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THE ANATOMY AND TAXONOMIC SIGNIFICANCE OF THE MALE ACCESSORY REPRODUCTIVE GLANDS OF MUROID RODENTS

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SYNOPSIS: The structures of the male reproductive tracts of 24 genera of muroid rodents were compared to assay characters of potential taxonomic utility. One form, *Sigmodon hispidus*, was studied in detail to serve as a basis for comparison.

Analysis of the accessory reproductive gland complement in 24 genera of murid, cricetine, and microtine rodents reveals that these structures vary in both number and form. The bulbo-urethral glands are the least variable elements while the preputial, ampullary, vesicular, and prostate glands show considerable modifications. The prostates, though variable in form and occasionally lacking one or more of the three usual pairs of glandular material, are never totally absent. The vesicular, ampullary, and preputial glands are lost singly or in various combinations in 8 of 22 genera for which such information is available.

The accessory reproductive glands show greater similarity between certain genera currently placed in separate families than between some genera classified within the same family. Certain cricetines, such as *Oryzomys* and *Sigmodon*, have reproductive tracts of a basic pattern shared by both murids and microtines; other cricetines including *Peromyscus*, *Neotoma*, *Onychomys*, and *Tylomys*, differ radically from this basic pattern. This indicates a polyphyletic origin of the Cricetidae and suggests that genera currently classified as cricetines should be assigned to different taxa.

[1] This paper represents, in part, a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Biology of the University of Florida. The author is currently an Assistant Professor in the Zoology Department at Tulane University. His major research interests are the anatomy and systematics of mammals and the vertebrate paleontology of the southeastern United States. Manuscript received 15 April 1964.—ED.

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Introduction

Studies of the genitalia of rodents to date have dealt with forms widely scattered throughout the order, and most have been descriptive rather than comparative. Detailed comparative anatomical studies of the accessory reproductive glands are available only for the Sciuridae (Mossman, *et al.*, 1932; Prasad, 1957). Accessory glands of the following muroid genera have been described: *Cricetus, Arvicola, Nectomys, Mus* (Tullberg, 1899); *Microtus* (Hamilton, 1941; Delost, 1955); *Rattus* (Walker, 1910; Price, 1936); *Mus* (a number of papers, summarized by Snell, 1941); *Mesocricetus* (Ortiz, 1947); *Neotoma* (Howell, 1926).

A recent series of papers by Hooper (1958; 1959; 1960; 1962) and Hooper and Hart (1962) demonstrate that different phallic forms exist within the Cricetidae, and suggest a polyphyletic origin of the family.

The purposes of this study were to determine the extent and nature of the variations occurring in the accessory glandular complements of male muroid rodents, to see if and how they relate to the current taxonomic arrangement of the group. As a basis for comparison with other muroids, I studied the anatomy of the male accessory glands of a representative form (*Sigmodon hispidus*) in detail.

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Male Accessory Reproductive Glands of *Sigmodon hispidus*

The reproductive tract of *Sigmodon hispidus* (Fig. 3) is of the general type possessed by most muroid genera examined. The glandular complement includes preputial, bulbo-urethral, vesicular, ampullary, prostate, and urethral glands. Examination of more than 50 specimens reveals that basic structure and number of accessory reproductive glands is constant, though superficial shape and size vary seasonally. Haines (1961) demonstrated a 336-fold annual change in

seminal vesicle weight in *Sigmodon*. Sizes given in the following accounts are not intended to represent absolutes, but merely to afford criteria for comparison of the relative sizes of the different glands.

Preputial Glands.

Two pairs of these glands are recognized. A small ventral pair lies within the confines of the prepuce, and a larger lateral pair encroaches upon the ventral border of M. rectus abdominis. Each of the four glands is drained by a single duct. The small ventral glands measure about 10 x 3 mm in greatest length and width, respectively. Corresponding measurements for the larger pair are 18 x 5 mm.

The preputial glands are modified sebaceous glands. The large polyhedral cells are best seen in the basal part of each unit, prior to degeneration and formation of sebum. The nuclei are centrally located in the secretory cells and the ducts are lined with squamous epithelium (Fig. 1a).

The preputial glands are supplied by the superior epigastric artery and the superior external pudendal artery and are drained by the superior external pudendal vein.

Bulbo-urethral Glands.

These paired, tubulo-alveolar glands lie craniad and laterad to the urethral bulb. Each pear-shaped gland is drained by a single duct and measures about 5 x 6 mm. The glands are bordered by the M. bulbocavernosus (caudad), the M. ischiocavernosus (cephalad), and the M. externa caudae media (medially). The ducts pass between the M. ischiocavernosus and M. bulbocavernosus and enter the dorsolateral walls of the urethra just anterior to the urethral bulb. The ducts pass through the tissues of the membranous urethra to enter the lumen at the point where the urethra turns ventrad to form the penile urethra.

The secretory cells of the bulbo-urethral glands average 30 x 20 microns. When stained with hemotoxylin and eosin the nuclei are dark blue, the cytoplasm is eosinophilic. The nuclei lie at the base of the cell adjacent to the well developed basement membrane (Fig. 1b).

The bulbo-urethral glands are supplied by a small branch of the artery of the urethral bulb which is a branch of the artery of the penis. The veins from these glands drain into the vein of the urethral bulb which is continuous with the internal pudendal vein.

Vesicular Glands.

The vesicular glands are the largest of the accessory glands of *Sigmodon*. They lie dorsad to the bladder and form the most anterior portion of the tract. Frequently they are pushed together by pressure from the caecum. The vesiculars are recurved, lumpy, and frequently lobate along the outside margin of the curve. From the duct to the terminal portion along the greater curve they may measure as much as 40 mm. The maximum thickness is generally about 10 mm. Each gland is drained by a single duct, which enters the urethra dorsolateral to the ampulla.

The vesicular glands are surrounded by a thick layer of smooth muscle covered by a thick tunic of connective tissue. The mucuous membrane is thrown into an amazing series of folds which provide a large secretory surface (Fig. 1c). The secretory cells are columnar (15 x 5 microns) with the nuclei situated at the basal portion adjacent to the basement membrane. The waxy secretion is eosinophilic.

The superior vesicular artery gives off branches to the following glands: vesicular; ampullary; dorsal, ventral, and lateral prostates. Other branches supply the vas deferens and the bladder. The inferior vesicular artery has a similar distribution, but is not so large. All structures mentioned above are drained by veins which unite to form the superior vesicular vein.

Ampullary Glands.

These paired glands lie directly anterior to the neck of the bladder. They are closely associated with their respective vasa deferentia and are contained within the same connective tissue sheath. These are the smallest of the accessory glands, the pair measuring about 6 mm in width, and 4 mm in thickness at maturity.

The ampullary glands are branched tubulo-alveolar glands. The epithelium is heavily contorted, but the small size of the glands does not afford an extensive secretory surface. The secretory cells average 10-15 microns (Fig. 1d). Each gland is drained by numerous ducts which enter the vas deferens near its termination and the vestibule of the ampulla.

Prostate Glands.

These are the most confusing glands in the reproductive tract. They attain a large size, are large in number, variable in color, and inconstant in shape. The homologies of glands designated as prostates in different mammalian groups are not clear.

Walker (1910) described the glands that lie in the lesser curve of the vesiculars of *Rattus* as "coagulating" glands and emphatically denied their association with the prostatic series. Most subsequent authors have used the name "coagulating" for these glands. Price (1936) demonstrated that the prostates of *Rattus* arise embryologically from three cords, destined to be the three main prostatic groups. The "coagulating" are the most anterior of these three lobes, and are, therefore, prostates. Price (1936) termed these three prostatic groups "posterior", "mid", and "coagulating". Hamilton (1941) discussing *Microtus* used the term "ventral lobes" and "ventro-lateral" lobes. The "ventral" lobes of Hamilton are the ampullaries, not part of the prostatic series. The "ventro-lateral" lobes of Hamilton are the "coagulating" glands of Walker.

The difficulty in the naming of these glands becomes especially involved when comparing different genera whose prostatic complements may not be alike. As the prostates are clearly divisible into three major groups in *Rattus*, *Sigmodon*, and many of the other genera examined in this study, I have chosen to designate these groups as "anterior", "dorsal", and "ventral".

The anterior prostates correspond to the "coagulating" of Walker (1910), Price (1936), and Snell (1941); and the "ventro-lateral" of Hamilton (1941). I have not used "coagulating" because we are not certain of the function of these glands in the numerous genera in which they occur. I have not used "ventro-lateral" because there are other ventral and lateral prostates. I have chosen "anterior" because of all the prostates these are the most anterior, and because their ducts enter the anterior portion of the prostatic urethra.

The dorsal prostates lie on the dorsal border of the prostatic urethra and are the same as those so designated by Snell (1941) and as the "mid lobe" by Price (1936). Hamilton (1941) does not mention these glands in *Microtus* though they are present.

The ventral prostates lie on the ventral surface of the prostatic urethra, posterior to the bladder. They are the "posterior prostates" of Price (1936), the "prostates" of Walker (1910), and the "ventral" prostates of Snell (1941). As previously mentioned, the "ventral" prostates of Hamilton (1941) are ampullary glands. *Sigmodon* and many other muroid genera have two sets of ventral prostates.

The two pairs of ventral prostates in *Sigmodon hispidus* consist of median and lateral pairs (Fig. 3). The median pair lies posterior to the bladder and are elongate, filiform, branched and tubular. They are highly irregular in shape, twisted about fatty tissue, and pushed against the bladder or the vesiculars. When straightened each gland

may be 15-25 mm long at maximum development. As many as 50-75 tubules may be present at the terminal portion. At the base of each gland 8 to 10 tubules are visible, and sections of the prostatic urethra suggest the presence of a corresponding number of ducts from each of the glands. The ducts enter the ventral wall of the prostatic urethra caudad and slightly ventrad to the neck of the bladder. These glands are white when preserved in formalin or FAA.

The tubules are loosely bound together by connective tissue and are lined by secretory epithelium, the cells measuring 20 to 25 microns in length and 10 to 15 microns in width. The mucous membranes are thrown into heavy folds. The smooth muscle between the tubules is not extensive. These glands do not section easily because the fixative crystallizes their secretions.

The second pair of ventral prostates lie laterad to the median pair and equal them in size and number of tubules. They are branched, tubular glands with as many as 75 tubules present at the terminal edge; they closely resemble the median ventral prostates, except that their secretory epithelial cells are more elongate, averaging 25 to 30 microns in length (Fig. 2a). Each member of the pair has 7 to 9 ducts which enter the ventral wall of the prostatic urethra laterad to the neck of the bladder. These glands become reddish to purple when preserved in formalin or FAA.

