70	104	22	51	27	36	47	33
<i>eremicus</i>	55	60	90	24	59	38	26	33	22
<i>interparietalis</i>	65	55	95	24	56	37	33	35	31
<i>californicus</i>	52	48	85	25	54	34	31	35	17
<i>lepturus</i>	30	44	60	12	19	—	12	54	14
<i>bonderanus</i>	86	86	80	68	—	—	—	27	42
<i>floridanus</i>	74	78	88	48	41	21	16	31	43
<i>flavidus</i>	59	75	^a	26	40	29	18	20	25
<i>pirrensis</i>	71	82	^a	42	58	42	16	31	33
<i>thomasi</i>	94	114	145	57	82	42	35	52	59
Mean of all species	65	64	93	25	46	28	25	31	26

^a No data.

The deferent ducts are relatively short. The mucosa of the duct is thrown into prominent folds and consists of columnar epithelium that appears to be pseudostratified in at least some regions (fig. 6A). The majority of the cells possess prominent cilia, and small "blebs" of secretion are attached to the surfaces of some. The nuclei are oval and centrally situated in the cell. Their position is so uniform that they tend to form a distinct zone. The lumen of the deferent duct narrows markedly just before the ampulla. The epithelial lining of the ampulla is lower than that of the more distal portion of the deferent duct, and the cells have darker-staining nuclei. Cilia, if present, are scarce.

The urethra is comparatively short. Urethral glands (fig. 6B) are abundant and are of a simple alveolar type, with short ducts opening directly into the lumen of the urethra. The individual cells of these glands have dark-staining, round nuclei, and pinkish cytoplasm. The urethral glands are distributed from about the level of the colliculus seminalis to just anterior to the bulb of the penis. The latter contains bulbar glands that closely resemble the urethral glands and form a dense, dark-staining mass between the layers of epithelial and connective tissue (fig. 6C). The bulbar glands are abundant and uniformly distributed in the ventral and lateral wall of the bulb but are sparse in the dorsal portion. The dorsal margin of the bulb of the penis is truncate, with no sign of bifurcation in the specimens examined.

The accessory gland complement consists of a single pair each of ampullary, vesicular, anterior and dorsal prostate, bulbo-urethral, and vestigial preputial glands, and two pairs of ventral prostates.

The ampullary glands are compact masses of tightly coiled, branched tubules, with numerous ducts opening into the ampulla. The tubular nature of these glands is hardly evident externally, even in fully mature animals. The tubules are lined with a simple cuboidal or low-columnar epithelium that is only slightly infolded and possess an inner layer of smooth muscle and an outer one of connective tissue. The dark-staining, oval nuclei lie close to the basement membrane. In some specimens, the ampullary gland completely surrounds the base of the deferent duct; in other cases the duct is only partially enclosed by the glandular tissue.

The vesicular glands are the largest and most distinctive components of the accessory gland complex. They are elongated, J-shaped structures, with a somewhat lumpy or knobby outer curvature and smoother inner curvature. This difference is also reflected in a greater infolding of the epithelium lining the large central lumen on the outer surface. A thin layer of smooth muscle tissue lies between the epithelium and the thick connective tissue coat that invests the gland. The epithelial cells are

low columnar with dark, round, or oval nuclei situated next to the basement membrane (fig. 6D). A characteristic of these epithelial cells is the presence in the cytoplasm of dark secretion granules surrounded by lighter "halos." This feature is also found in *Mus* (Hummel, Richardson, and Fekete, 1966). The secretion of these glands is clear and viscous in the fresh state. When it is fixed, it assumes a hyaline appearance and becomes brittle, cracking in parallel fissures when sectioned. The secretion stains purple toward the center of the lumen and reddish at the periphery.

Each vesicular gland possesses a single large duct that enters the anterior portion of the urethra, opening onto a well-developed colliculus seminalis. In specimens examined histologically, the vesicular and deferent duct on each side joined immediately before opening into the urethra. Whether this condition is constant in *leucopus* is not known; but in all probability there is individual variation, as occurs in *Mus*, as to whether the vesicular ducts enter the urethra separately or fuse with the deferent ducts first.

There is some variation in the degree of curvature and extent of irregularity of the outer margin of the vesiculars among breeding adults. The vesiculars of immature animals are much smaller, saclike, and flaccid. The lumen contains no secretion, and the epithelium is only slightly folded. The cells are cuboidal rather than low columnar.

The three groups of prostate glands together encircle the prostatic urethra. The anterior prostates are elongate, slender glands consisting of a mass of loosely bound tubules that distally range from about five to 10 in number. They lie along the lesser curvature of, and in contact with, the vesicular glands, the two being bound together by connective tissue. The tubules are lined with cuboidal or low-columnar epithelium that is only moderately infolded in comparison with that of the vesicular gland (fig. 7A). The secretion of these glands appears entirely granular in fixed and stained material. The cells have round nuclei that stain less heavily than those of the vesicular or ampullary gland epithelia. Individual tubules are surrounded by a thin layer of connective tissue and smooth muscle fibers. Each gland is drained by a single duct that enters the urethra laterally just posterior to the entrance of the deferent duct. There was no marked variation in position or appearance of these glands in the series of mature specimens examined. The tubules are fewer and smaller in diameter in immature animals.

The dorsal prostate glands are situated on the dorsolateral aspect of the urethra posterior to the bases of the vesicular glands. Each gland is composed of a medial and a lateral lobe. The former is compact and

has a relatively smooth surface, whereas the latter tends to be more diffuse, and the tubules more distinct. The tubules are lined with a cuboidal or low-columnar epithelium that is not thrown into folds (fig. 7B). The cells have pale-staining cytoplasm and round or oval nuclei situated in the basal half of the cell. The eosinophilic secretion is granular in appearance and tends to shrink away from the sides of the lumen, leaving strands attached to the walls in some specimens; in others it is homogeneous and does not exhibit such shrinkage. Each gland drains into the prostatic urethra by approximately nine ducts. Each medial lobe has about five ducts that lie along the dorsal aspect of the corresponding vesicular duct and enter the urethra dorsad to the vesicular and deferent ducts. The lateral lobe has about four ducts that enter the urethra anteriorly with the group from the medial lobe. There is little variation in the appearance of these glands in breeding specimens. In some instances, however, a small tuft of tubules from these glands projects forward between the bases of the vesicular glands.

The two pairs of ventral prostate glands comprise discrete masses of tubules and associated ducts that are held together by connective tissue. A medial pair is attached to the urethra just below the stalk of the bladder. Their tubules are lined with a moderately folded, tall-columnar epithelium the cells of which have pale-staining cytoplasm and round nuclei basal in position (fig. 7C). The epithelium is remarkably uniform, with all cells approximately of the same height and all nuclei situated at about the same level in the cell. The secretion has a granular appearance and stains magenta. The number of ducts in 11 specimens ranged from two to four on a side, with a mean of 2.9.

The remaining pair of ventral prostates is situated lateral to the above, and the glands tend to have a more opaque appearance. The epithelial cells of the tubules are tall columnar, and the lining is slightly infolded. The secretion is granular in nature. The connective tissue covering the tubules is thinner than that of the medial pair, and the diameter of the individual tubules is smaller. The ducts of the lateral pair enter the urethra in the same region as those of the anterior prostates and lateral lobe of the dorsal prostates. The number of ducts in 10 specimens ranged from one to three.

In mature individuals, one pair of ventral prostates is in some cases larger than the other, but there is no consistent size difference between the medial and lateral components.

The bulbo-urethral glands consist of a wedge-shaped body situated in the bulbocavernosus muscle mass and a tail that passes between the ischiocavernosus and bulbocavernosus muscles to enter the cephalic por-

tion of the bulb of the penis. These glands consist of a compact mass of tightly packed tubules and alveoli discharging into a central lumen. The tubules are lined with a low-columnar epithelium the cells of which have pale-staining cytoplasm and flattened nuclei lying close to the basement membrane (fig. 7D). A small quantity of connective tissue surrounds each tubule and a thick layer of striated muscle occurs between the tubules and the outer connective tissue coat. The tail of the gland is composed of a single large duct that is surrounded by additional glandular tissue along its distal portion.

A pair of glands of sebaceous type observed within the prepuce near the tip of the glans penis in two of four specimens examined histologically are believed to represent preputial glands. These structures could not be demonstrated in gross dissections. The identification as preputials is based on size, position, and structural details. They are distinctly larger and more complex than other sebaceous glands found in the prepuce, and they possess a distinct duct that opens into the space between the prepuce and the tip of the glans in the same manner as do the preputial glands in species that have these glands well developed. The glands lie near the inner fold of the prepuce and are not associated with hair follicles, whereas typical sebaceous glands are more abundant toward the outside of the prepuce and are usually associated with hair follicles.

Peromyscus gossypinus

The only other member of the *leucopus* group (*gossypinus*) is very similar to *leucopus*. Eighty per cent of 55 adult males in breeding condition had some pigment developed on the cremaster. When maximally developed, pigment occurs over about the posterior half of the cremaster and is darkest on the caudal extremity. Adult females may also have pigmented areas lateral to the vulva-anal area in the same relative position as the pigmentation of the cremaster in males.

The tracts of *gossypinus* examined were larger in all dimensions than those of *leucopus*. Although the absolute size differences probably reflect merely the difference in adult body size, there is some suggestion of actual proportional differences between some of the genital organs of the two species (table 2). A few other morphological differences were also noted, some of which might have been the result of variation in sexual condition, age, or effect of preservation rather than actual differences between species. There were seven efferent ducts in one specimen of *gossypinus* compared with six in *leucopus*. The urethral glands in

gossypinus first appear ventral to the vesicular duct rather than dorsal to the duct as in *leucopus*. The secretion of the anterior prostate was more homogeneous in *gossypinus*, and preputials were present in all three specimens examined and were larger and better developed than in *leucopus*, although still not grossly discernible (fig. 8A, B).

Maniculatus GROUP

The tracts of four of the seven species included here were studied. These tracts differ in size and minor features, some of which may be only individual differences. This group and the remaining groups of the subgenus *Peromyscus* do not differ in any fundamental way from the *leucopus* group except for the complete absence of preputial glands (fig. 8C). The urethral glands seem to be somewhat more abundant in the *maniculatus* group as compared with *leucopus*, and, with the possible exception of *melanotis*, the ducts of the ventral prostate glands seem to average fewer.

Peromyscus polionotus

Full breeding adults of *P. polionotus* show reduction of hair on the posterior portion of the cremaster and development of pigmentation as in the *leucopus* group. In keeping with the small body, the tract in *polionotus* is small. With the exception of an unusually short urethra, however, the proportions of the various structures do not differ appreciably from those of the genus as a whole.