The small leaf-like dorsal prostate glands lie along the dorso-anterior border of the prostatic urethra (Fig. 3) and the colon passes medially between them. The glands are compact and bound tightly in a sheath of connective tissue. Each gland is about 7 mm long, 5 mm wide, and 2 mm thick and each drains into the dorso-anterior wall of the prostatic urethra through four to six ducts. About 15 tubules, visible only upon dissection, can be distinguished in each of these glands. The tubules are of smaller caliber than those of the ventral prostates, and the mucous membrane is not so heavily folded. The columnar epithelial cells are small, averaging 15 to 20 microns. The smooth muscle is thicker than in other members of the prostate series (Fig. 2b).

The anterior prostate glands lie in the lesser curve of the vesicular glands. They consist of long, branched tubules lying on either the medial or the lateral or on both surfaces of the vesiculars. The tubules are large, averaging 3 to 5 times the diameter of those of the ventral prostates. Each gland of the pair may have 25 to 35 tubules. These are drained by anastomosing ducts which lie adjacent to the duct of the corresponding vesicular gland.

Histologically, the anterior prostate glands are quite similar to

the other prostate divisions. The compound tubules are larger, however, and the mucous membranes are not so extensively folded. The columnar epithelial cells are small, averaging 15-20 microns in length. The smooth muscle is not so extensive as that of the dorsal prostates (Fig. 2c).

Urethral Glands.

The prostatic urethra receives the neck of the bladder, the ampullae, and the ducts of prostate and vesicular glands. The illustration of this region in *Mus* in Snell (1941) is identical to that in *Sigmodon*. Posterior to the prostatic region the urethra is surrounded by a mass of striated muscle, the sphincter urethrae membranaceae. Between the muscular wall and the lumen a mass of loose, simple alveolar glandular tissue forms the diffuse urethral glands (Fig. 2d). A small amount of smooth muscle is presented in the lamina propria.

Comparative Morphology of the Male Genitalia of Muroid Rodents

Description and illustrations of the male accessory glands are available for only six genera of cricetid rodents: *Mesocricetus* and *Cricetus* (Cricetinae, Cricetini), *Neotoma* and *Nectomys* (Cricetinae, Hesperomyini), and *Microtus* and *Arvicola* (Microtinae, Microtini). This dearth of information is disappointing in comparison with the vast literature dealing with other reproductive structures, especially the baculum.

Several introductory comments may help view the following descriptions in proper perspective. All genera included are not truly of equal taxonomic rank. For example, *Peromyscus* and *Microtus* are composed of numerous species, many rather diverse, which may be subdivided upon further examination. On the other hand *Ochrotomys*, until recently considered a subgenus of *Peromyscus*, is monotypic, and *Onychomys* and *Baiomys* include but two species each. As it was impossible to treat all the species of each genus included, I examined one species (Table 1), fully aware that further study of the larger genera may necessitate additions to or revisions of certain of my conclusions.

Variations within each form must be considered. My examination of the genitalia of 50 *Sigmodon hispidus*, showed no variation in the basic number and morphology of the accessory organs. This was also true for *Ondatra, Microtus, Neofiber, Oryzomys,* and several other genera of which I was able to dissect two or more specimens.

Therefore I feel that the data obtained for genera for which but a single adult specimen was available are trustworthy.

Of all the genera examined, only *Rattus*, *Mus*, and *Mesocricetus* showed variation in the accessory glandular structures. One specimen of *Mesocricetus* had only one vesicular gland. In one *Rattus* the number of prostates on the left and right sides of the urethra was not equal. These were the only specimens examined from inbred strains of laboratory animals. Osteological variations in such strains of *Rattus* are well known, so there is little reason that genital structures might not show similar aberrations.

Age and seasonal changes in forms where a seasonal reproductive cycle occurs are other important sources of variation. Unless otherwise noted, descriptions and illustrations are based upon adult specimens with scrotal testes and in which the tubules of the cauda epididymis were visible. It is difficult, and probably fallacious, to give accurate measurements of glands subject to such seasonal variability. Where given, the measurements in this section are for the greatest length by the greatest width of organs, unless otherwise specified. Care was taken that a similar orientation of glands was used in all measurements.

Unless otherwise stated, the bulbo-urethral glands and their duct systems are similar to those found in *Sigmodon*. These glands are so alike in all genera examined that individual descriptions are not warranted.

With certain forms it is difficult to determine whether a prostate is bilobed, or if two pairs are involved. I have attempted to follow a conservative course; unless the glands are distinctly separate with clearly discrete duct systems, I consider them to constitute a single bilobed gland.

Mesocricetus Nehring 1898

(Fig. 4a)

Ortiz (1947) described the accessory glands in part. His discussions of the embryology of the tract and hormonally induced variations are noteworthy. Although he mentions the prostatic ducts, he gives no information on the number of lobes, their extent, and other aspects of interest from a taxonomic standpoint.

No preputial glands were present in the specimens examined.

The vesicular glands are large and strongly recurved ventrally. They are lumpy and irregular in shape, and bulbous on the median surface near the ducts. A single duct from each gland enters the anterior aspect of the prostatic urethra dorsad and laterad to the vas

deferens. The greater curve of the gland is heavily lobate, and many of the lobes are compoundly branched. Although a number of genera exhibit some degree of lobation of the vesicular, this condition is most pronounced in *Mesocricetus*.

The ampullary glands are large and lie at the point of contact of the two vasa deferentia. The glandular tissue is not so tightly bound by connective tissue as in *Sigmodon* and it forms a more amorphous mass.

Three pairs of prostates are present in *Mesocricetus*. A single elongate (12 x 5 mm) pair of ventral prostates lies laterad, and caudad to the bladder. The ducts enter the ventral wall of the prostatic urethra laterad to the neck of the bladder. The paired dorsal prostates are situated on the antero-dorsal wall of the prostatic urethra through which the ducts pass. These prostates encroach upon the dorsal margin of the vesicular glands for a short distance. The colon passes between the two lobes of this gland. The paired anterior prostates lie within the lesser curves of the vesiculars and in contact with their lateral borders. The ducts of the anterior prostates, two on each side, enter the prostatic urethra adjacent to the vesicular ducts.

Oryzomys Baird 1857

(Fig. 4b)

A single pair of large preputial glands is present. These flare proximally, and most of their mass lies on the sides of the glans penis. Each is drained by a single duct that opens at the distal, lateral edge of the prepuce.

The lobate vesicular glands are large and recurved, their distal tips in contact with the base of the gland. Laterally each gland appears to be a solid mass, but its recurved nature is readily apparent on dissection. The single duct of each gland enters the prostatic urethra immediately laterad to the vas deferens.

The compact ampullary glands are adjacent to their respective vasa deferentia. Each gland is drained by numerous ducts that open into the vas deferens and ampulla.

Four pairs of prostates are present. The two pairs of ventral prostates consist of a median pair (10 x 3 mm) lying caudad to the bladder, and a more lateral, bulbous pair (6 x 5 mm) situated on either side of the median pair. The ducts of the median pair enter the urethra posterior to the neck of the bladder, while those of the bulbous pair enter slightly more laterally. In formalin or FAA the

median ventral prostates are white and the laterals red. A single pair of elongate dorsal prostates (8 x 4 mm) is situated on the dorsal surface of the urethra, encroaching anteriorly onto the dorsal border of the vesiculars with the colon passing medially between them. Their ducts enter the antero-dorsal wall of the prostatic urethra. The anterior prostates are filiform, fanlike glands lying upon the median surfaces of the vesiculars. They are drained by two ducts on each side which enter the urethra laterad to the vesicular ducts.

Oecomys Thomas 1906

(Fig. 4c)

As I was able to obtain only the proximal portion of the tract, I cannot describe the preputial or bulbo-urethral glands.

The vesicular glands are lumpy and recurved. The median border and the greater curve are both irregular in shape. The recurved tip is strongly notched. Each gland is drained by a single duct entering the urethra dorsad and laterad to the ampulla.

The ampullary glands lie on their corresponding vasa deferentia, to which their numerous ducts pass immediately proximal to the ampulla.

Four pairs of prostates are recognizable in this genus. An elongate (9 x 3 mm), median pair of ventral prostates lies directly caudad of the bladder, and a second, more bulbous (3 x 3 mm), lateral pair is located on the sides of the prostatic urethra. The median pair is white in formalin, the lateral pair a reddish purple. The ducts of the median pair enter the prostatic urethra posterior to the neck of the bladder; those of the lateral pair enter the urethra through the side walls. The dorsal prostates are represented by a pair of compact glands at the anterior end of the urethra; their ducts enter the urethra through the antero-dorsal wall. The anterior prostates are a loose, filiform set of glands lying in the lesser curve of the vesiculars. They are drained by a pair of ducts on each side that enter the urethra laterad to the ducts of the vesiculars.

Nectomys Peters 1861

(Fig. 4d)

A single pair of preputial glands is present, situated on the lateral borders of the glans penis. These are long and narrow, each measuring 14 x 4 mm and are drained by a single duct.

The bulbo-urethral glands lie in approximately the same position as in *Sigmodon*, though in *Nectomys* the median border of each gland is in contact with the rectum. In the other genera examined the glands are not so deeply situated. Each gland is drained by a single duct that enters the dorso-lateral wall of the membranous urethra craniad to the origin of the phallus.

The vesiculars are large and recurve ventrally. Their gross appearance is one of extreme lumpiness. Members of the pair are asymmetrical, their median borders being the more irregular. The greater curve is grossly lobate, as opposed to the fine compound lobations in *Mesocricetus*. Each gland has a single duct that opens into the cephalic end of the prostatic urethra adjacent to the ampulla.

The compact ampullary glands lie about the vasa deferentia within an area about 4 x 3 x 2 mm. Numerous ducts drain each gland.

Nectomys has five pairs of prostates. Of the two elongate pairs of ventral prostates, the median pair lies directly caudad of the bladder, its ducts entering the prostatic urethra through the ventral wall posterior to the neck of the bladder. The lateral pair is of the same size (9 x 3 mm), but is drained by ducts entering the urethra laterad to the neck of the bladder. The median pair remains white in FAA; the lateral pair assumes a red color. A typical pair of dorsal prostates lies in the anterior part of the tract on the dorsal surface of the prostatic urethra with one lobe on each side of the colon, their bodies encroaching on the dorsal surface of the vesiculars. The ducts from these glands enter the urethra through the antero-dorsal wall. A smaller, more lateral pair of glands lies on the sides of the prostatic urethra below the dorsal prostates. Their ducts appear to open into the prostatic urethra next to those of the dorsal prostates. Because of their proximity and similar morphology (their tubules appear identical to those of the dorsal prostates) I consider these glands to be a second, more laterally located dorsal set. Both sets of dorsal prostates are white in FAA. The filiform anterior prostate glands lie mainly within the lesser curve of the highly asymmetrical vesiculars, but may extend over both their lateral and median aspects. Each gland is drained by a pair of ducts entering the prostatic urethra close to the ducts of the vesiculars.