The cells of the deferent duct epithelium have pale-staining, oval nuclei which, although tending to be in the middle of the cell, do not form the distinct zone observed in the *leucopus* group. The cilia are relatively short as compared with those of *gossypinus*. Urethral glands first appear anteriorly in the region dorsal to the vesicular duct and in the prostatic urethra are more abundant ventrally than dorsally or laterally, forming a ventral prominence.

The duct of the anterior prostate is very large, being about equal in size to the vesicular duct, and each lobe of the dorsal prostate has five or six ducts. The tubules of the lateral ventral prostate are larger than those of the following species and less infolded than those of the median portion of the gland. There are two or three ducts associated with the medial ventral prostate. The bulbo-urethral glands are relatively larger than those of *maniculatus*. Sebaceous glands associated with hair follicles are abundant in the general area of the prepuce occupied by preputial glands when present.

Peromyscus maniculatus

The cremaster area of several subspecies (*gracilis*, *bairdii*, and *nubiterrae*) available for examination in the flesh may become sparsely haired and posteriorly pigmented in active breeding animals. Six efferent ducts were present in two specimens. The cilia of the deferent duct epithelium are about one-third to one-fourth of the length of the cells, as in *polionotus*. The nuclei are narrowly oval and do not form a well-marked zone. The urethral glands first appear posterior to the entrance of the vesicular duct and are evenly distributed around the wall of the prostatic urethra. Sebaceous glands do not seem to be so abundant in the prepuce as in *polionotus*.

Peromyscus oreas

No differences in gross morphology between *P. oreas* and *maniculatus* were observed in the one tract available for study. Although the specimen had spermatozoa in the cauda epididymis, the tract had a somewhat immature appearance. It is thus possible that differences in morphology would be evident in a more mature individual.

Peromyscus melanotis

The single tract examined was generally similar to that of *maniculatus* in morphology and dimensions. It had four lateral ventral prostate ducts, exceeding the number in all the examined specimens of *polionotus* and *maniculatus*, and two medial ventral prostate ducts. The penile bulb was slightly bifurcate.

Crinitus GROUP*Peromyscus crinitus*

Except for the complete absence of preputial glands, the accessory gland complement of this species is essentially as in the *leucopus* group. The urethra is proportionally short, and the small size of the ventral prostate of the specimens that were examined contrasts with the general condition in the subgenus. The lateral ventral prostate gland of one specimen had three ducts, and the medial had one. The bulb of the penis was slightly bifurcate in two of the specimens, whereas a third showed only the faintest suggestion of this condition.

Boylei GROUP

Tracts of three of the eight species were examined. Except for the

absence of preputials, as determined by gross dissection of each species and histological examination of one, the members of this group do not exhibit any trenchant differences from the *leucopus* group.

Peromyscus boylei

The bulb of the penis was moderately bifurcate in five specimens and slightly so in a sixth. The ampullary glands of the specimens available were of average size; the tubules were clearly visible to the unaided eye. The vesicular glands are more strongly recurved than is typical of *leucopus*, and the medial ventral prostates are distinctly smaller than the lateral pair. The number of ducts ranged from two to four in the lateral pair, but only one was associated with the medial pair.

Peromyscus pectoralis

Three of four specimens exhibited bifurcation of the penile bulb, whereas the fourth showed no evidence of this condition. The ampullary glands are relatively small compared with those of *boylei*, and the tubules are not visible on the surface. The vesicular glands are not so strongly recurved as those of *boylei*, having a relatively longer, straight, proximal segment. All groups of prostate glands, especially the medial ventral pair, are smaller and more diffuse than those in *boylei*. The ducts of the lateral ventral prostates numbered three and four in two of the specimens, whereas there were two medial ducts in each. Although all examined specimens of this species had spermatozoa in the cauda epididymis, the tracts had a somewhat immature appearance. Thus, possibly some or all of the differences in morphology or size noted between *pectoralis* and *boylei* are the result of variation in reproductive state rather than actual specific differences.

Peromyscus oaxacensis

The deferent duct of the single specimen examined histologically differed in certain details from that of *leucopus*. The cilia were relatively short, approximating only about one-fifth of the height of the cell. In addition, the nuclei were much more elongate in shape and situated closer to the base of the cell. The extent to which these features apply to other members of the species group was not determined. The bulb of the penis was not bifurcate in either of our two specimens. The bulbar glands occur in scattered bundles rather than in a relatively continuous mass as in *leucopus* and other species of the subgenus. The ampullary and vesicular glands resemble those of *pectoralis* more than those of

boylei. The epithelial cells of the anterior prostate gland tubules are taller than in *leucopus*. The median lobe of the dorsal prostate has about 10 ducts, and the lateral lobe has seven. Although the typical two pairs of ventral prostates were evident in the one specimen examined grossly, only a medial pair with two ducts could be identified in the sectioned material. Preputial tissue was not observed in sections of the glans penis, although ordinary sebaceous glands were abundant.

Truei GROUP

The genital organs of the representatives of this group were essentially similar to those of *leucopus*. Preputial glands were not evident in gross dissection; the available material did not permit a clear determination of the presence or absence of vestigial preputials.

Peromyscus truei

The deferent duct of this species is relatively long and appears to possess a heavier muscle layer than other members of the subgenus. The ampulla of the specimen studied histologically was unusually capacious, and its wall was strongly folded to produce many large compartments. These compartments were packed with spermatozoa that were regularly arranged with the heads directed toward, and usually in contact with, the lining epithelium. Although sperm were frequently observed in the deferent ducts and ampullae of other species examined histologically, only in *truei* was such a uniform orientation of the sperm with respect to the walls of the ampulla observed. This condition is suggestive of some sort of trophic relationship. The urethra is long, and urethral glands appear to be more numerous in the anterior portion than in other species. Posteriorly, urethral glands first begin to diminish on the dorsal wall of the urethra. Bulbar glands are more numerous in the ventral part of the bulb than in the dorsal or lateral areas. The bulb of all specimens examined was moderately bifurcate. The medial and lateral lobes of the dorsal prostate are compact and have eight and five ducts, respectively. Five or six ducts are associated with the lateral ventral prostate; and one or two, with the medial division. Although a short piece of the tip of the penis was missing in the specimen sectioned, no trace of preputial glands was observed in the remaining portion.

Peromyscus difficilis

Compared with the preceding species, the deferent duct is proportionally quite short, the bulb is not bifurcate, and the dorsal and ventral

prostate glands are more diffuse.

Mexicanus GROUP

Specimens of about one-half of the species of the largest species group of the subgenus *Peromyscus* were available. Although the morphology of the genital tract of all species is fundamentally similar to that of other representatives of the subgenus, a greater degree of intraspecific and interspecific variation in genital structure than is the case in other species groups is exhibited. This variability concerns chiefly the number and position of the ventral prostate glands and the shape of the bulb of the penis. The dorsal prostate in all species examined is bilobed, as in *leucopus* and other groups, but the lateral lobe is extremely diffuse and divided into more or less separate lobes. The bulbo-urethral glands are relatively large in all species. No grossly discernible preputial glands were present in any species, and no trace of these structures was evident in the histological material of one species.

Peromyscus mexicanus

Bifurcation of the bulb of the penis was pronounced in one, slight in one, and absent from two of the four specimens examined. Three specimens had a single pair of ventral prostates, whereas one had both medial and lateral pairs, as is the case in other members of the subgenus. In the first instance, the position of the glands and arrangement of the ducts suggested that they represented the lateral pair. The number of lateral ducts averaged 2.3, and three ducts were associated with the medial ventral prostates in the one individual with this set of glands.

Peromyscus nudipes

Four of five specimens exhibited a slight to moderately bifurcate penile bulb, whereas the fifth showed no trace of bifurcation. All specimens possessed two pairs of ventral prostates, although in one case the point of attachment of the medial pair was shifted laterally as compared with the usual condition.

Peromyscus furvus

Both specimens studied had a relatively well-marked bifurcation of the bulb and both pairs of ventral prostates in the typical position. In the one specimen in which the ducts could be counted, there were six

associated with the lateral ventral prostate and three with the medial.

Peromyscus guatemalensis

The bulb was not bifurcate in either of two specimens available. Both pairs of ventral prostates are present, and both join the urethra ventrolaterally. Each member of the medial and lateral pairs has three and four ducts, respectively.

Peromyscus megalops

Urethral glands in this species do not appear to be so numerous as in *leucopus* and tend to be concentrated laterally and ventrally in the urethra. The glands first appear posterior to the point where the ducts of the anterior accessory glands enter the urethra. The bulb of the one specimen studied histologically possessed a thick layer of bulbar glands and was different in shape from all other examined specimens of *Peromyscus*. It was deeply cleft in the center, and each side was in turn shallowly bifurcate. The lateral lobe of the dorsal prostate is proportionally large and overlies the base of the anterior prostate to a considerable extent. It has about five ducts, and the medial segment has 10. Both pairs of ventral prostates are developed, and each had four ducts in the specimen examined. The ducts of the lateral pair come to lie dorsal to those of the medial pair, entering the urethra anterior instead of lateral to them as in other species. No trace of preputials was noted in sections of the prepuce and glans penis.

Peromyscus zarhynchus

The bulb of the penis was moderately invaginated in the specimen examined. Two pairs of ventral prostates were present and joined the urethra in the typical manner. The lateral pair had two ducts on a side, and the medial pair had three.

Peromyscus grandis

The bulb of the single specimen available was not bifurcate. Both pairs of ventral prostates were developed, and three and four ducts, respectively, were associated with each member of the lateral and medial pairs.

SUBGENUS *HAPLOMYLOMYS*

Figure 1

The genital tracts of three species in this subgenus that were examined

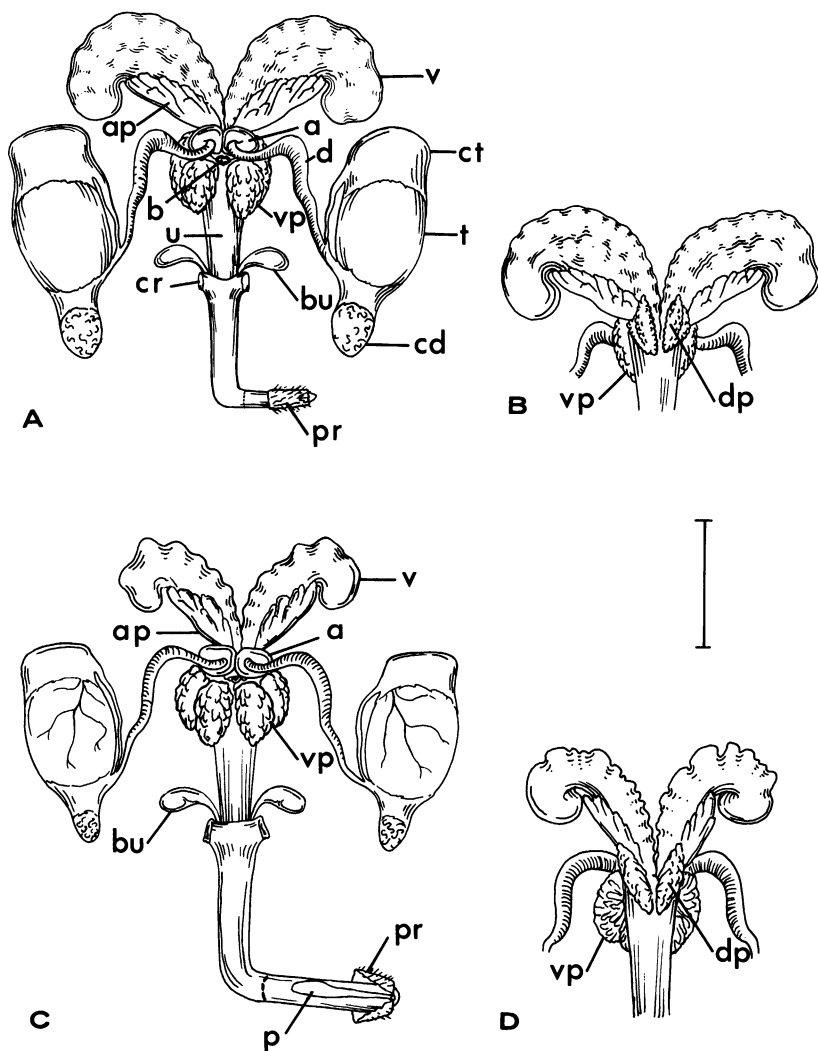


FIG. 1. Male genital tracts of *Peromyscus*. A, B. *P. (Peromyscus) leucopus*. A. Ventral view. B. Dorsal view. C, D. *P. (Haplomylomys) interparietalis*. C. Ventral view. D. Dorsal view. Scale equals 1 cm.

Abbreviations: a, ampullary gland; ap, anterior prostate gland; b, bulb of penis; bu, bulbo-urethral gland; cd, cauda epididymis; cr, crus penis; ct, caput epididymis; d, deferent duct; dp, dorsal prostate gland; p, preputial gland; pr, prepuce; t, testis; u, urethra; v, vesicular gland; vp, ventral prostate gland.

possess the same complement of accessory glands as does the subgenus *Peromyscus* and have, in addition, a single pair of well-developed preputial glands.

Peromyscus eremicus

The testes of the available specimens were proportionally small. Five efferent tubules were present in one individual. The deferent ducts are of average length for the genus and are essentially similar to those of *leucopus* in gross structure and histology. Urethral glands first appear posterior to the region of the colliculus and, although present throughout the urethra proximal to the bulb, seem to be less abundant than in the subgenus *Peromyscus*. In addition, the ducts of the ventrally situated urethral glands in the anterior region of the urethra appear to be larger than those in the previous subgenus. The bulb of the penis was strongly bifurcate in three of five specimens, but showed no evidence of invagination as in other cases. Bulbar glands are present and appear not to differ in abundance or distribution from those of *leucopus*.

The tubules of the ampullary glands are easily visible to the unaided eye, and their epithelial lining is unfolded. The vesicular glands resemble those of the subgenus *Peromyscus* in gross morphology and general histological features. The epithelium lining the lumen is moderately infolded. The anterior prostates also are similar to those of the subgenus *Peromyscus*. The dorsal prostates are partially divided into a lateral and medial lobe. The lateral lobe tends to be more diffuse than the medial element. A tuft of dorsal prostate tissue extended between the bases of the vesiculars in four of six specimens that were examined. In fixed and stained material, the secretion of the medial lobe appears to be almost entirely granular, whereas that of the lateral lobe is more homogeneous, with only scattered granules. The individual tubules of both lobes are lined with cuboidal epithelium, that of the lateral lobe being less folded than that of the medial. Each lateral lobe has about six ducts as compared with about five for the medial lobe.

The medial pair of ventral prostates tends to be smaller than the lateral pair. The epithelial lining of the tubules of both pairs of glands is moderately infolded. The cells are columnar in both cases, but those of the medial pair tend to be taller. The mean numbers of median and lateral ventral prostate ducts in six specimens were 1.3 (from one to two) and 3.3 (from three to four), respectively.

The bulbo-urethral glands are similar in shape and structure to those of *leucopus*, although the duct appears to be convoluted in *Haplomylomys*.

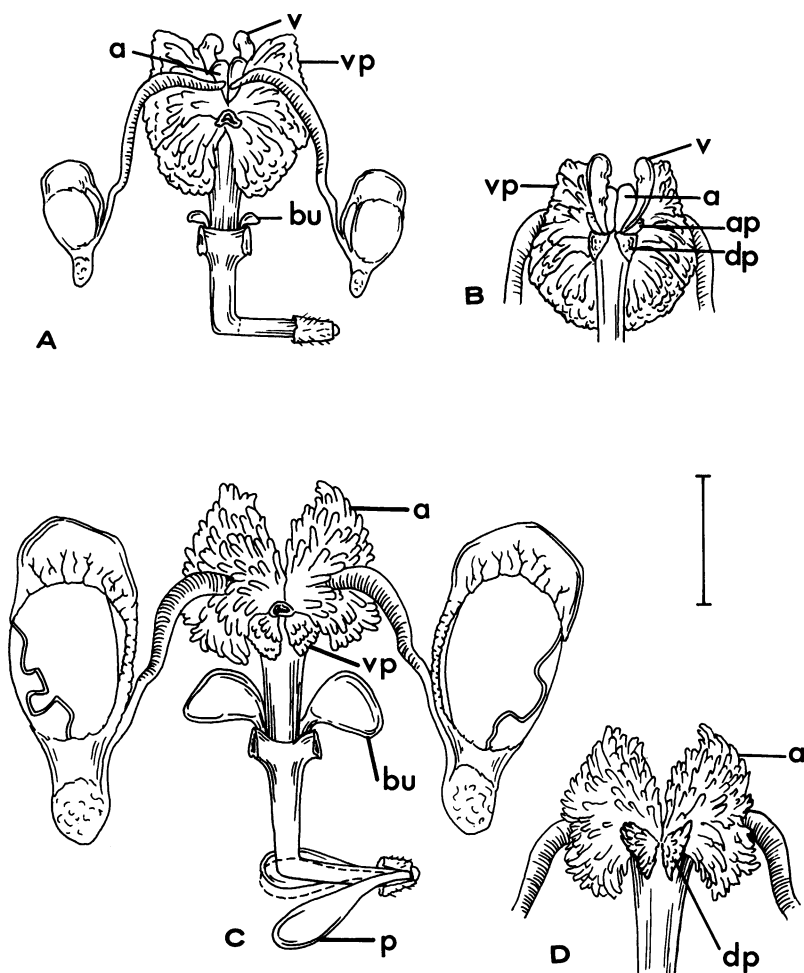


FIG. 2. Male genital tracts of *Peromyscus*. A, B. *P. (Hobomys) lepturus*. A. Ventral view. B. Dorsal view. C, D. *P. (Osgoodomys) banderanus*. C. Ventral view. D. Dorsal view. Scale equals 1 cm.

Abbreviations: a, ampullary gland; ap, anterior prostate gland; bu, bulbo-urethral gland; dp, dorsal prostate; p, preputial gland; v, vesicular gland; vp, ventral prostate gland.

The preputial glands lie laterad of the penis between the folds of the prepuce (fig. 8D). The glands are elongate, narrow, and taper gradually at the base. They discharge by a single duct that opens into the space between the glans surface and inner fold of the prepuce. Each gland is

composed of many individual groups of cells separated by connective tissue. Each cluster tends to have distinct, large, round cells at the periphery and less distinct cells internally that are degenerating in the process of formation of secretion. The nuclei are round and centrally situated. The mean length and width of the preputials of five specimens were 5.8 and 1.4 mm., respectively. Ordinary sebaceous glands in association with hair follicles are also abundant in the skin of the prepuce.

Peromyscus interparietalis

Figure 1

The tract of this species agrees closely with that of the foregoing. The bulb of the penis of the specimens examined, however, was not bifurcate, and the vesicular glands were less strongly recurved. The median tuft of the dorsal prostates extending forward between the vesiculars observed in *eremicus* was not noted in this species, and the two pairs of ventral prostates were about equal in size. The lateral ventral prostates appeared to have three ducts each in the one specimen examined; the number associated with the medial pair could not be determined. The preputials of three specimens had an average length and width of 7.1 and 1.8 mm., respectively.

Peromyscus californicus

The tract of this species agrees generally with that of the other species in the proportional size of the various genital organs, with the exception of a relatively short deferent duct. As in *interparietalis*, the bulb of the penis was not bifurcate. The vesiculars are also less recurved than in *eremicus*, although a tuft of dorsal prostate tissue extends forward between their bases as in the latter species. The two pairs of ventral prostates are of approximately equal size. Each medial member had two ducts, and each lateral, four. The preputial glands of one specimen were 10.0 mm. long and 2.0 mm. wide.

SUBGENUS *HABROMYS*

Figure 2

Only one of the three species assigned to this taxon by Hooper and Musser (1964) was available for study. Although all the accessory glands found in this group can be homologized with those of the subgenera *Peromyscus* and *Haplomylomys*, there are striking differences in both gross and microscopic anatomy.

Peromyscus lepturus

Figure 2

When the large body size of this species is considered, all four of the tracts available seem unusually small, even in the case of specimens with abundant sperm in the cauda epididymis. It is possible that none of the specimens was in full reproductive condition. We are convinced, however, that the differences observed in the tract of this species are far too pronounced to be attributable to this factor alone.

The deferent ducts of two specimens examined in cross section are unlike those of *leucopus* in having a less infolded epithelial lining. The cells are not so tall as in *leucopus*, and the cilia are shorter. The nuclei also tend to be rounder and are not situated at so uniform a level in the cell. The walls of the ampulla are extensively folded, and some of the epithelial cells in this part of the tract appear to bear cilia, unlike the usual condition in the species previously described.

Urethral glands are less abundant than in *leucopus* and are aggregated in a small number (four or five) of relatively discrete masses, one of which is situated in the ventral wall of the urethra, whereas the remainder are situated on the dorsal aspect. The bulb of the penis is distinctly bifurcate, and, as in the case of the urethral glands, the bulbar glands occur in scattered aggregations.