Tullberg (1899) illustrated the male reproductive tract of *Nectomys*, but did not distinguish between the various prostatic units. At least four are recognizable in his illustration.

Akodon Meyen 1833

(Fig. 4e)

Two pairs of preputials occur as in *Sigmodon,* a small ventral pair (2 x 1 mm) and a larger lateral pair (5 x 3 mm). Each gland is drained by a separate duct. The lateral pair has a flaring proximal end and a ventral concavity within which the smaller pair lies.

The vesicular glands are small, recurved, and slightly scalloped along the greater curve. Each is drained by a single duct which enters the anterior wall of the prostatic urethra adjacent to the vas deferens.

The paired ampullary glands do not differ essentially from those of *Sigmodon.*

Three pairs of prostate glands are recognizable in this genus. The single pair of ventral prostate glands is median in position, the ducts entering the prostatic urethra through the ventral wall posterior to the bladder. The dorsal prostates lie somewhat anterior to the urethra and encroach upon the dorsal border of the vesiculars. The colon passes medially between the two lobes. Their ducts enter the antero-dorsal wall of the urethra. A single pair of anterior prostate glands is present, although each appears bilobed. One lobe is directed craniad along the lateral border of the corresponding vesicular, the other is a small rosette of prostatic tissue situated on the ventral border of the vesicular craniad to its entrance into the prostatic urethra. I could not distinguish the ducts of either lobe. All prostates were white in preservative.

Phyllotis Waterhouse 1873

(Fig. 4f)

The only specimen I examined, a carcass remaining from a skin preparation, lacked preputial glands which may have been lost in skinning.

The paired bulbo-urethral glands lie in the same position described for *Sigmodon.* The gland body is not pear-shaped as in *Sigmodon,* but is concave on one side and somewhat saucer-like.

The vesiculars are large and recurved ventrally toward the rear. The outer margin is slightly lumpy, while the lesser curve is smooth. The duct arrangement is similar to that of *Sigmodon.*

The ampullary glands are well developed, with the greatest mass of each gland concentrated on the dorsal aspect of the vas deferens. Each gland is slightly bilobed.

There are four pairs of prostate glands. A bulbous, median pair of ventral prostates lies caudad of the bladder; its ducts enter the urethra through the dorsal wall posterior to the neck of the bladder, paralleling the neck into the prostatic urethra. A smaller, lateral pair of ventral prostates lies along the neck of the bladder, below which the ducts enter the urethra. The dorsal prostates lie on the dorsal wall of the prostatic urethra and partially encircle the colon. Their ducts enter the antero-dorsal wall of the prostatic urethra. The paired anterior prostates lie in the lesser curve of the vesiculars. One duct from each enters the prostatic urethra at its anterior border. All prostates are white in preservative.

Nyctomys De Saussure 1860

(Fig. 5a)

No preputials were found in the specimen examined.

The paired bulbo-urethral glands lie in the same position as described for *Sigmodon*, but are more ovate than in the latter. A single duct drains each gland and enters the membranous urethra anterior to the origin of the phallus.

No vesiculars were present in the specimen examined.

The ampullary glands are large, 5 x 5 mm, and are loosely filiform in contrast to the more compact type in *Sigmodon* and some other genera. Each gland discharges into its corresponding vas deferens through numerous ducts. This genus has only a single set of prostates which forms the most anterior extension of the tract and apparently represent the anterior prostate series. On each side are four units, each drained by a single duct entering the antero-dorsal wall of the prostatic urethra laterad and dorsad to the ampulla. These long, thin (15 x 3 mm) units are each composed of two to eight branching tubules. The only other genus with similar prostates is *Neotoma*, which has ventral prostates which *Nyctomys* lacks.

Peromyscus Gloger 1841

(Fig. 5b)

The specimens of this genus I examined had no preputial glands.

The vesicular glands are large and recurved, and measure about 50 mm along the greater curve. The margin of the greater curve is prominently notched; the lesser curve is smooth. A single duct drains each gland.

The ampullary glands lie along the vas deferens and join craniad to the neck of the bladder. The ventral aspect of the vas deferens is

not covered by ampullary tissue. The total area of the glands is about 4 x 4 x 3 mm, a considerable portion of which lies on the anterior border of the vas deferens.

The specimens examined had four pairs of prostate glands. The medial pair of ventral prostates (8 x 5 mm) lies directly caudad of the bladder; the second pair (10 x 7 mm) lies laterad to the bladder. The ducts of both pairs of ventral prostates enter the ventral side of the urethra. The dorsal prostate glands lie on the most antero-dorsal portion of the prostatic region and abut against the vesiculars. The descending colon passes between their two lobes. The ducts enter the urethra dorsally. The anterior prostate glands are long attenuate glands (12 x 3 mm) lying in the lesser curve of the vesiculars. Each gland is drained by two ducts entering the urethra laterad to and in contact with the vesicular ducts. All prostates are white in preservative.

Reithrodontomys Giglioli 1873

(Fig. 5c)

No preputial glands were observed in the specimens examined.

The lumpy horns of the recurved vesiculars curve ventrally and fold back upon themselves. Along the greater curve they measure about 15 mm. Their ducts lie laterad and dorsad to the vas deferens.

Each of the compact, paired ampullary glands lies along and is adnate to the corresponding vas deferens, and covers all but its ventral surface.

Four distinct pairs of prostates are developed in this genus. A bulbous (4 x 3 mm), median pair of ventral prostate glands lies caudad to the bladder. This pair is white when fixed in FAA. Dorsad and laterad to the median pair is a smaller (1 x 1 mm) set, also white in FAA. The ducts of both these pairs of glands enter the ventral and lateral walls of the urethra. The dorsal prostates lie on the dorsal and most anterior portion of the prostatic urethra, are separated by the colon, and drain into the antero-dorsal portion of the urethra. These glands are pink in FAA. The anterior prostates are elongate (6 x 3 mm) and situated in the lesser curve of the vesicular. They are drained by two ducts on each side, which lie parallel to the ductus deferens and the openings of the vesicular ducts.

Neotoma Say and Ord 1825

(Fig. 5d)

In his description of the male accessory glands of this genus Howell (1926) comments on a small sac-like structure in *N. intermedia*

that may have represented a vestigial preputial. I have not examined this species; the members of the genus I dissected showed no preputials.

The bulbo-urethral glands lie in the usual position but are more flattened than those in the other genera examined.

I found no vesicular glands in the specimens I examined.

The ampullary glands are quite large and diffuse. Combined they measure 15 x 10 mm and extend some 5 mm craniad of the anterior extension of the vas deferens. Numerous ducts from each lobe enter the final 5-7 mm of the corresponding vas deferens.

There are two pairs of prostate glands. The ventral prostates are long and narrow (12 x 6 mm) and have filiform tubules; their ducts enter the ventral aspect of the urethra laterad to the neck of the bladder. A very large and diffuse pair of anterior prostate glands lies in the position usually occupied by the vesicular. Their heavily branched tubules present a fan-like appearance, spreading 25-30 mm wide; the individual tubules are widest near the bladder and become narrower as they continue to branch. Two ducts from each side enter the prostatic urethra laterad to the ductus deferens.

The glands Howell (1926) designated as "coagulating" are the ampullary glands, while those he called "vesicular" represent, from their branched, filiform nature, one of the prostate series. According to my interpretation, vesiculars are not present in this genus. Which prostate glands Howell's "vesiculars" represent is not clear. As *Neotoma* has no typical dorsal prostate, these fan-shaped glands could be either highly modified anterior or dorsal prostates. I consider them anterior prostates because (1) the tubules of the dorsal prostates are generally of a smaller diameter than those of the glands in question, (2) the ducts (two on each side) enter the prostatic urethra laterad to the vasa deferentia, and (3) their fan-like structure is more typical of anterior than dorsal prostates. Most forms that have a large anterior prostate also have a large, recurved vesicular, within the lesser curve of which the anterior prostate usually lies. In the absence of vesicular glands, the anterior prostates would probably expand, which could produce the condition found in *Neotoma*.

Tylomys Peters 1866

(Fig. 5e and 5f)

I cannot confirm the presence or absence of preputial glands in this genus as the specimen I had lacked the distal portion.

The ampullary glands are the most distinctive feature of the male

tract of this genus. Each ampullary gland is associated with a corresponding ampulla (Fig. 5f), into which several ducts from each gland enter laterad to the entrance of the vas deferens. The ampulla is the largest and most well developed of any cricetid examined, about 3 mm long, and folded upon itself. It is bulbous, and the ampullary gland laterally attached appears as a diverticulum. This condition is unlike that found in any other cricetid genus examined in this study.

The vesicular glands are lumpy and irregular. They are not truly recurved as in *Sigmodon,* but instead have the anterior ends twisted and lying upon the main body of the gland.

This genus has only two pairs of prostate glands. A small (5 x 3 mm) median, compact pair of ventral prostate glands lies caudad of the bladder, the ducts entering the ventral wall of the urethra just posterior to the bladder neck. A second more diffuse pair is situated at the anterior end of the prostatic urethra on the dorsal border where its ducts enter the urethra. These glands are filiform, as anterior prostates often are, but occupy the position of the dorsal prostates of the other genera. Each part of the gland is composed of about six to eight unconvoluted tubules.

Baiomys True 1894

(Fig. 6a)

A single pair of preputials lies on the sides of the glans. They are small (5 x 2 mm), expanded proximally, and drained by a single duct on each side.

The vesicular glands of *Baiomys* are quite simple and small (8 x 2 mm). They are straight for most of their length, and recurved only at the tip.

The ampullary glands are the most reduced of any genus studied. They consist of four to six simple tubular glands draining directly into the corresponding vas deferens. The individual tubular elements are unconnected and small (less than 1 mm).

Paired ventral, dorsal, and anterior prostates are present. The former are located posterior to the bladder and measure 4 x 3 mm. Their ducts enter the ventral wall of the prostatic urethra caudad of the neck of the bladder. The dorsal prostate glands lie on the anterior cephalic border of the prostatic urethra, and the descending colon passes between their two lobes. Their ducts enter the dorsal wall of the prostatic urethra. The anterior prostates lie at the cephalic end of the urethra and extend along the border of the vesic-

ulars but are not adnate thereupon. They are about 4 mm long, and filiform in appearance. All prostates are white in FAA.

Ochrotomys Osgood 1909

(Fig. 6b)

A single pair of preputial glands lies on the sides of the glans penis. They are small, about 4 x 1 mm, and a single duct drains each.

Ochrotomys is characterized by small vesicular glands which appear as simple tubular structures. They are about 10 x 2 mm and slightly recurved near the tip. The recurving appears to follow no consistent pattern.