The ampullary glands are about the same size as those of *leucopus* but are somewhat different in shape, being dorsoventrally flattened. The tubules are large, and the lumina are spacious (fig. 9A). The slightly folded epithelium of the tubules is cuboidal, with round nuclei. Some of the epithelial cells of the ampullary gland tubules seem to possess cilia.

The vesicular glands are extremely atypical. They are tiny, simple, saclike structures with connective and muscle tissue layers that are only as thick as the glandular epithelium (fig. 9A). The secretion seen in sections of the vesicular glands resembled that of the ampullary glands.

In correlation with the poorly developed vesicular glands, the anterior prostates are very small. The cuboidal epithelium of the tubules is only slightly infolded in contrast to the condition in *leucopus*, and there was no evidence of secretion in the serial sections examined.

A pair of small dorsal prostates is present. Each gland has two or three ducts that extend between the bases of the vesiculars to enter the urethra anteriorly. The tubules of the dorsal prostates are lined with cuboidal epithelium, and the secretion has a granular appearance in sections.

The most conspicuous of the accessory glands are the ventral prostates. In some specimens only a single pair, believed to represent the lateral pair of other species, could be demonstrated. Each gland possessed about seven ducts. In other tracts tiny tufts of tissue that appeared to be separate from the main pair of ventral prostates are believed to represent the medial pair. In one specimen examined histologically, the medial prostatic tissue was closely associated with the main glands but possessed a separate duct that entered the urethra independently of those of the former. Both lateral and medial ventral prostate glands are similar histologically (fig. 9B). The epithelium of the tubules is tall columnar, with pale-staining cytoplasm and nuclei lying close to the basement membrane.

The bulbo-urethral glands are unusually small but typical in structure. There is no gross or microscopic evidence of preputial glands, although typical sebaceous glands are fairly abundant on the outer surface of the prepuce.

SUBGENUS *OSGOODOMYS*

Figure 2

The sole representative of this subgenus is strikingly divergent from all other species of *Peromyscus* in genital structure.

Peromyscus banderanus

The testes are proportionally large. Two specimens examined possessed seven and eight efferent ducts. The deferent ducts are relatively long.

The most conspicuous of the accessory glands are extensive masses of elongate tubules surrounding the bases of the deferent ducts in the same anatomical relationship as the ampullary glands of other species. Although these glands more closely resemble prostates, with their long, slender tubules, than the more compact ampullaries of other species of *Peromyscus*, we provisionally regard them as ampullaries on the basis of position and arrangement of ducts. The latter are numerous and, upon careful dissection, are seen to enter the ampulla in the same manner as typical ampullary ducts. Although the material available for histological study was poorly fixed and unsuited for detailed examination, the epithelial cells lining the tubules of these glands are tall columnar, in contrast to the cuboidal type found in the ampullaries of *leucopus*. The epithelium is moderately infolded. Spermatozoa were visible in the lumina of sectioned ampullary gland tubules.

Vesicular and anterior prostate glands were not grossly evident, and

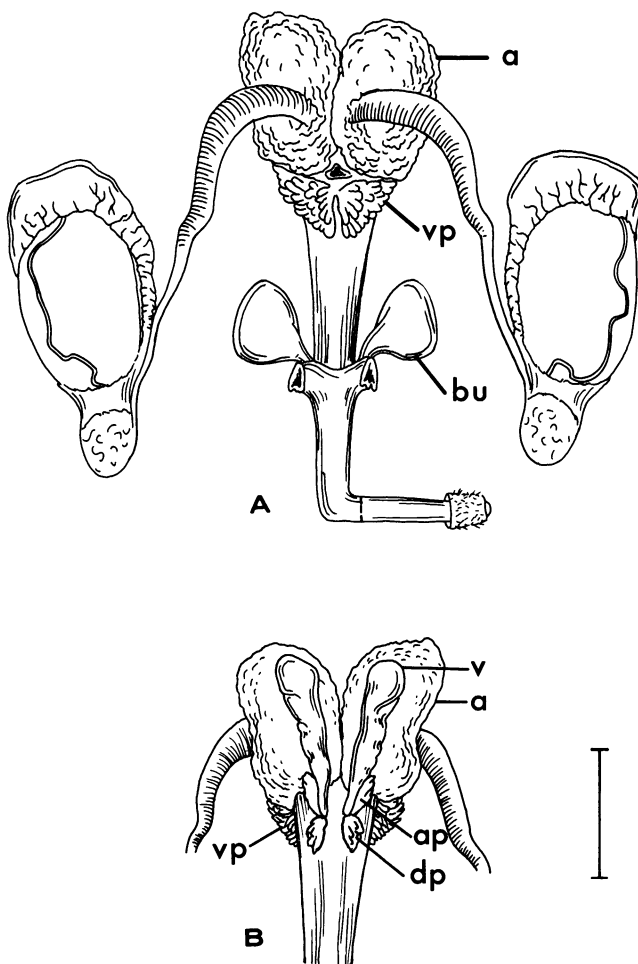


FIG. 3. Male genital tract of *P. (Podomys) floridanus*. A. Ventral view. B. Dorsal view. Scale equals 1 cm.

Abbreviations: a, ampullary gland; ap, anterior prostate gland; bu, bulbo-urethral gland; dp, dorsal prostate; v, vesicular gland; vp, ventral prostate gland.

no traces of these glands were observed in histological preparations. Dorsal prostates could be seen in only two of the five specimens examined and were extremely small and not bilobed as is typical in other species.

The ventral prostates appear to be represented by a single pair only, although in one specimen each gland was divisible into two lobes. The

bulbo-urethral glands are relatively large but exhibit no essential difference in structure from those of other subgenera.

Peromyscus banderanus possesses well-developed preputial glands, which are considerably larger than those of members of the subgenus *Haplomylomys*. The body of the gland extends well beyond the flexure of the penis, and its medial aspect is concave to accommodate the penile shaft. The body tapers smoothly into the duct, which opens in the typical position. The mean length and width of the preputials of five specimens were 15.6 and 2.8 mm., respectively.

SUBGENUS *PODOMYS*

Figure 3

The tract of the sole representative of this subgenus also departs to a significant degree from the pattern of the subgenera *Peromyscus* and *Haplomylomys*.

Peromyscus floridanus

The cremaster of full breeding adults becomes partially hairless in the posterior region as in other species of *Peromyscus* but does not develop such intense pigmentation as seen in the *leucopus* or *maniculatus* groups. The maximum extent of pigmentation observed consisted of small, irregular, scattered blotches. Only 41 per cent of 119 breeding males examined exhibited any trace of pigment, and only 2 per cent showed maximum development as described above.

Seven efferent ducts were present in one specimen examined. The deferent ducts are relatively long and differ in structure from those of all other species of *Peromyscus* included in this study. The distal portion is rather narrow as in other species, but instead of increasing its diameter gradually as it approaches the urethra, it does so rather abruptly, producing a distinctly expanded proximal segment. In one specimen, the narrow distal segment was 9 mm. long, with a maximum diameter of 0.5 mm., whereas the proximal segment was 15 mm. long and 2.3 mm. in diameter. The lumen of the proximal segment is extensively partitioned by deep infoldings of the walls (fig. 9C, D). The compartments are lined with columnar epithelium, although the cells are not so tall as in *leucopus*. The oval nuclei are large and tend to be situated in the basal half of the cells, although their position is not constant enough to form a distinct zone as in *leucopus*. The epithelium in this region of the deferent duct appears to be less extensively ciliated than that in *leucopus* and other species with typical deferent ducts. The cilia

are relatively long, approximating one-third of the length of the cell.

The complex partitioning of the lumen of the proximal segment becomes less as the duct narrows to enter the ampulla. The ampulla is much expanded and also highly compartmentalized. Its outer wall is relatively thin owing to the reduction of the muscle layer. No cilia were noted in the ampulla region. The nature of the proximal portion of the deferent duct of *floridanus* appears to be closely similar to that described for several other unrelated genera of mammals (Kowalska-Dyrz, 1966) and may represent an adaptation for sperm storage.

The urethral glands are similar to those of *leucopus*. They first appear dorsal to the ducts of the vesicular gland and are confined to the dorsal wall of the anterior portion of the prostatic urethra. Distally they become more evenly distributed, but sparser. The bulb of the penis was distinctly bifurcate in all specimens examined. Bulbar glands are present (fig. 10A).

The ampullary glands are the most conspicuous of the accessory glands of breeding individuals. Externally the glands have a relatively smooth contour, although the limits of individual tubules are discernible to the naked eye. The tubules are lined with a moderately folded columnar epithelium. In two of four breeding specimens, the tubules of the ampullary glands contained large quantities of sperm (fig. 10B). This condition, although possibly an artifact of preservation, was not seen in other species; in some cases a few isolated spermatozoa were occasionally observed in the ampullary gland tubules.

The vesicular glands are extremely reduced as in *lepturus*. They are tiny and saclike and appear to contain no secretion even in full breeding adults. Some indication of the small size of these glands in *floridanus* is given by volumetric comparison with those of *gossypinus*, a species with vesiculars of normal proportions. The volume of the vesiculars of an adult *floridanus*, as determined by water displacement, was 0.015 ml. as compared with 0.600 ml. for *gossypinus*. The lumen of the gland in *floridanus* is lined with a highly infolded cuboidal epithelium (fig. 6C).

In correlation with the rudimentary vesiculars, the anterior prostates are poorly developed, consisting of only one or two tubules. The tubules are lined with a cuboidal epithelium that is not folded, and there was no evidence of secretory activity in the sections of these glands.

The dorsal prostates are also small. In gross dissection, only a medial lobe is evident, although traces of lateral lobes appear in section. The latter consist mainly of five ducts with little or no associated glandular tissue. The tubules of the medial lobes are lined with a cuboidal epithelium, which showed no sign of secretory activity in the histological

material available. Each medial lobe possesses four ducts.

Two pairs of ventral prostates are clearly distinguishable histologically but are not so evident in gross dissection. The lateral pair is closely bound to the medial one and is considerably smaller. The tubules of the lateral glands are lined with a very slightly infolded cuboidal epithelium, whereas the epithelium of the medial pair is columnar and moderately infolded. The medial ventral prostates have two to four ducts each; the lateral ones, about six.

The bulbo-urethral glands are similar to those of other members of the genus and are proportionally large as compared with *leucopus*. There is no evidence of preputial glands.

SUBGENUS *ISTHMOMYS*

Figure 4

Both species included in this subgenus, established by Hooper and Musser (1964), were studied. Although generally similar to the *leucopus* group in over-all genital morphology, the tracts are easily distinguishable.

Peromyscus flavidus

Figure 4

The entire tract is quite large in actual measurements, but the majority of the structures are not proportionally larger than those of other members of the genus. One specimen possessed eight efferent ducts. The wall of the urethra is relatively thick as a result of a heavy muscle layer. The bulb of the penis of the single specimen examined was bifurcate. The ampullary glands are fairly large and conspicuous, the individual tubules being so prominent that they produce a very irregular surface. The tubules are oriented more or less parallel to one another as in *banderanus* rather than being tightly coiled as in *leucopus*.

The vesicular glands of mature individuals are oddly shaped compared with those in the subgenera *Peromyscus* and *Haplomylomys*. They are not recurved, and the anterior edge bears a fringe of tubules up to 7 mm. long. Some of the tubules are secondarily branched. In less-developed tracts, the vesiculars are more recurved and more like those of *leucopus* in appearance, although still more strongly lobulated.

The anterior prostates tend to be fan-shaped instead of elongate and filamentous as in *leucopus*. The dorsal prostates are lobed as in other species. The ventral prostates are proportionally small, and all specimens examined appeared to have only a single pair. In some specimens, however, each gland was partially divisible into several lobes. As the

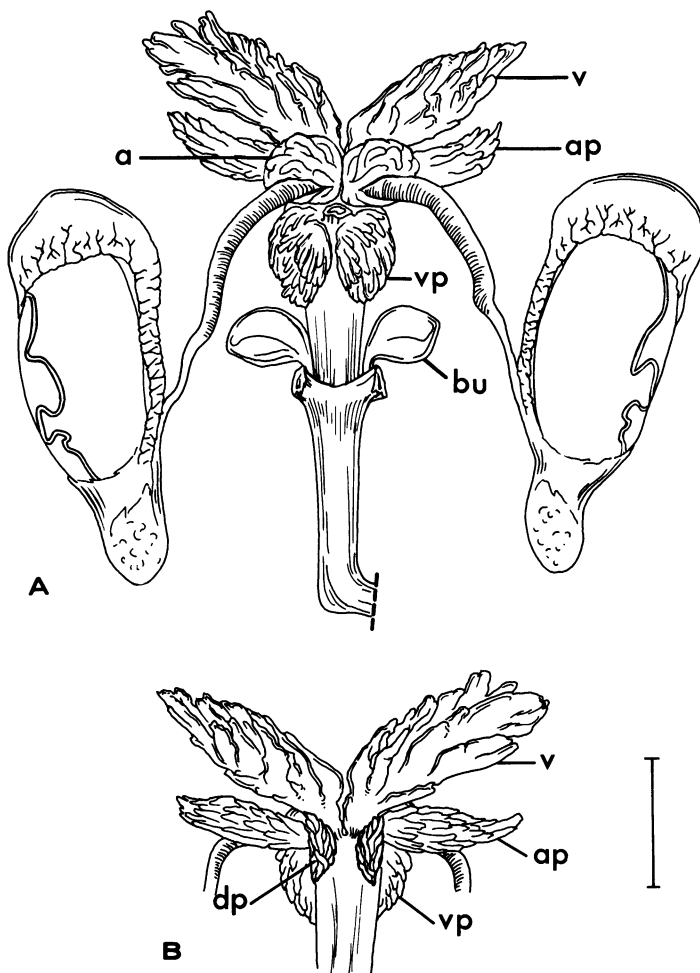


FIG. 4. Male genital tract of *P. (Isthmomys) flavidus*. A. Ventral view. B. Dorsal view. Scale equals 1 cm.

Abbreviations: a, ampullary gland; ap, anterior prostate gland; bu, bulbo-urethral gland; dp, dorsal prostate; v, vesicular gland; vp, ventral prostate gland.

ventral prostate glands join the urethra on its ventral aspect just posterior to the bladder stalk, they may represent the medial elements of the two pairs of other species.

The bulbo-urethral glands are typical, and there is no evidence of preputial glands.

Peromyscus pirrensis

The tract of this species averages larger in absolute size than the preceding, and the majority of structures are relatively larger as well. The urethral wall is thick, as in *flavidus*, but the bulb showed no evidence of bifurcation in any of the specimens examined. In other respects, the tract closely resembles that of *flavidus*.

SUBGENUS *MEGADONTOMYS*

Figure 5

Peromyscus thomasi

The most impressive feature of the genital tract of this species is its large over-all size. In addition, most of the individual elements are proportionally large. In general morphology, the tract of this species bears a fundamental resemblance to that of *leucopus*, although there are some trenchant differences.

Eleven efferent ducts were counted in one specimen. The deferent ducts, although exceptionally long, are similar in shape to those of *leucopus*. They appear to differ, however, in certain histological details from those of species in other subgenera. The epithelial lining of the duct in one specimen studied histologically was more prominently folded than in any other species except *floridanus*, although it did not approach the latter in complexity (fig. 10D). There was also a much broader zone of loose connective tissue between the epithelium and muscle layer than in other forms. The ampulla is relatively large and extensively compartmentalized.

The long and relatively thin-walled urethra contains typical urethral glands, which are numerous in the prostatic and anterior portions of the membranous urethra, but become sparser posteriorly. The bulb of the penis is not bifurcate. Bulbar glands are fairly abundant, but do not form aggregations as dense as in the *leucopus* group.

The ampullary glands are comparatively large. The tubules have a relatively small diameter and thick walls compared with the *leucopus* group. The cells of the moderately infolded epithelium of the tubules range from low to tall columnar, and in fixed and stained sections the secretion has a granular appearance.

The vesicular glands resemble those of the subgenera *Peromyscus* and *Haplomylomys*. The columnar epithelium lining the lumen is highly infolded. The anterior prostate glands are not especially enlarged and in other respects are generally like those of *leucopus*. The tubules are lined with tall-columnar epithelium, and the secretion has a granular ap-

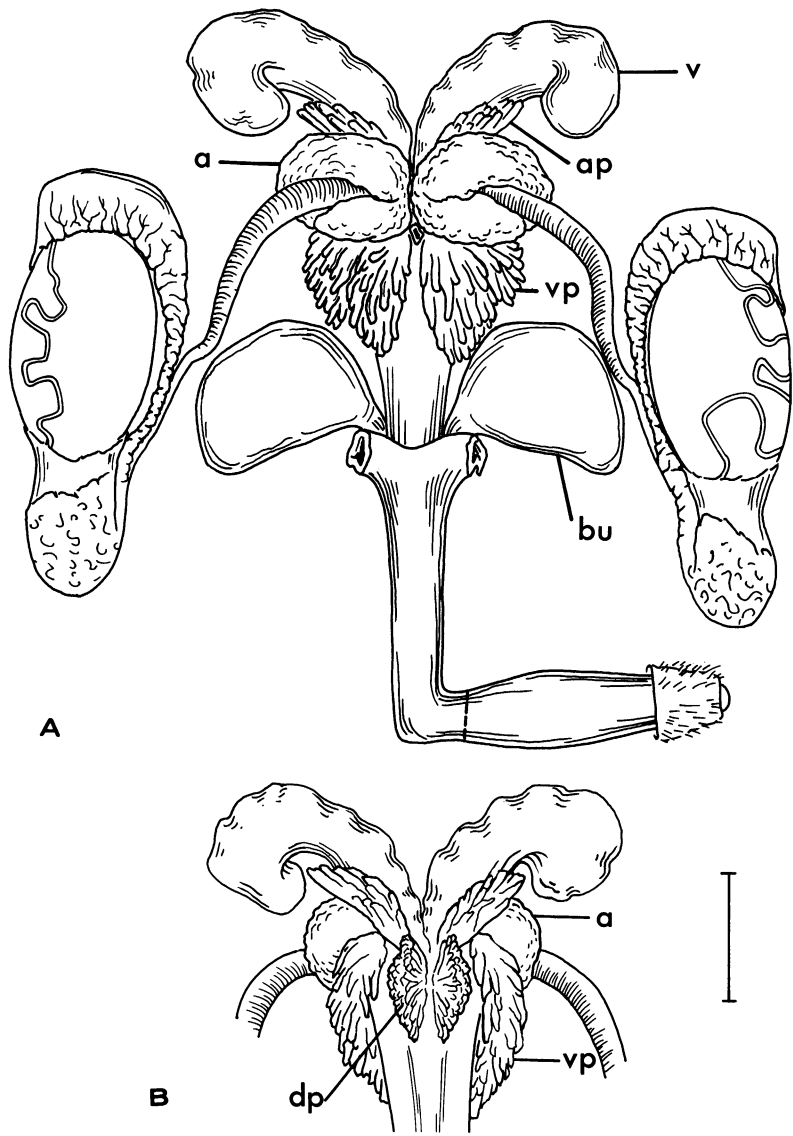


FIG. 5. Male genital tract of *P. (Megadontomys) thomasi*. A. Ventral view. B. Dorsal view. Scale equals 1 cm.
Abbreviations: a, ampullary gland; ap, anterior prostate gland; bu, bulbo-urethral gland; v, vesicular gland; vp, ventral prostate gland.

pearance. The dorsal prostates are bilobed, each lobe being rather diffuse. The medial and lateral lobes have about eight and four ducts, respectively. The epithelium of the tubules is tall columnar and slightly infolded.

Ventral prostates appear to be represented by two or three pairs of glands, which differ histologically as well as in position. The innermost pair has one duct on each side that enters the urethra on the ventral side below the neck of the bladder. The tubules are lined with a tall-columnar epithelium that is moderately infolded. The outer pair has three ducts on a side which enter the lateral wall of the urethra. The epithelium lining these tubules is cuboidal to low columnar and only slightly infolded. In those specimens with three pairs of ventral prostates (two of three tracts examined), the third pair was situated between the last described above and the dorsal prostates. They were drained by three ducts on a side, and the epithelium of the tubules was tall columnar.

The bulbo-urethral glands of *thomasi* are similar in shape and histology to those of the *Leucopus* group but are proportionally much more robust. The ducts lie adjacent to one another on the ventral surface of the bulb, whereas in *leucopus* they are rather well separated. There was no trace of preputial glands in gross dissections or sectioned material. Typical sebaceous glands are present on the outer aspect of the prepuce but do not seem so numerous as in *leucopus* and some other species.