Ochrotomys has the most poorly defined prostates of the genera examined. Four pairs are tentatively recognized. A small and bulbous pair of ventral prostates lie posterior to the bladder. A second ventral set, loosely divided into two lobes on each side, is situated laterad to the neck of the bladder. The ducts of both of these sets enter the dorsal aspect of the urethra posteriad and laterad to the bladder. Both ventral sets are white in FAA. The dorsal prostates are small and lie at the anterior, dorsal side of the urethra where the ducts enter the urethra. The anterior prostate glands are compact and lie at the base of the vesiculars. They discharge into the prostatic urethra by what appears to be a single duct on each side, situated next to the vas deferens. Most other genera examined have two ducts draining each member of the anterior prostate pair.

Onychomys Baird 1857

(Fig. 6c)

A pair of long and narrow (8 x 2 mm) preputial glands lies on the lateral sides of the glans penis. Their ducts open near the distal end of the prepuce.

The male genital tract of *Onychomys* is distinctive in that both vesicular and ampullary glands are absent.

This genus has two pairs of prostate glands. A single median pair (4 x 3 mm) of bulbous ventral prostates are white when preserved in FAA. Their ducts enter the urethra on the ventral surface lateral to the neck of the bladder. A median pair of dorsal prostate glands (4 x 3 mm each) is located at the anterior portion of the prostatic urethra in the position usually occupied by the absent vesicular. The lobes are not separated by the colon. The ducts enter the urethra dorsad to the vas deferens.

Taylor (1963) describes the accessory male glands of *O. torridus* (I used *O. leucogaster* here). She considers the dorsal prostates of this study to be "seminal vesicles", *i.e.* vesicular glands. However, the numerous and branching ducts of this gland that she describes are more characteristic of prostatic tissue. As was pointed out above, only embryological studies of the origin of such questionable glands will determine true homologies.

Synaptomys Baird 1857

(Fig. 6d)

A single pair of preputials spreads out upon the M. rectus abdominis from an origin in the tissues of the prepuce. Each is 15 x 10 mm in an adult specimen and is drained by a single duct on its respective side of the glans penis. These broad flaring preputials are a particularly striking feature of the male tract of *Synaptomys*, even among the microtines, whose preputials average proportionally larger than those of any other group examined.

The vesicular glands are simple and tubular, irregular in diameter, and lumpy at certain points. Though their general appearance is not one of extreme irregularity, they are convoluted at the ends in no particular pattern. One measured 15 x 3 mm when straightened. The vesiculars empty into the prostatic urethra adjacent to the vas deferens by means of a single duct from each gland.

The ampullary glands are small, tightly knit glands lying adnate to their corresponding vas deferens into which they drain through numerous ducts. Each ampullary gland appears to contain about eight compound bulbous units, tightly bound about the vas deferens.

Four pairs of prostate glands are recognized. One major pair of elongate (8 x 4 mm) ventral prostates lies slightly posteriad and laterad to the neck of the bladder. A second smaller pair of ventral prostates lies at their base and their ducts are slightly closer to the lateral border of the neck of the bladder. These two sets of glands are not so clearly distinct as those of some other genera. Both are white in FAA. The ducts of both sets pass through the ventral wall of the prostatic urethra, posteriad and laterad to the neck of the bladder. The dorsal prostates are large (8 x 3 mm), situated on the antero-dorsal border of the prostatic urethra, and extend anteriorly for a short distance. Their ducts enter the antero-dorsal wall of the prostatic urethra. The anterior prostates are attenuate glands lying adnate to the dorsal border of the vesiculars for about 8 mm. They are more compact than anterior prostates of some of the cricetids such

as *Sigmodon* or some other microtines such as *Ondatra*. The ducts, two on each side, enter the anterior wall of the prostatic urethra ventrad and laterad to the ducts of the vesicular glands.

Ondatra Link 1795

(Fig. 6e)

The large, paired preputial glands spread across the M. rectus abdominis. The largest gland measured was 50 mm x 10 mm. Each gland is drained by a single duct lying on the dorsal aspect of the glans penis.

The large, heavily convoluted, tubular vesicular glands are very irregular. They twist and turn in no apparent pattern other than accommodation to the other organs of the abdominal cavity. They are moderately branched and lobated but this does not obscure their simple tubular nature. Straightened, a single vesicular may measure as much as 75 mm. Each gland drains through the anterior wall of the prostatic urethra by means of a single duct that lies dorsad and laterad to the ampulla.

The ampullary glands are attached to the vas deferens and drain into it through numerous ducts at the point where it enters the ampulla. These glands cover an area approximately 15 x 10 mm. Three ventral and four dorsal lobes are distinguished in each gland.

There are four pairs of prostates. An elongate (20 x 10 mm) pair of median ventral prostate glands lies posteriad to the bladder. The ducts enter the ventral wall of the prostatic urethra directly caudad of the neck of the bladder. These glands are white in FAA. A smaller (5 x 4 mm), more bulbous and lateral pair of ventral prostate glands that is purple in FAA lies at the base of the larger glands. The ducts enter the urethra near the neck of the bladder. The large (15 x 10 mm) dorsal prostates lie on each side of the colon and on the antero-dorsal border of the prostatic urethra. Large (25 x 8 mm) anterior prostate glands lie upon the ventro-lateral surfaces of the vesiculars. Each opens into the prostatic urethra by four ducts next to the vesicular ducts.

Neofiber True 1884

(Fig. 6f)

A large pair of preputial glands covers part of the M. rectus abdominis. Expanded terminally, they measure 20 x 10 mm. Each gland is drained by a single duct that lies on the lateral aspect of the glans penis.

The vesiculars are large, convoluted tubular glands that measure as much as 50 mm when straightened. They are of fairly uniform (about 5 to 7 mm) thickness. The convolutions are either medial or lateral, and appear to have no constant pattern. Each vesicular gland is drained by a single duct which opens into the prostatic urethra adjacent to the vas deferens.

The ampullary glands partially surround the vasa deferentia, anterior to the neck of the bladder. Each gland is associated with its corresponding vas deferens, into which numerous ducts enter. These glands, like the corresponding ones in *Ondatra,* are divided into several lobes bound tightly together.

Three sets of prostate glands are recognized. A large pair (18 x 11 mm) of ventral prostates lies directly posterior to the bladder. This pair of glands may be teased apart into two lobes on either side. However, since but one duct system seems to enter the prostatic urethra, posterior and slightly laterad to the neck of the bladder, the four lobes apparently represent only one pair of glands. A single pair of dorsal prostates is located on the antero-dorsal wall of the urethra, the colon passing between the two elements. The ducts enter the urethra through the antero-dorsal wall. The paired anterior prostate glands may lie on either the lateral, dorsal, or ventral borders of the vesiculars, and are drained by four ducts on each side. The ducts enter the prostatic region laterad to the ducts of the vesicular glands.

Microtus Schrank 1798

(Fig. 7a)

Hamilton (1941) described the tract of *Microtus pennsylvanicus.*

A single pair of preputial glands is present on the sides of the glans penis. A single duct drains each gland. As Hamilton (1941) states, these are smaller than those of *Synaptomys* and *Clethrionomys.*

The recurved vesicular glands are similar to those of *Clethrionomys* or *Sigmodon,* but smaller. The greater curvature is lumpy, the lesser one smoother. Each gland drains into the prostatic urethra through a single duct that courses dorsad and laterad to the vas deferens.

The paired ampullary glands lie upon the vasa deferentia where the latter converge and enter the urethra, each on its corresponding vas deferens. The glands here considered ampullaries are evidently the "ventral lobes" of the prostate of Hamilton (1941).

Four pairs of prostate glands are recognized in *Microtus.* A median, somewhat elongate (6 x 3 mm) pair of ventral prostate glands

lies posterior to the bladder. A second, more bulbous (4 x 3 mm) pair of ventral prostates is situated more laterally. The ducts of the median pair enter the prostatic urethra posterior to the neck of the bladder while those of the lateral pair enter the urethra near the sides of this structure. Hamilton (1941) did not mention these glands, though they appear in his illustration. The paired dorsal prostate glands lie along the anterior cranial border of the prostatic urethra. The anterior margins of these glands sometimes encroach upon the dorsal borders of the corresponding vesicular glands. The ducts enter the urethra through its antero-dorsal wall under the main body of the gland. Hamilton (1941) did not discuss these glands, though they are visible in his dorsal view of the tract. The paired anterior prostates lie in the lesser curves of the vesicular glands, along the lateral borders. They are drained by two ducts on each side which enter the urethra adjacent to the ducts of the vesicular glands. These are the "ventro-lateral lobes of the prostate" of Hamilton (1941).

Pedomys Baird 1857

(Fig. 7b)

A single pair of preputial glands lies on the sides of the glans penis. They were small (5 x 2 mm) in the specimen examined, and I am not certain they were fully developed for usually the preputials of the Microtinae are large.

The simple tubular vesicular glands are irregular, lumpy, and seem to represent an intermediate condition between the recurved and convoluted types. They are slightly recurved at the terminal portion. A single gland, when straightened, measured 12 x 3 mm. A single duct drains each one.

There is little ampullary glandular tissue evident on the ventral surface of the vas deferens, most of it being concentrated on the cephalic, dorsal and caudal aspects.

There are four pairs of prostate glands. A median, bulbous pair of ventral prostate glands lies caudad to the bladder, where its ducts enter the ventral wall of the prostatic urethra. Each member of the pair is composed of two lobes. As the ducts are confluent and the tubules of the glands appear identical, I recognize only a single set of glands in this position. A second, more lateral pair of ventral prostates lies laterad to the neck of the bladder, where its ducts enter the prostatic urethra. All ventral prostates are white in FAA and formalin. The dorsal prostates lie at the antero-dorsal border of the prostatic urethra, and their cephalic edges encroach upon the dorsal aspect

of the vesiculars. Their ducts enter the dorsal wall of the urethra. The colon passes between these paired glands. The anterior prostates lie along the ventral and lateral aspects of the vesiculars. Each gland is loosely bilobed, the longest lobe (7 x 2 mm) being situated dorsally and projecting farther cephalically. The smaller (3 x 1 mm) is ventral to the larger. These glands empty into the urethra through two ducts on each side, one from each lobe, adjacent to the ducts of the vesicular glands.

Pitymys McMurtrie 1831

(Fig. 7c)

A single pair of preputial glands lies on the sides of the glans penis and is drained by a single duct on each side. These glands encroach slightly upon the M. rectus abdominis.

The vesicular glands are large and irregular, intermediate between convoluted and recurved. The terminal portion is lobate. A single gland measures 10 x 4 mm. The terminal lobes are depressed ventrally, but do not then curve posteriorly. Each gland is drained by a single duct that enters the prostate adjacent to the vas deferens.

The ampullary glands lie in the usual position at the junction of the vasa deferentia, and each is adnate to its corresponding vas deferens. The glands are divided into two major portions, lying massed on the cephalic and caudal aspects respectively of the vas deferens. Several ducts appear to be associated with each ampullary gland.

There are four pairs of prostate glands. A median, bulbous (4 x 4 mm) pair of ventral prostates lies caudad of the bladder, the ducts entering the ventral wall of the urethra posterior to the neck of the bladder. A second, smaller pair of glands (2 x 1 mm) lies laterad to the neck of the bladder, when its ducts enter the prostatic urethra. All ventral prostates are white in FAA and formalin. The paired dorsal prostates lie at the antero-dorsal border of the prostatic urethra, their cephalic edges upon the dorsal aspect of the vesiculars. Their ducts enter the antero-dorsal wall of the urethra. The anterior prostates lie on the ventral border of the vesiculars and are drained by a pair of ducts on each side which enter the urethra adjacent to the ducts of the vesiculars.

Clethrionomys Tilesius 1850

(Fig. 7d)

The vesiculars are recurved and slightly lobate along the greater curve. The inner margins are heavily lobate. They are drained by

a single duct from each gland that enters the anterior border of the prostatic urethra adjacent to the vas deferens. Of the microtines examined, *Clethrionomys* has the most heavily recurved vesiculars. This genus and *Microtus* stand in marked contrast to other microtines with large convoluted vesicular glands, though in other details of the tract all microtines are constant.

The ampullary glands surround the vasa deferentia and open into them through a number of ducts prior to the ampullae. In the specimen examined these glands were dark purple. The original preservative is not known, but they were the only ampullaries studied that were so deeply colored in preservative. In some genera these organs were pink, but never a deep purple. It is interesting to note that the lateral pair of ventral prostates was identical in color to the ampullaries.

Four pairs of prostates are recognized. A small (3 x 5 mm) bulbous median pair of ventral prostates lies directly behind the bladder. These glands are white in the preservative. The ducts enter the ventral wall of the prostatic urethra posterior to the neck of the bladder. A second, more elongate (10 x 4 mm) pair of ventral prostates lies laterad to the bladder; their ducts enter the prostatic urethra laterad to the neck of the bladder. These are the same purple color as the ampullary glands. A large (8 x 5 mm) leaflike pair of dorsal prostate glands lies on the antero-dorsal border of the prostatic urethra through which its ducts pass. The colon passes between the two lobes of this gland. The anterior prostates lie in the lesser curve of the vesiculars, either laterally or medially depending on the nature of the recurving of the corresponding vesicular gland. Each anterior prostate gland is drained by two ducts that enter the prostatic urethra ventrad and laterad to the corresponding vesicular duct.

Rattus Frisch 1775

(Fig. 7e)

The accessory glands have been well studied in *Rattus*, as would be expected in an animal so frequently used in experimental research. The majority of the work on this species has been concerned with the effect of removal of certain prostatic lobes, or effects of hormone treatments. Walker (1910) described the anterior prostates as "coagulating glands" and disclaimed any connection between these and other prostates. Price (1936) considered these glands to be members of the prostatic series, as do most modern workers, although the name "coagulating gland" is still frequently applied.

Price (1936) figured all the accessory glands in *Rattus* grossly and histologically and described their ducts as did Walker (1910) in part. Though further description is unnecessary, I recognize an additional pair of prostates probably of the ventral series, based on what appears to be a separate duct system.

The possibility of a high frequency of morphological aberrations exists in inbred strains of *Rattus*.

Mus Linnaeus 1758

(Fig. 7f)

Snell (1941) gives a very adequate gross description and histology of the male genitalia of *Mus*. The only discrepancy between my observations and those he and others have reported previously is that I recognize two pairs of ventral prostates (as I do for *Rattus*) where Snell and others note only one.

Possible morphological aberrations produced by inbreeding exist in *Mus*.

Discussion

The male accessory reproductive glands of rodents were first considered to be of taxonomic import by Tullberg (1899). Mossman, *et al.* (1932) demonstrated their utility in the Sciuridae, but to date they have received little consideration in studies of the muroid rodents.

Phallic characters, especially the baculum, have been the genital characters most frequently employed in muroid systematics. Neither of the two distinct phallic forms found in the muroids is restricted to any currently recognized taxonomic group (Hooper, 1960). Many New World cricetines have a simple phallic form, distinct from the complex phallus built around a baculum with three distal processes.

The accessory glands of the male reproductive tract of muroid rodents also fall into two groups, almost coinciding with the phallic groupings of Hooper (1960). Surely as more forms are studied these groupings will have to be modified, but among the forms studied, certain patterns are evident (Table 2).

Preputial glands are most common among those genera with a complex phallus. Of the cricetines with a complex phallus only *Mesocricetus* lacks these glands. Two genera, *Sigmodon* and *Akodon*, have two pairs of preputials, a small ventral and a large lateral pair. These glands are most highly developed in the microtines, in which they flare upon the abdominal muscles. Preputial glands were not

noted in *Peromyscus, Reithrodontomys,* and *Neotoma,* all of which have simple phalli. Three other genera (*Ochrotomys, Baiomys,* and *Onychomys*) have both the simple phallic type and preputial glands (Table 2).

The bulbo-urethral glands exhibit the greatest uniformity of all accessory glands in the muroid rodents. With but minor variations these glands are identical in all genera studied. Within the Sciuridae, however, these glands are highly modified (Mossman, *et al.,* 1932).

With the exception of *Nyctomys,* all genera with a complex phallus have vesicular glands (Table 2). Of the genera with the simple phallic type, only *Neotoma* and *Onychomys* lack vesiculars. *Baiomys* and *Ochrotomys* have markedly reduced glands. Only *Peromyscus* and *Reithrodontomys* of the genera with the simple phallus have well developed vesiculars.

The fully developed vesicular glands are usually the largest accessory glands in the forms in which they occur. Basically these are simple tubular glands which upon distention are thrown into convolutions of two types. In cricetines and muroids they become recurved and highly irregular on the greater curve of the gland. In some microtines (and those cricetines in which these glands are reduced) the tubular nature of the vesiculars remains apparent, and numerous fortuitous bends occur. In some genera (e.g., *Ondatra* and *Neofiber*) the convolutions of the vesiculars are evidently determined by the positions of other internal organs. *Clethrionomys* has the generalized, recurved type, while *Microtus, Pitymys* and *Pedomys* are intermediate in form.

The ampullary glands are generally constant in shape. In *Baiomys* these are reduced to several small, unconnected, simple tubular glands draining into their respective vasa deferentia. *Ochrotomys* and *Onychomys* lack these glands. In two genera (*Neotoma* and *Nyctomys*) the ampullaries are large and filiform, probably because of the absence of the vesicular glands which, when present, generally constrict them along the anterior border. *Tylomys* has most distinctive ampullary glands, draining directly into a bulbous ampulla. All others enter the corresponding vas deferens as well as the ampulla by numerous ducts.

The prostate glands vary in form and number of pairs among the various muroid genera and are the most diversified glands of the accessory set. The dorsal prostates occur in all but two genera (*Neotoma* and *Nyctomys*). The ventral prostates are represented by either one pair (7 genera), two pairs (16 genera), or are absent (*Nyctomys* only). If two pairs of ventral prostates are present, one (lateral)

usually assumes a red color in FAA or formalin, and the other (medial) remains white. Although this can probably be safely attributed to the nature of the secretions of the glands, no further information is available. The anterior prostates are present in 22 of 24 genera studied, absent only in *Tylomys* and *Onychomys*. In two other genera, *Neotoma* and *Nyctomys*, these are greatly enlarged. This modification of the anterior prostates occurs in the only two genera in which the vesicular glands are concurrently absent. In *Nyctomys* these are the only prostate glands present.

Variation in the form and number of accessory glands is greater in those genera with the simple phallus type. Four groupings are recognizable among these genera. *Peromyscus* and *Reithrodontomys* lack preputial glands. The remainder of the accessory glands are not highly modified. *Baiomys, Ochrotomys,* and *Onychomys* are the only forms examined with a simple phallic type that have retained preputial glands. Further, the vesicular glands are reduced in *Baiomys* and *Ochrotomys,* and absent in *Onychomys,* while the ampullary glands are greatly reduced in *Baiomys* and absent in the other two genera. A third condition is exhibited by *Neotoma,* in which the condition of the prostates is somewhat similar to that of *Nyctomys,* which has a reduced complex phallus. The anterior prostates are highly modified in both genera, and the vesiculars are absent. Finally, the unusual condition of the ampullary glands of *Tylomys* are unlike those of any rodent examined. I have not studied the remaining genera (*Neotomodon, Sciotionomys, Nelsonia, Xenomys,* and *Ototylomys*) that are known to have a simple phallus (Hooper, 1960), which must be done before they can be positioned by their accessory genitalia.

Genera with the complex phallic type generally show much greater uniformity of accessory glandular structures. *Nyctomys,* which has lost vesicular glands and all prostates except the highly modified anterior elements, is the only exception. The most significant differences between the genera with the complex phallic type are the modifications of the phallus itself, not glandular differences. The diverse assortment of accessory gland complements described above suggest certain generic affinities. These affinities are not, however, in agreement with the commonly accepted taxonomic arrangement of the muroid rodents as outlined by Simpson (1945). The morphology of the phallus (Hooper, 1960) further suggests that the present arrangement of genera is not a natural one. The most frequently encountered combination of genital characters in the forms examined includes the presence of a complex phallus, preputial glands, ampullary glands,

bulbo-urethral glands, well developed vesicular glands of either the recurved or convoluted types, and three basic sets of prostates.

Genera currently classified in three major muroid subfamilies (containing nearly 80% of the Recent Muroidea) exhibit this condition. Among others, *Oryzomys* (Cricetinae), *Clethrionomys* (Microtinae), and *Rattus* (Murinae) demonstrate this basic pattern. The similarity of the reproductive tract in such supposedly diverse forms, coupled with the complexity of the structures involved, leads to the assumption that this combination of genital characters is a generalized, or primitive, condition for muroid rodents, and possibly for the Myomorpha in general.

Although slight variation in number of prostatic pairs was noted, neither genus of the Murinae examined diverged far from the basic pattern shared with the cricetines and microtines.

The microtines are conservative in the characters of the male accessory glands with but slight generic differences noted. This is not surprising, as this group of rodents is closely knit in most morphological features (Simpson, 1945; Hooper and Hart, 1962). The adherence to the basic pattern of reproductive structures is perhaps unexpected, however, as the microtines are commonly assumed to be one of the more specialized branches of the Cricetidae.