DISCUSSION

Based on differences in the accessory gland complement (table 3) and other features of the male genital tract exclusive of the phallus, the species included in this study segregate into seven major groups that correspond to the subgenera of Hooper and Musser (1964). Our data thus support those departures from Osgood's (1909) classification proposed by Hooper and Musser primarily on the basis of phallic characteristics, namely, the removal of *P. banderanus* and *P. lepturus* from the subgenus *Peromyscus*; the separation of *P. flavidus* and *P. pirrensis* from the group containing *P. thomasi*; and the allocation of *P. crinitus* to the subgenus *Peromyscus* rather than *Haplomylomys*. We did not examine either *P. lophurus* or *simulatus*, the other representatives of Hooper and Musser's subgenus *Habromys*, but anticipate that they will be found to agree with *lepturus* in their genital anatomy.

Although phallic structure and the morphology of the remainder of the tract reveal a similar pattern of species grouping within the genus *Peromyscus*, the distinctiveness of some of the groups varies with the

TABLE 3
STATUS OF THE COMPLEMENTS OF ACCESSORY GLANDS IN *Peromyscus*

Subgenus	Ampullary	Vesicular	Anterior Prostate	Dorsal Prostate	Ventral Prostate	Bulbo-urethral	Preputial
<i>Peromyscus</i>	^a	+	+	+	+	+	—/0
<i>Haplomylomys</i>	+	+	+	+	+	+	+
<i>Habronomys</i>	+	—	—	—	+	+	0
<i>Osgoodomys</i>	++ (?)	0	0 (?)	—	+	+	+
<i>Podomys</i>	+	—	—	—	+	+	0
<i>Isthmimys</i>	+	+	+	+	+	+	0 (?)
<i>Megadontomys</i>	+	+	+	+	+	+	0

^a Symbols: 0, absent; +, present and of normal proportions; ++, present and larger than normal; —, present but smaller than normal.

particular component of the reproductive system utilized. In phallic structure, *Podomys*, *Habromys*, and *Osgoodomys* have certain characteristics in common, whereas in the remainder of its genital features *Osgoodomys* is far removed from the other two groups. Similarly, the differences between *Podomys* and *Habromys* in accessory glands, structure of the deferent duct, and other aspects of the proximal genitalia are suggestive of greater divergence than is indicated by the glans penis alone. In contrast, *Megadontomys* seems to be more distinct from the subgenus *Peromyscus* in phallic structure than in the remainder of its tract. Our over-all impression is that major groups of species within *Peromyscus* are more sharply differentiated by the structure of the more proximal regions of the reproductive tract than by the phallus.

With regard to the species groups of the subgenus *Peromyscus*, the only group clearly set off by genital structure is the *leucopus* group with its vestigial preputial glands. There is some suggestion from the limited material available of species group differences in absolute size or relative proportions of certain glands or other structures, minor morphological differences, such as the shape of the bulb of the penis, or numbers of prostate ducts. For example, the *truei* group appears to have a relatively high number of lateral ventral prostate ducts, whereas the *mexicanus* group, although variable, tends to have a large number of medial ventral prostate ducts. The *boylei* group seems to be characterized by relatively small anterior and ventral prostates and short deferent ducts. From genital features, the *leucopus* group would seem to be the most primitive by virtue of its retention of remnants of preputials. The *mexicanus* group is most variable and may prove to be a more heterogeneous assemblage than other species groups of *Peromyscus*. In terms of total numbers of ventral prostate ducts, the *boylei*, *crinitus*, and *maniculatus* groups are more similar to one another than to the *truei* and *mexicanus* groups. We agree with Hooper's (1958) conclusion from observations on the phallus that *crinitus* is intermediate between the *maniculatus* and *boylei* groups.

Our observations also indicate the occurrence of significant differences in genital structure between species within a given species group or subgenus, and we suspect that differences at the subspecific level could be demonstrated with adequate material. In general, however, examination of larger series of specimens with greater attention to more subtle quantitative and qualitative differences in reproductive structures would be necessary to substantiate these impressions fully.

Aside from any possible taxonomic significance, trends in the development of the accessory glands within the genus are intrinsically interesting. The tendency toward greater variability in the complement of

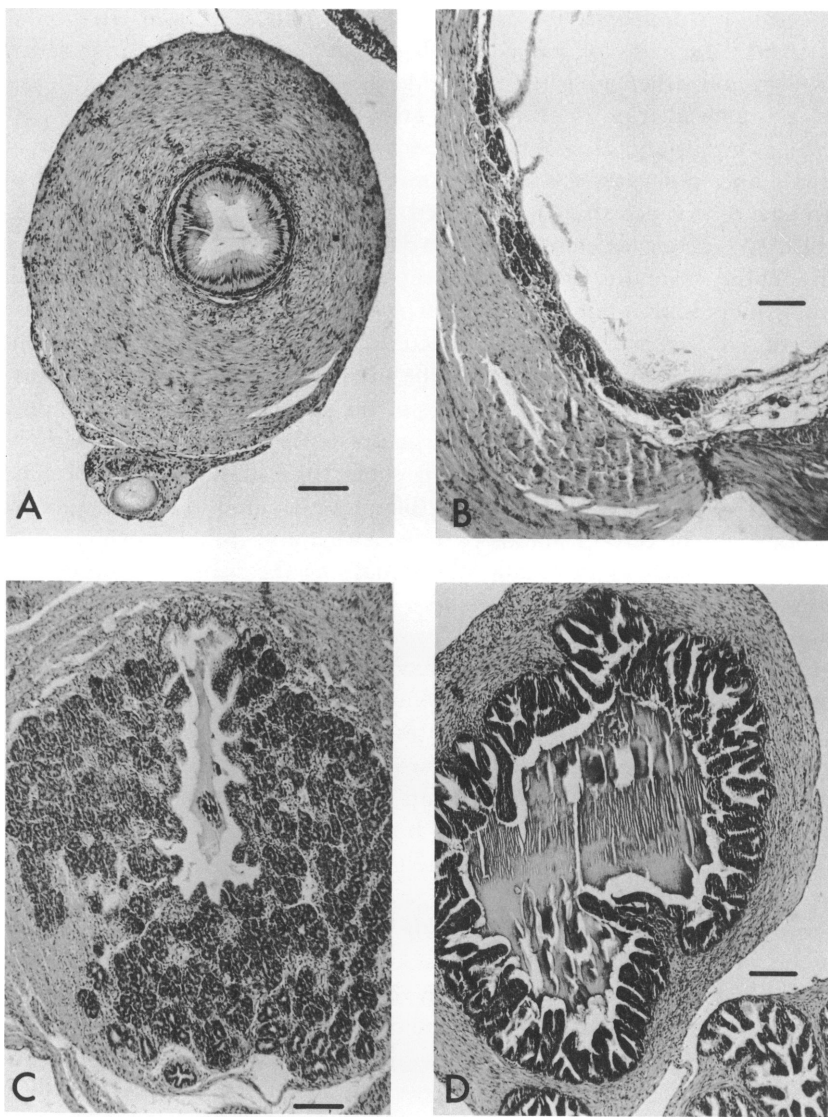


FIG. 6. *Peromyscus (Peromyscus) leucopus*. A. Deferent duct. B. Urethra, showing urethral glands. C. Bulb of penis, showing bulbar glands. D. Vesicular gland. Scale equals 0.1 mm.

accessory glands in association with the simple type of penis noted for murid rodents as a whole (Arata, 1964; Hershkovitz, 1966) is exempli-

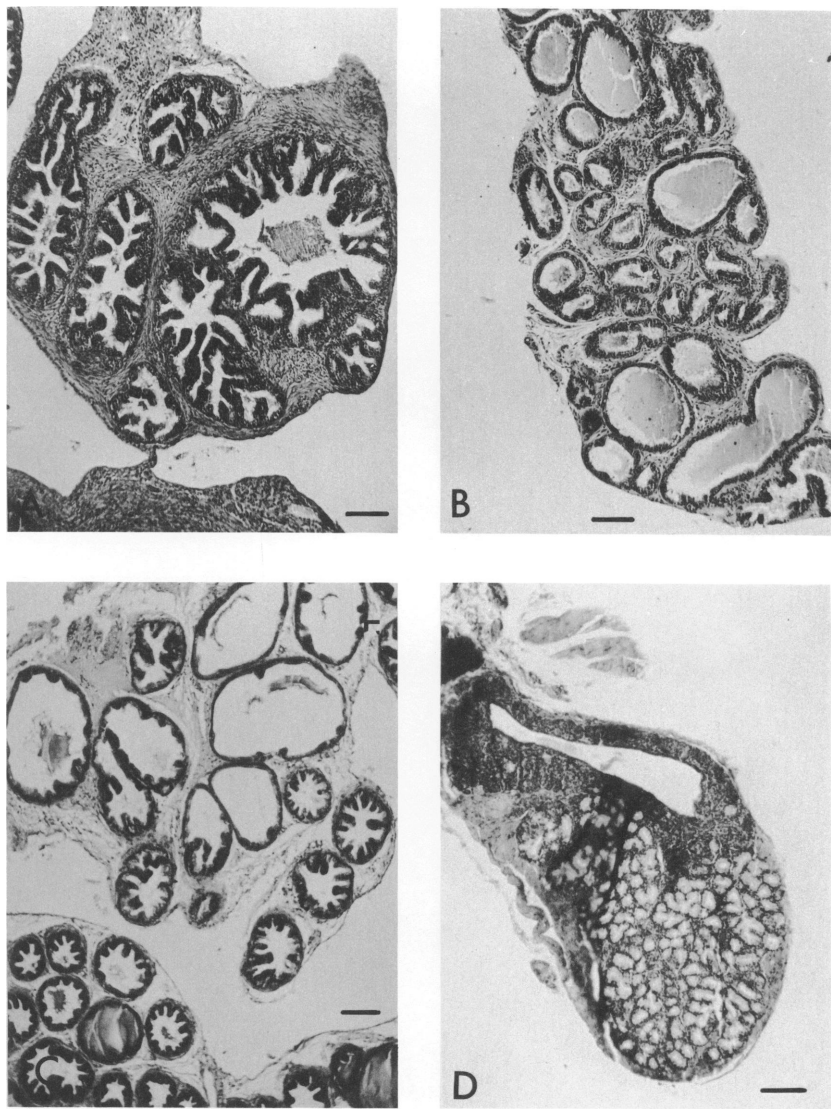


FIG. 7. *Peromyscus* (*Peromyscus*) *leucopus*. A. Anterior prostate gland. B. Dorsal prostate gland. C. Ventral prostate gland, showing portions of lateral and medial elements. D. Bulbo-urethral gland. Scale equals 0.1 mm.

fied by *Peromyscus*. The bulbo-urethral, ampullary, and ventral prostate glands are the most stable components of the tract. Of these, the bulbo-