It is within the cricetines as currently constituted that the greatest divergence from the generalized pattern occurs. The Old World members (Cricetini) are similar to the Microtinae and the Muridae. The New World cricetines (Hesperomyini) fall into two distinct groups. Those of basically Neotropical affinities (*Sigmodon, Oryzomys, Akodon, Phyllotis, Nectomys, Oecomys,* and doubtlessly others not examined) resemble the Cricetini, Microtinae, and Muridae. Those of essentially Nearctic affinities differ strongly from these groups. As pointed out by Hooper (1960) the North American forms (and a few others) have the simple phallus. Of these *Peromyscus* and *Reithrodontomys* have retained relatively complete sets of accessory glands, but others (*Neotoma, Onychomys, Ochrotomys, Baiomys,* and *Tylomys*) possess highly modified accessory gland complements. This dichotomy in the Hesperomyini is substantiated by Rinker (1954) who demonstrated that *Sigmodon* and *Oryzomys* are myologically quite distinct from such forms as *Neotoma* and *Peromyscus.*

Hooper and Hart (1962) have shown that a trend toward simplification of the complex phallic type can be seen in the microtines. The murid phallus is but a modification of the complex type. The Hesperomyini of the simple phallic type may not be a homogeneous group. The wide diversity in accessory glandular complements sug-

gests that they are not, but may result from more than one modification of the basic cricetine stock. The condition of *Nyctomys* further suggests that this trend is still in progress. *Nyctomys* has a glandular complement similar to *Neotoma*, but the most simplified of the complete types of phallus examined.

The murids are assumed to have a cricetid ancestry (Simpson, 1945). On the basis of the reproductive tract, this would have to have been a cricetid with a complex phallus and a complete set of accessory glands. Numerous cricetines with such reproductive structures, and typified by such modern genera as *Sigmodon* or *Oryzomys*, could be similar to the murid ancestral stock.

An interpretation of muroid phylogeny based solely on the morphology of the male reproductive tract is contrasted to the currently accepted classification in Figures 8 and 9. Such an arrangement is purely speculative and is not meant to propose taxonomic revision at this time. It seems obvious however, from the data presented herein, and those of other workers, that the Cricetinae is not a natural group. The New World cricetines (Hesperomyini) in particular are in need of revision. If the Cricetinae is to be retained in its currently accepted vastness, encompassing microtines, Cricetini, and the diverse Hesperomyini, among others, then from the evidence afforded by the morphology of the male reproductive tract, the Muridae should be included as well. This would essentially conform to the all-inclusive Muridae of Ellerman (1940) or of Hershkovitz (1962). It is possible however, that as more information becomes available, some of the muroid groups will be placed into newly constituted taxa, and the Muridae and Cricetidae will be retained in a more restricted usage.

TABLE 1

LIST OF SPECIES AND NUMBER OF SPECIMENS (IN PARENTHESIS) EXAMINED

Order: Rodentia
Suborder: Myomorpha
Superfamily: Muroidea
Family: Cricetidae
Subfamily: Cricetinae
Tribe: Cricetini
Mesocricetus auratus (5)
Tribe: Hesperomyini
Oryzomys palustris (10)
Oecomys tectus (2)
Nectomys alfari (2)
Tylomys fulviventer (2)
Nyctomys sumicrasti (1)
Reithrodontomys humulis (2)
Peromyscus gossypinus (4)
Ochrotomys nuttali (2)
Baiomys taylori (1)
Onychomys leucogaster (1)
Akodon sp. (1)
Phyllotis darwini (1)
Sigmodon hispidus (50)
Neotoma floridana (3)
Subfamily: Microtinae
Tribe: Lemmini
Synaptomys cooperi (2)
Tribe: Microtini
Clethrionomys gapperi (1)
Ondatra zibethicus (6)
Neofiber alleni (4)
Pitymys pinetorum (3)
Microtus pennsylvanicus (2)
Pedomys ochrogaster (1)
Family: Muridae
Subfamily: Murinae
Rattus norvegicus (10)
Mus musculus (5)
Total number examined . . . 120

TABLE 2

SUMMARY OF THE VARIATION IN ACCESSORY GLANDS OF 24 MUROID GENERA

Genera	*Phallus*	*Preputial*	*Bulbo-Urethral*	*Ampullary*	*Vesicular*	*Prostates (Pairs)*		
						Dorsal	Ventral	Anterior
Mesocricetus	C	0	X	X	X	1	1	1
Sigmodon	C	X*	X	X	X	1	2	1
Akodon	C	X*	X	X	X	1	1	1
Oryzomys	C	X	X	X	X	1	2	1
Oecomys	C	?	X	X	X	1	2	1
Nectomys	C	X	X	X	X	2	2	1
Phyllotis	C	?	X	X	X	1	2	1
Nyctomys	C	0	X	X	0	0	0	1-4?
Neotoma	S	0	X	X	0	0	1	1-4?
Tylomys	S	?	X	X	X	1	1	0
Peromyscus	S	0	X	X	X	1	2	1
Reithrodontomys	S	0	X	X	X	1	2	1
Baiomys	S	X	X	X	X	1	1	1
Ochrotomys	S	X	X	0	X	1	2	1
Onychomys	S	X	X	0	0	1	1	0
Synaptomys	C	X	X	X	X	1	2	1
Ondatra	C	X	X	X	X	1	2	1
Neofiber	C	X	X	X	X	1	1	1
Microtus	C	X	X	X	X	1	2	1
Pitymys	C	X	X	X	X	1	2	1
Pedomys	C	X	X	X	X	1	2	1
Clethrionomys	C	X	X	X	X	1	2	1
Rattus	C	X	X	X	X	1	2	1
Mus	C	X	X	X	X	1	2	1

Phallus Types: C = complex, S = simple, X = glands present, 0 = glands absent, * = two pairs present

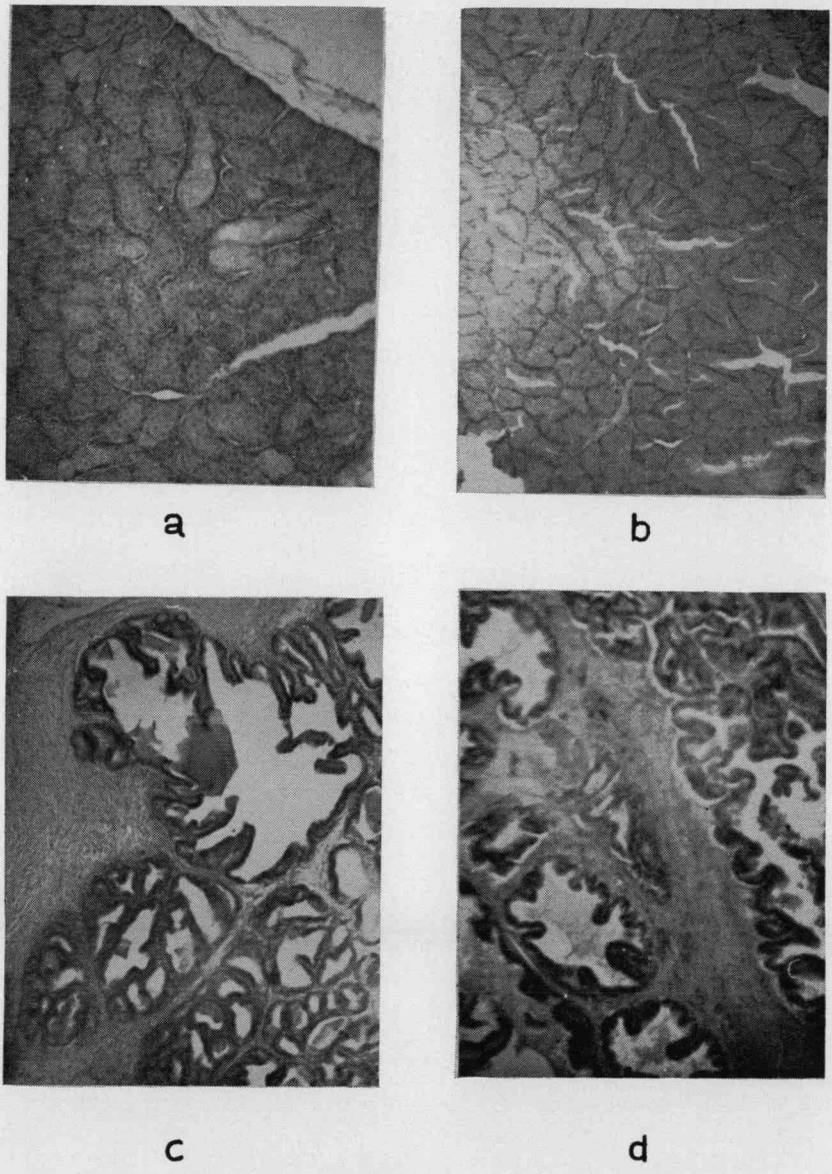

Figure 1. Cross sections of accessory reproductive glands of *Sigmodon hispidus:* a, preputial; b, bulbo-urethral; c, vesicular; d, ampullary. x 100.

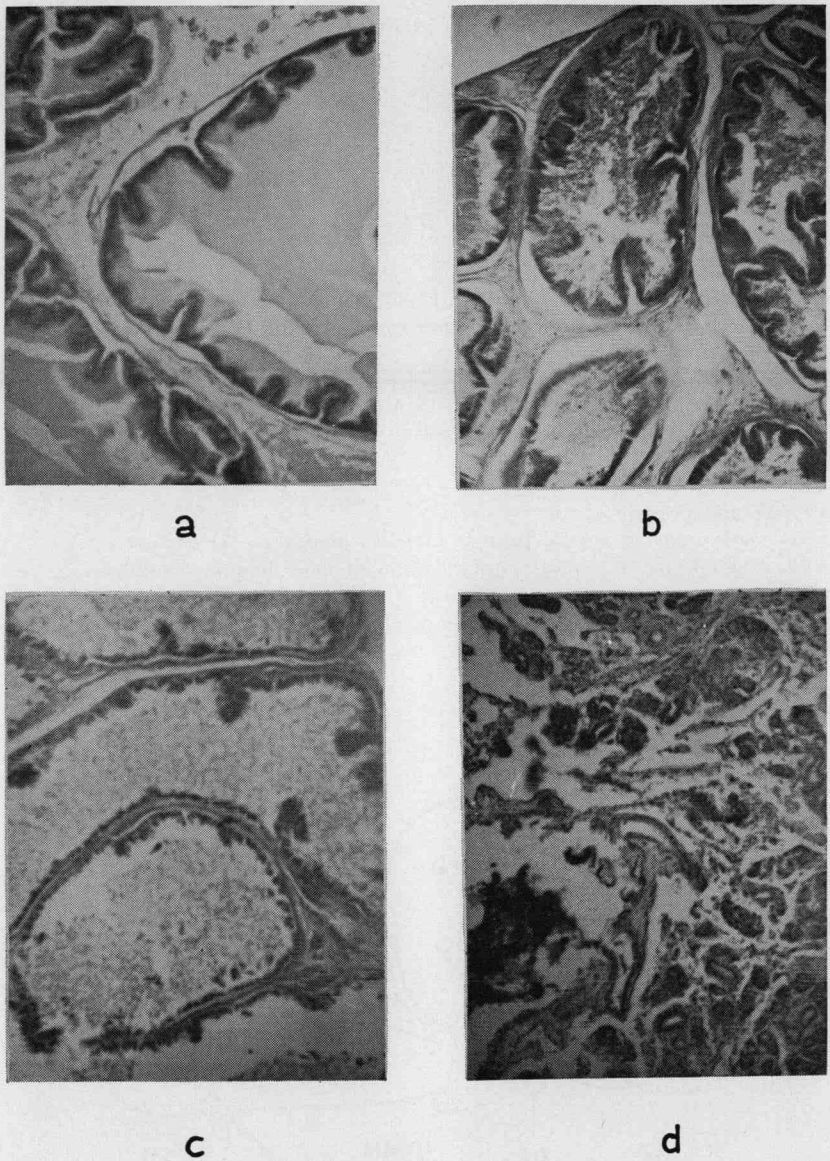

Figure 2. Cross sections of accessory reproductive glands of *Sigmodon hispidus:* a, ventral prostate; b, dorsal prostate; c, anterior prostate; d, urethral glands. x 100.

ABBREVIATIONS USED IN FIGURES 3, 4, 5, 6, 7

A—Ampullary gland
AMP—Ampulla of vas deferens
AP—Anterior prostate gland
B—Bladder
B(C)—Bladder (neck cut)
BU—Bulbo-urethral gland
D-A—Duct of ampullary gland
DP—Dorsal prostate gland
DPI—Primary lobe of dorsal prostate gland (if more than one present)
DPII—Secondary lobe of dorsal prostate gland (if more than one present)
P—Phallus
PR—Preputial gland
PRI—Primary lobe of preputial gland (if more than one present)
PRII—Secondary lobe of preputial gland (if more than one present)
V—Vesicular gland
VD—Vas deferens
VP—Ventral prostate gland
VPI—Median lobe of ventral prostate gland (if more than one present)
VPII—Lateral lobe of ventral prostate gland (if more than one present)

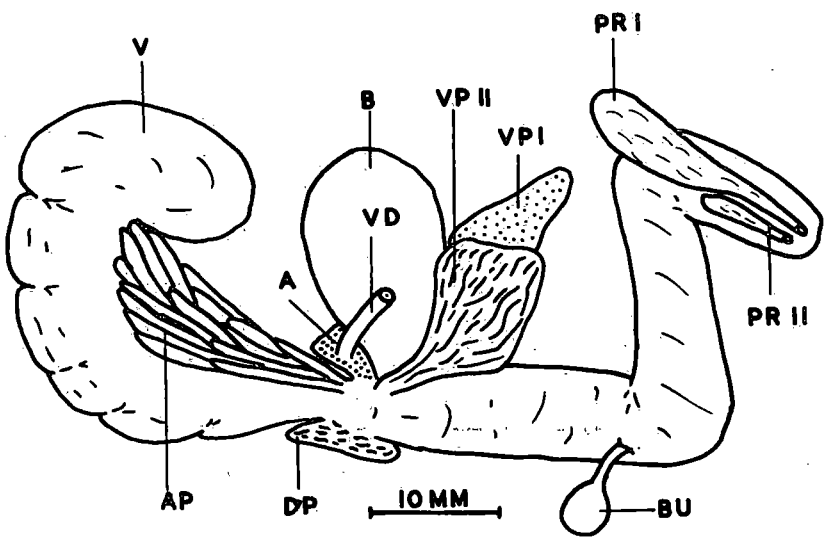

Figure 3. Lateral view of the male reproductive tract of *Sigmodon hispidus*.

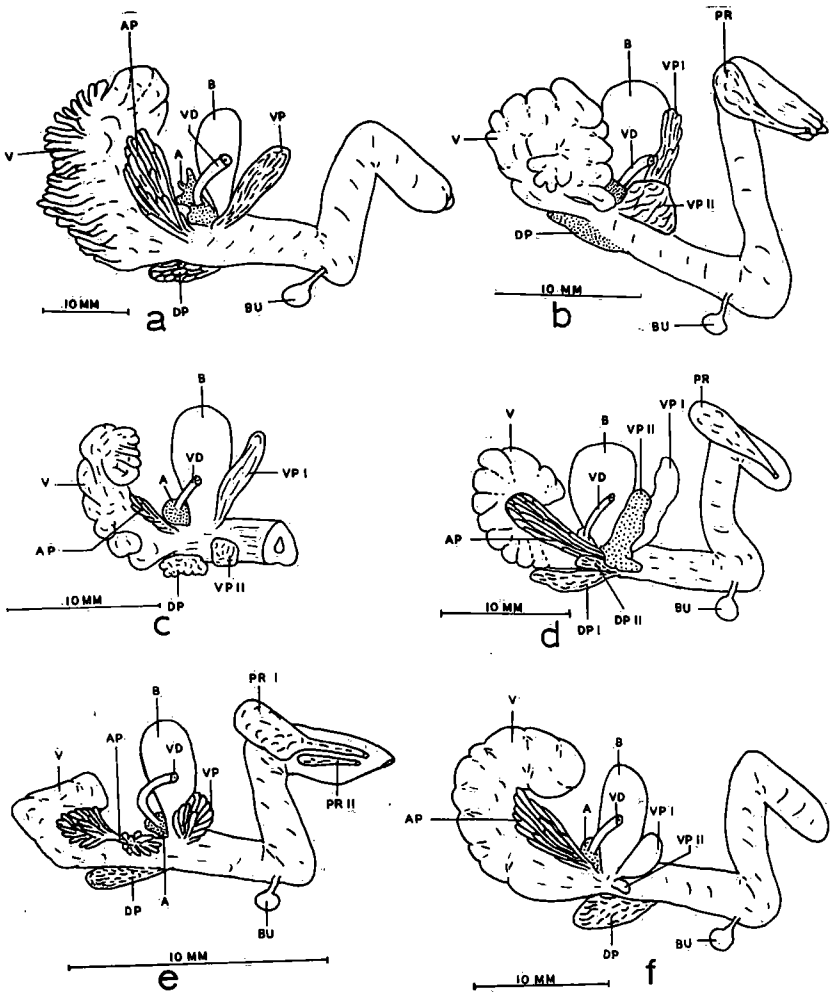

Figure 4. Male reproductive tracts of muroid rodents: a, *Mesocricetus*; b, *Oryzomys;* c, *Oecomys;* d, *Nectomys;* e, *Akodon;* f, *Phyllotis.* (For key to abbreviations see page 34.)

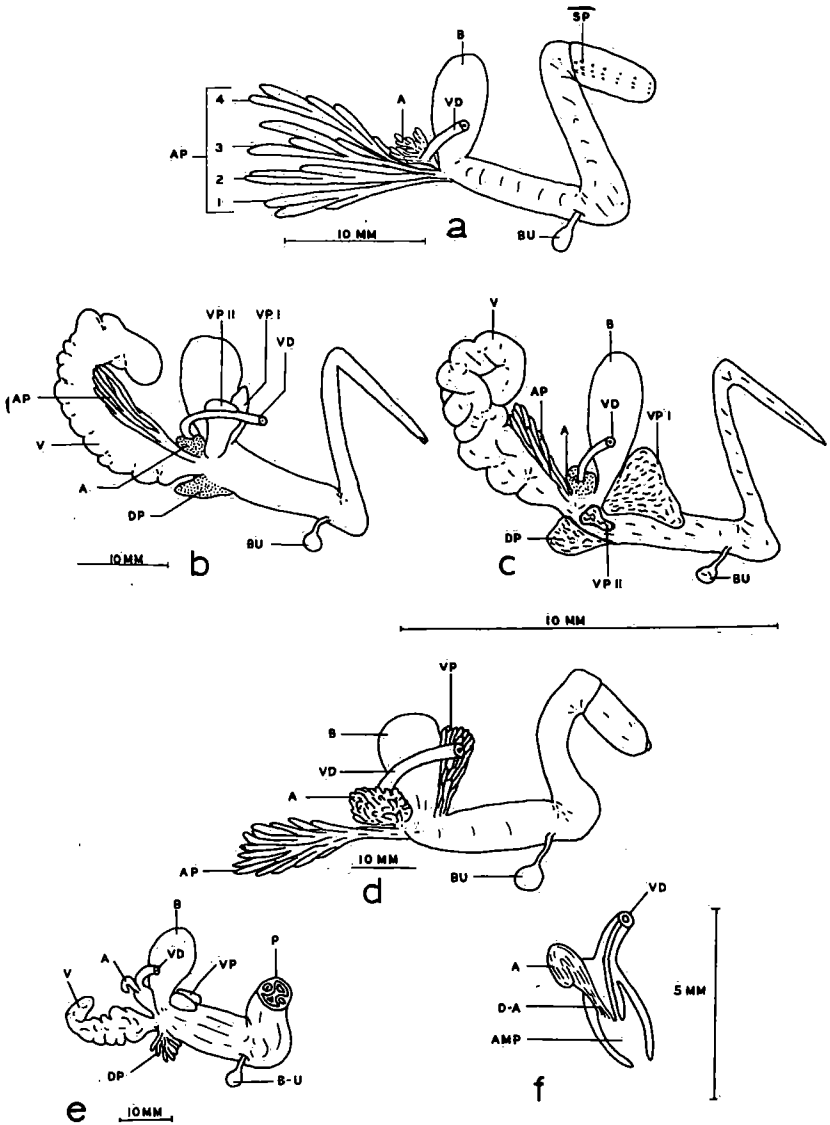

Figure 5. Male reproductive tracts of muroid rodents: a, *Nyctomys*; b, *Peromyscus*; c, *Reithrodontomys*; d, *Neotoma*; e, *Tylomys*; f, diagrammatic cross section of the ampulla of *Tylomys*. (For key to abbreviations see page 34.)