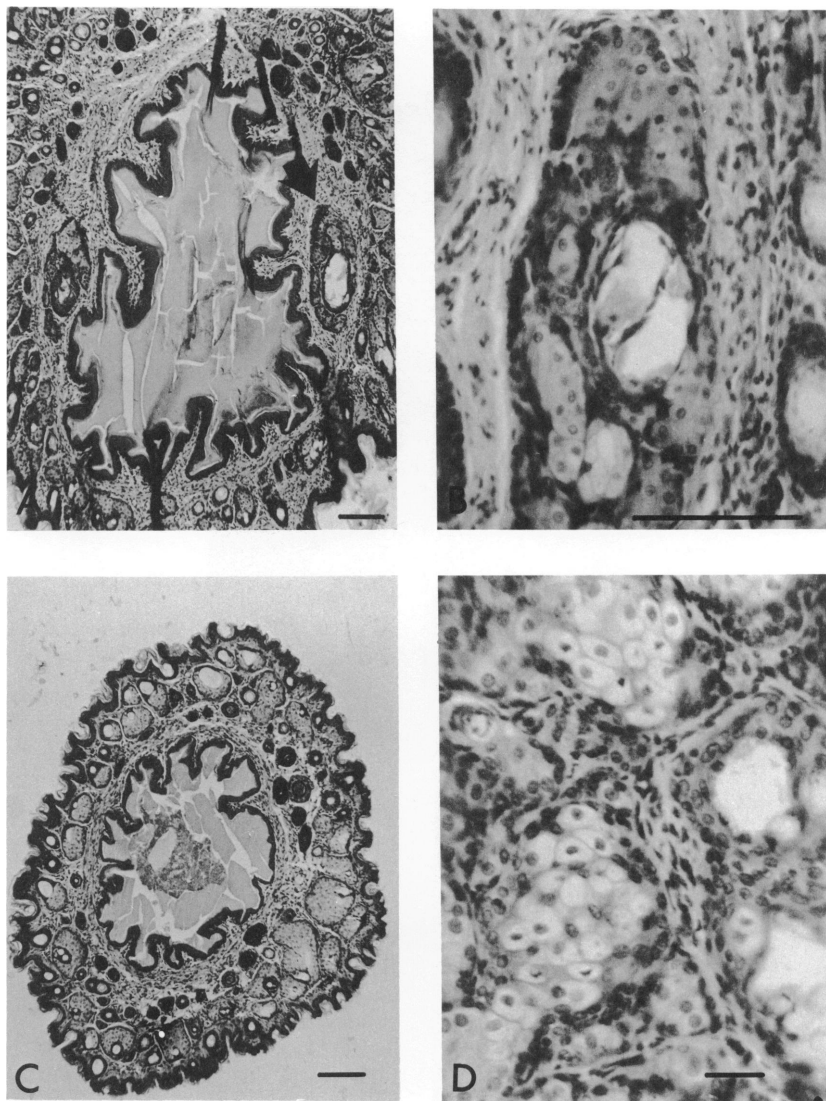


FIG. 8. A, B. *Peromyscus gossypinus*. A. Glans penis, showing vestigial preputials (arrow). B. Detail of preputial gland. C. *Peromyscus polionotus*. Glans penis, showing absence of preputials but abundance of typical sebaceous glands associated with hair follicles. D. *Peromyscus eremicus*. Detail of preputial tissue. Scale equals 0.1 mm.

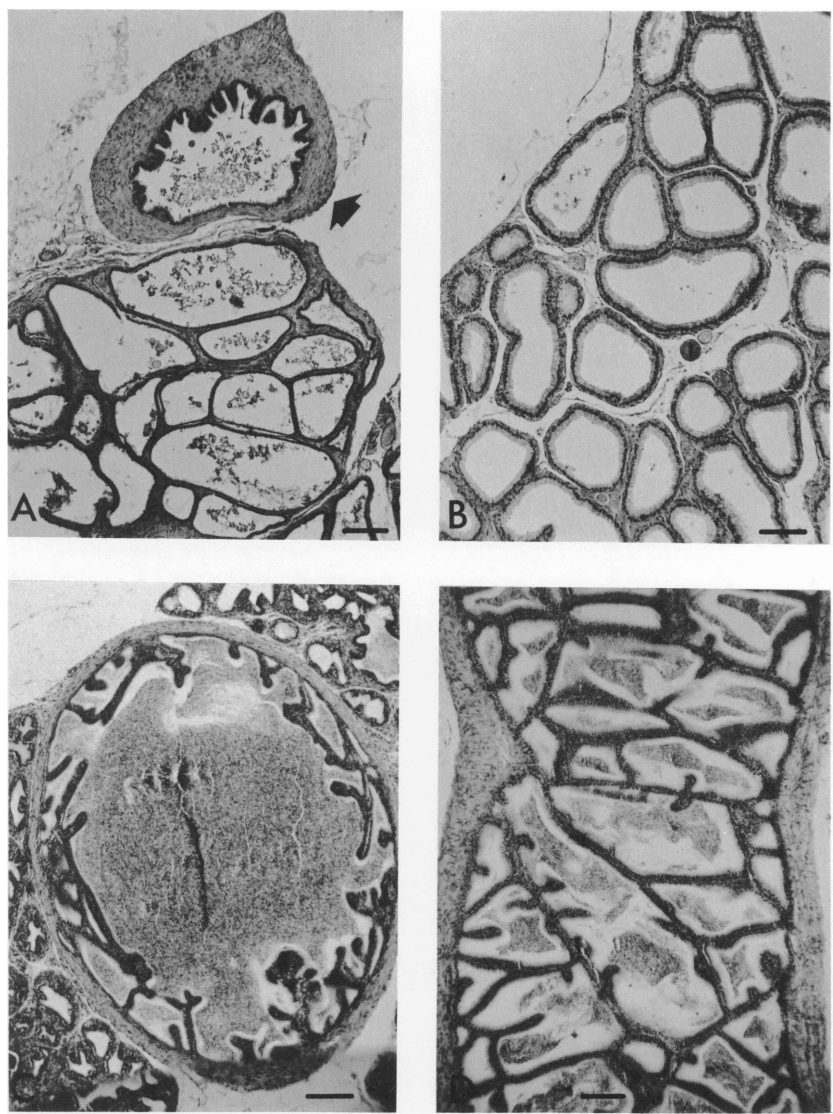


FIG. 9. A, B. *Peromyscus lepturus*. A. Vesicular (arrow) and portion of ampullary gland. B. Ventral prostate gland. C, D. *Peromyscus floridanus*. C. Cross section of proximal portion of deferent duct. D. Longitudinal section of proximal segment of deferent duct. Scale equals 0.1 mm.

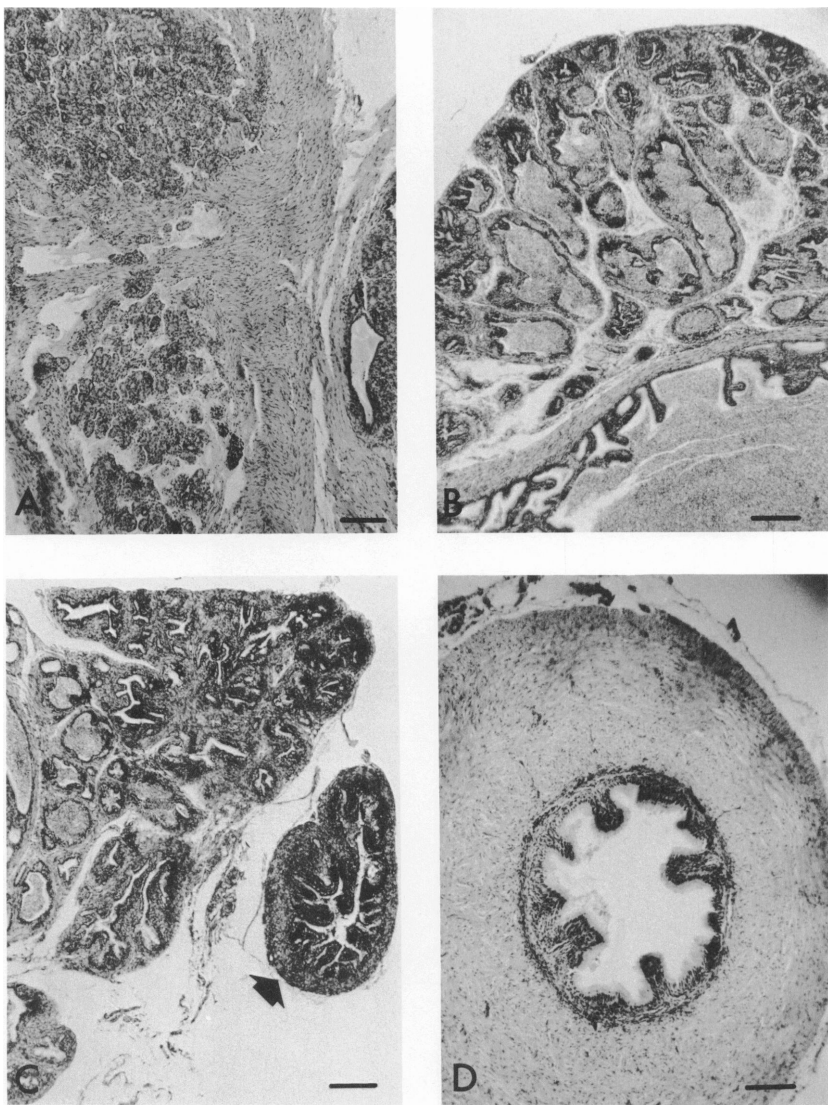


FIG. 10. A-C. *Peromyscus floridanus*. A. Bulb of penis, showing bulbar glands and bifurcate condition. B. Ampullary gland. Note masses of sperm in lumina of tubules. C. Vesicular gland (arrow). D. *Peromyscus thomasi*. Deferent duct. Scale equals 0.1 mm.

urethra exhibit the least variation in size and appearance. The uniformity of these structures extends to the entire group of murids (Arata, 1964). In contrast, the preputials, vesiculars, anterior prostates, and dorsal prostates are variable in both occurrence and morphology. The degree of development of the ampullaries, vesiculars, and prostates seems to be interrelated, a reduction or absence of the vesicular glands invariably being accompanied by a corresponding decrease in the size of anterior and dorsal prostates together with "compensatory" enlargement of either the ampullary or ventral prostates. The presence or absence of preputials, or a variation in their size when present, on the other hand, does not appear to be correlated with the development of more proximal elements of the tract. We are also unable to see any obvious relationships between preputial glands and phallic type. For example, *Haplomyloms* and *Osgoodomys* both possess well-developed preputials, but they differ markedly in phallic structure; *Osgoodomys*, *Habromys*, and *Podomys* exhibit similarities in the phallus, but contrast sharply with respect to the presence of preputials.