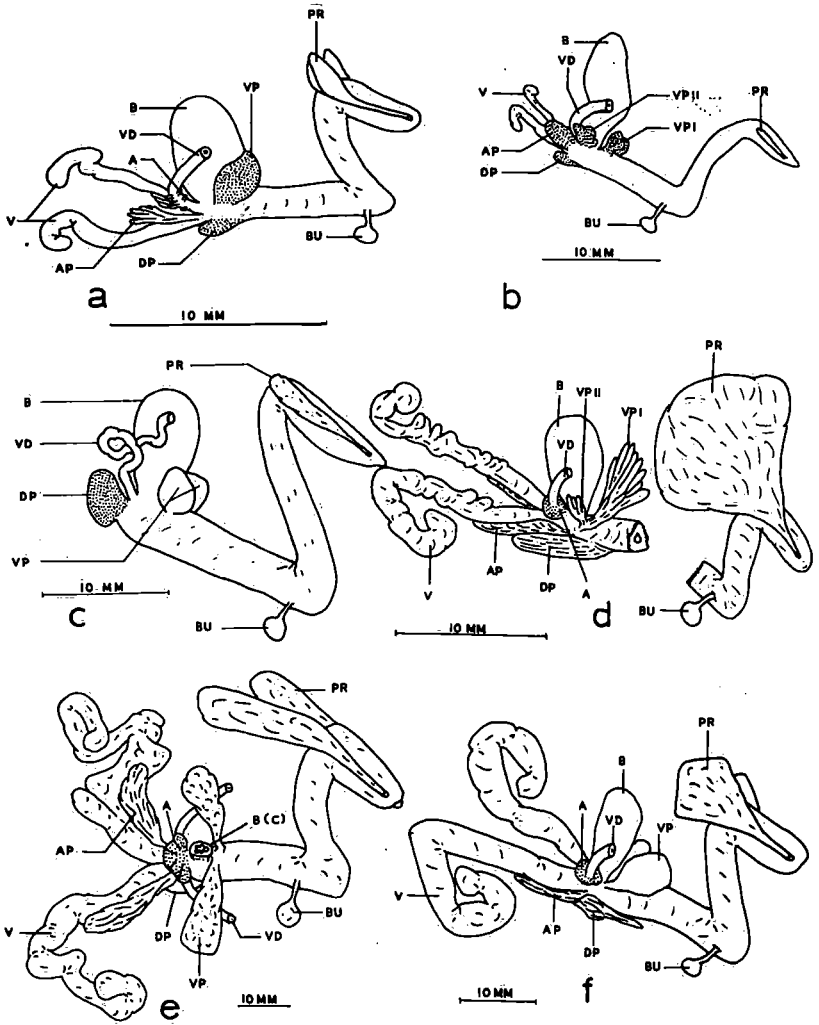

Figure 6. Male reproductive tracts of muroid rodents: a, *Baiomys*; b, *Ochrotomys;* c, *Onychomys;* d, *Synaptomys;* e, *Ondatra;* f, *Neofiber.* (For key to abbreviations see page 34.)

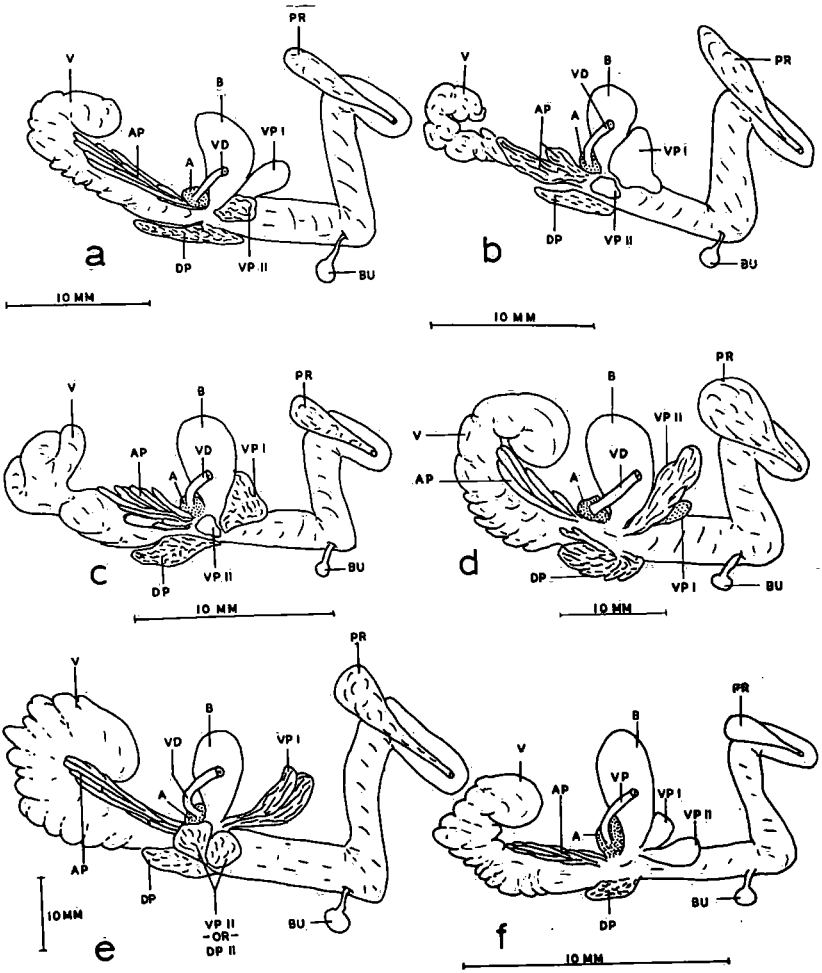

Figure 7. Male reproductive tract of muroid rodents: a, *Microtus*; b, *Pedomys*; c, *Pitymys;* d, *Clethrionomys;* e, *Rattus;* f, *Mus.* (For key to abbreviations see page 34.)

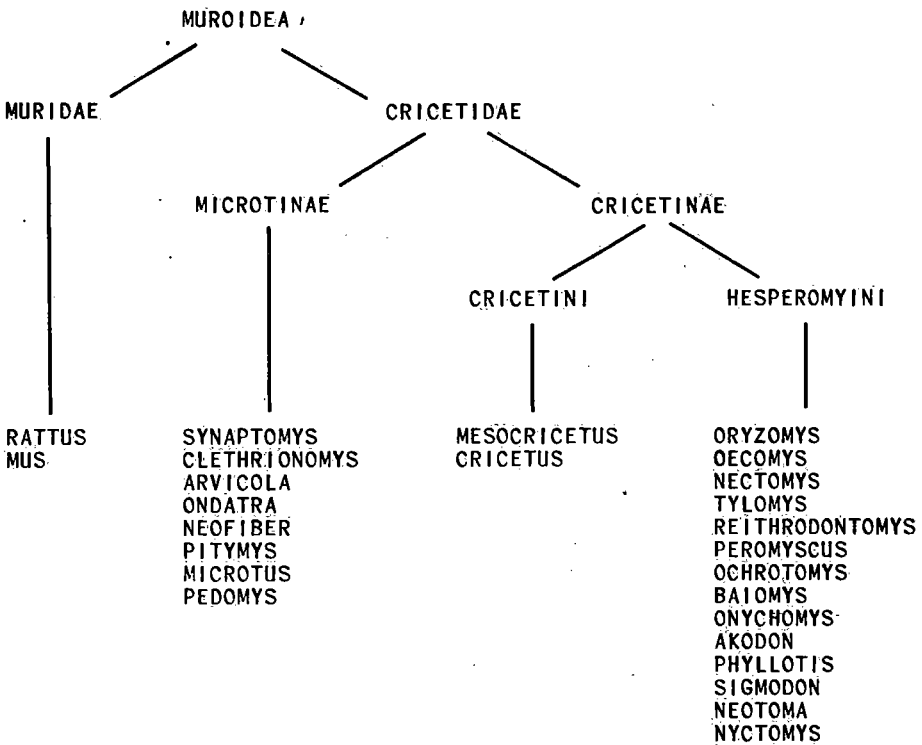

Figure 8. Interrelationships of certain muroid genera according to the currently accepted classification (Simpson, 1945).

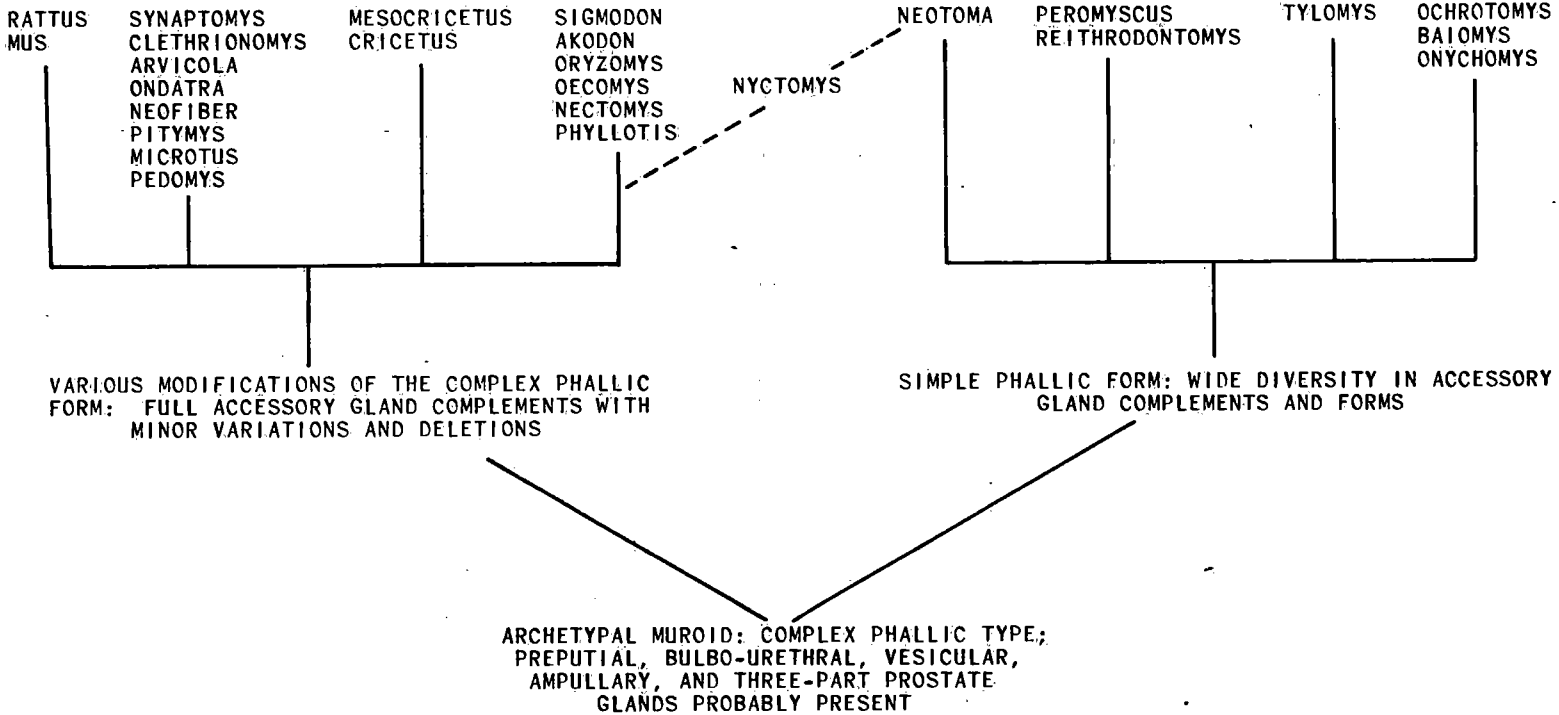

Figure 9. Interpretation of the relationships of the genera in figure 8 based on the morphology of the male reproductive tract. As explained on page 29, no taxonomic levels are indicated because too few genera have been examined to establish them soundly.

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