The relative variability of genital structures also appears to exhibit some zoogeographic correlation. With the exception of *Podomys*, all the species occurring north of Mexico have the basic *Peromyscus-Haplomyloms* pattern, whereas the groups that are the most divergent with regard to genitalia, such as *Osgoodomys*, *Habromys*, and *Isthmomy*, occur in Mexico or Central America. It is of interest to note that *Podomys* appears to have some zoogeographic affinity with the general southwestern region of the United States, Mexico, or Central America (Johnson and Layne, 1961). The majority of the reproductively aberrant subgenera thus fall into Hooper and Musser's (1964) tropical-species category of *Peromyscus*, which is distinguished from temperate species by details of the skull structure and tail coloration.

A question also arises as to the functional significance of the marked variation in genital structure found in *Peromyscus*. So little is presently known about the physiological role of the various mammalian accessory glands and the ecology and behavior of most of the species involved that any consideration of this subject must be speculative. The apparent correlations noted above in the developmental status of ampullary, vesicular, and prostate glands may in turn reflect some functional interrelationship between them. The retention of preputials in the subgenus *Haplomyloms* may be an adaptation to conserve water. This group is associated primarily with xeric habitats, and the use of the oily secretion of the preputials rather than urine for marking objects in the environment (Eisenberg, 1962) may aid in reducing water re-

quirements. It is not clear whether or not such an explanation applies in the case of *Osgoodomys*.

The reduced size of some of the accessory glands in *P. floridanus* may be partially a reflection of a genetically determined low level of testosterone production, which in turn may be an adaptation to insure more precise synchronization of breeding activity with appropriate environmental conditions (Layne, 1966). Evidence for such a suggestion, in addition to the reduction in size of the glands themselves, is the lesser pigmentation of the cremaster and the relatively smaller bulbo-cavernosus and ischiocavernosus muscle mass in sexually active males, as compared with individuals of *leucopus* or *gossypinus* that have a normal accessory complement. The modification of the proximal segment of the deferent duct of *floridanus* as a possible sperm reservoir may represent an adaptation to insure higher breeding success during times of sparse populations when the probability of encounters between individuals at the proper stage of the reproductive cycle is low.

Hooper and Musser (1964) considered that, exclusive of *Ochrotomys* and *Baiomys*, the remaining species of *Peromyscus* probably constitute a close phyletic unit. They viewed the genus as consisting of a large central group (subgenus *Peromyscus*) and six small peripheral groups, each representing an independent line of divergence from the central stock. The data from the present study provide a further basis for attempting an interpretation of the relationships between the subgenera of *Peromyscus*.

If the genus as presently defined is assumed to represent a single phyletic unit, the evidence of the genital system points to the subgenus *Haplomylomys*, with its complete set of accessory glands of "normal" proportions, as the basal or "primitive" type from which the other groups were derived. This interpretation, which differs from Hooper and Musser's concept, receives some support from the myological study of Rinker (1963). The large preputials and highly modified, proximal, accessory-gland complement of *Osgoodomys* suggest that it is a highly divergent offshoot of the *Haplomylomys* group or some earlier common stock. The subgenus *Peromyscus* closely resembles *Haplomylomys* in genital morphology, except for the reduction or loss of the preputial glands, and thus can reasonably be considered to have evolved from the latter group. The *leucopus* group occupies a somewhat transitional position between the two subgenera. *Isthmomy*s and *Megadontomys* most probably came from the line represented by the subgenus *Peromyscus*. Although *Isthmomy*s seems somewhat more distinct from *Peromyscus* than *Megadontomys* in over-all genital features, the three groups share a fundamentally similar pattern of reproductive structures.

Podomys and *Habromys* are less aberrant in their genital features than is *Osgoodomys* yet are well removed from the subgenera *Haplomylomys* and *Peromyscus*. The condition of reduced vesicular, anterior prostate, and dorsal prostate glands shared by these groups may represent either relatively close affinity or convergence. Similarities in phallic structure (Hooper, 1958) and circumstantial zoogeographic evidence (Johnson and Layne, 1961) offer some support for the first possibility. The differences in the remaining accessories, however, and the unique structure of the deferent duct of *Podomys* could be cited as proof that the genital similarities in these two stocks are of independent origin. We are inclined to favor slightly the interpretation of some basic affinity between *Podomys* and *Habromys*. They may have been derived from a common stock, or closely related stocks, in which trends of reduction of the vesiculars and prostate elements were initiated prior to the divergence of the two groups, and with compensatory changes involving different accessories in each line occurring after separation. The absence of preputials from *Podomys* and *Habromys* argues in favor of the subgenus *Peromyscus* as the ultimate ancestral group. On the other hand, the reduction of vesiculars and associated prostates is reminiscent of *Osgoodomys*, and an alternative possibility is that *Podomys* and *Habromys* derive from some stock near *Osgoodomys* and have lost the preputials in the course of evolution. We regard a *Peromyscus* affinity as being the more likely possibility.

Figure 11 illustrates the relationships of the major groups of *Peromyscus* that in our opinion seem most probable on the basis of genital structure. Even if this interpretation of the phylogeny of the group is correct, *Osgoodomys*, *Podomys*, and *Habromys* have diverged from the typical members of the assemblage to such an extent that the advisability of retaining them within the genus seems open to question. The same might apply to *Isthmomys*.

Although it is possible to reconcile the divergent genital morphology of the present members of *Peromyscus* with the view of the genus as a natural assemblage, the data can also be interpreted as evidence for the opposite conclusion, namely, that the genus as currently constituted is polyphyletic. The reproductive tracts of *Podomys*, *Habromys*, and *Osgoodomys* are fully as distinct from those of the subgenus *Peromyscus* as are those of *Baiomys* and *Ochrotomys*, previously excluded from the genus, and even those of such supposedly more remotely related murid genera as *Mus*, *Rattus*, *Microtus*, *Phyllotis*, and others described by Arata (1964). It is possible, therefore, that these subgenera, and perhaps *Isthmomys* also, actually have no special relationship to "typical" *Peromyscus*, as

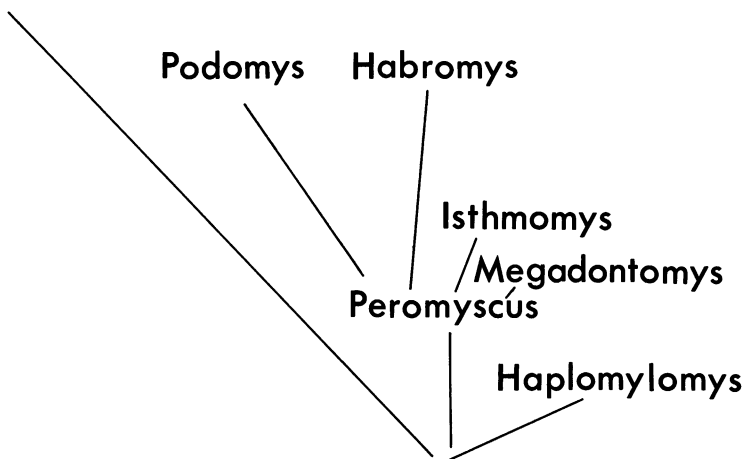
Osgoodomys

FIG 11. Possible relationships of the subgeneric groups of *Peromyscus* as suggested by the morphology of the male genital tract.

represented by the numerous species of the present subgenus *Peromyscus*. On the basis of genital morphology, *Haplomylomys* and *Megadontomys* appear to have a higher probability of a true relationship with *Peromyscus*, *sensu stricto*. As the genital organs of these groups are, however, of a general type found widely among murids with a complex phallus and in some forms with a simple phallus as well, such similarity does not necessarily provide unequivocal proof of basic affinity.

If the genus should prove to be an unnatural assemblage, the scheme presented in figure 11 might still stand as an illustration of the probable stages in the evolution of the various genital patterns from a generalized type occurring in separate ancestral stocks.

It should be emphasized that our primary objective in the foregoing discussion has been simply to compare the patterns of possible relationships of species of *Peromyscus* suggested by genital tract morphology with the current concept of the genus as represented by Hooper and Musser's classification and discussion rather than to advocate formal taxonomic changes. Although internal genital structure appears to be relatively conservative and thus of particular value in an assessment of fundamental relationships, all sources of information about the group in question, including other aspects of morphology as well as biochemical, genetic, ecological, and behavioral data, should of course be given due consideration in actual taxonomic decisions. In the case of *Peromyscus*,

genital data appear to give better insight into actual relationships than any one character, or combination of other characters thus far studied, including the dentition, skull morphology, baculum, number of teats, plantar tubercles, coloration, and size of appendages. The seven major groups distinguishable on the basis of genital morphology seem to be valid phyletic units. What is far from clear, however, is the true nature of the relationships among them. Perhaps the best taxonomic treatment for accurately expressing this uncertainty about their affinities would be to give each an independent generic status.

SUMMARY

The male genital tracts of 28 species of *Peromyscus* were examined. On the basis of the accessory glands and other structures seven major groups can be distinguished within the genus. These correspond to the subgenera of Hooper and Musser (1964). The subgenus *Haplomylomys* possesses a full complement of accessory glands, including ampullary, vesicular, anterior prostate, dorsal prostate, ventral prostate (two pairs), bulbo-urethral, and preputial glands. The subgenus *Peromyscus* differs only in lacking functional preputials, although these glands are present in rudimentary condition in some species. *Megadontomys* and *Isthmomys* are fundamentally similar to *Peromyscus*, although differing from that group and each other in numbers, proportional size, or morphology of certain glands. *Isthmomys* may diverge more from *Peromyscus* than *Megadontomys*. The remaining three groups are markedly different from other species in genital morphology. *Osgoodomys* lacks vesicular and both anterior and dorsal prostate glands but has exceptionally large and distinctive ampullaries and well-developed preputials. *Podomys* and *Habromys* share the condition of greatly reduced vesiculars and anterior and dorsal prostates but differ in other features. *Podomys* has enlarged ampullaries and a deferent duct of unique structure, whereas *Habromys* has normal ampullaries and a typical deferent duct but greatly enlarged ventral prostates. At least some of the species groups of the subgenus *Peromyscus* appear to be characterized by common genital features. These were more subtle than the differences between major groups and will require further study for verification. The genital data can be reconciled with the view that the genus *Peromyscus* is a natural assemblage of species in which some forms have diverged greatly, but they can also be interpreted in support of the hypothesis that the genus is polyphyletic. In either case, the present subgenera *Osgoodomys*, *Podomys*, and *Habromys* may warrant exclusion from the genus on the basis of their extremely divergent reproductive morphology.

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