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**THE GLANS PENIS IN FIVE GENERA
OF CRICETID RODENTS**

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THE rodent family Cricetidae consists of several hundred species comprised in some 90 genera and five subfamilies (Simpson, Bull. Amer. Mus. Nat. Hist., 85, 1945). Although it may be generally presumed that these genera and subfamilies are natural assemblages of closely related species, there is a strong possibility that all are not. The subfamily Cricetinae is a case in point. Recent work on the myology of some of these rodents (Rinker, Misc. Publ. Mus. Zool. Univ. Mich., 83, 1954) and my own studies of the male phallus indicate that an important dichotomy exists within the subfamily, and that dichotomy may, in fact, lead out of the Cricetinae into other subfamilies of muroid rodents. It seems clear, then, that although the many species of cricetids are classified in genera and subfamilies, the complex interrelationships of those species really are not well understood. Masses of new data need to be brought to bear on the problem. To serve that purpose a survey of cricetids, in regard to the anatomy of the glans penis, has been initiated.

This is the second of an intended series of reports on the subject. The initial one (Hooper, Misc. Publ. Mus. Zool. Univ. Mich., 105, 1958) dealt with variations of the phallus in *Peromyscus*. Present accounts describe the glandes in five other genera, namely *Reithrodontomys*, *Neotomodon*, *Onychomys*, *Baiomys*, and *Nelsonia*.

MATERIALS AND METHODS

The phalli described here are from fluid-preserved animals as follows:

Reithrodontomys megalotis: Arizona, Navaho Co., 1; Washington, Walla Walla Co., 1. *R. humulis*: Florida, Alachua Co., 1. *R. fulvescens*: Texas, Jeff Davis and Brewster counties, 2. *R. sumichrasti*:

Chiapas, near Pueblo Nuevo Solistahuacán, 2. *R. mexicanus*: Chiapas, near Pueblo Nuevo Solistahuacán, 2.

Neotomodon alstoni: México, Puerto Lengua de Vaca and Río Frío, 3; Morelos, near Distrito Federal line, 3.

Onychomys leucogaster: Colorado, Las Animas Co., 2. *O. torridus*: Texas, Brewster Co., 2.

Baiomys musculus: Oaxaca, near Tlacolula, 6. *B. taylori*: Michoacán, Tuxpan, 2.

Nelsonia neotomodon: Durango, near San Luis, 1.

In order to check various anatomical details I examined additional specimens of all of the five genera except *Nelsonia*, but those examples were not measured, sketched, and studied in detail and, therefore, they are not listed.

All specimens are contained in the University of Michigan Museum of Zoology with the exception of the example of *N. neotomodon* which was kindly provided by R. H. Baker from the collections at Michigan State University. I am indebted to J. H. Layne for specimens of *R. humulis*, to Balvir Saini who made the camera lucida sketches, and to W. L. Brudon for the completed drawings. The present study was initiated with financial aid provided by the Horace H. Rackham School of Graduate Studies, University of Michigan. Continued support is provided by the National Science Foundation.

The technique of processing the phalli is essentially that described elsewhere (Hooper, *op. cit.*). Each formalin-fixed specimen was partially cleared in 2 per cent KOH, stained in alkaline alizarin, in three stages passed through increasing concentrations of glycerine and water, and stored in pure glycerine. In contrast to the earlier procedure, the specimen was removed from KOH before it was translucent and before the spine-bearing epidermis had softened and begun to slough off. Two days in KOH at room temperature is usually sufficient for specimens of *Reithrodontomys* or *Onychomys*; longer periods are required for phalli of *Neotoma* and other larger animals. When not excessively cleared the specimen is intact and nicely pliable for dissection.

In measuring the specimens I used a micrometer disc calibrated to read to the nearest tenth of a millimeter. The measurements (Table I) are as follows:

Length of hind foot: Conventional length, from heel to tip of longest claw, of the right hind foot of fluid-preserved specimens.

Length of glans: Greatest distance on mid-longitudinal plane of

glans; measured from its base, where it joins the prepuce, to its distal limits.

Diameter of glans: Greatest diameter of glans, including spines.

Length of os penis: Straight-line length of osseous part of the baculum.

Length of cartilage tip: Length, distal to the bone, of the cartilaginous tip of the baculum.

Plates I-V, rendered directly from camera lucida tracings, accurately represent the shape of the glans and of some of its component parts. The baculum, situated deep within the glans, is indicated by dense stippling (osseous portion) and sparse stippling (cartilaginous part). The broken lines extending proximad from the base of the baculum mark the position of the corpora cavernosa penis. Immediately ventral to the corpora and baculum is the urethra, shown as a series of parallel stripes. Spinous areas on the surface of the glans are indicated by label and differential shading, and a few of the spines, highly magnified, are reproduced in an inset on each plate. In the longitudinal sections (Pls. IVc, Vb) some layers are distorted, pulled apart when the incised specimen was pinned open for sketching.

Since the specimens are drawn to different scales, vertical bars are provided on each plate to indicate relative size of each glans with respect to the length of the hind foot. Absolute sizes as well as ratios are listed in Table I.

DESCRIPTION OF PHALLI

REITHRODONTOMYS

In *Reithrodontomys* the glans penis is an elongate, rod-shaped structure similar in size and shape to the glans of *Peromyscus maniculatus*, *P. polionotus*, and other species of the *Maniculatus* Group (see Hooper, *op. cit.*). It consists of two topographic divisions; (1) a tapered, somewhat protractile tip, its outer tissues soft, pliable and non-spinous; and (2) a main body composed of comparatively dense tissues, some of which are spinous. The distal margin of the body, where it invaginates and joins the tip, is crenate and puckered ventrally; dorsally it is comparatively smooth. As in *Peromyscus*, the dorsal margin is situated well distal to the ventral one. Furthermore, in the specimens of *fulvescens* and *humulis*, but not the other species, the margin is slightly cleft middorsally, forming two lappets as seen in *Peromyscus*. Midventrally, it is lightly notched and the notch is

bounded by slight projections, but these processes are not as long and clear-cut as in *Peromyscus*. Situated immediately dorsal to these processes, and at the base of the protractile tip, is the meatus urinarius. The baculum is a simple osseous rod, enlarged basally and blunt distally, and apparently without a terminal cap or spine of cartilage; the bone is much longer than the glans.

In all species sampled to date, namely *humulis*, *megalotis*, *sumichrasti*, *fulvescens*, and *mexicanus*, the glans has the same basic shape and structure. Notwithstanding this basic similarity there appear to be slight interspecific differences in size and shape of glans and in distribution of spines on its outer surface. These differences are mentioned in the following brief accounts, in which *megalotis* is used as a standard for comparisons.

R. megalotis.—Glans an elongate modified cylinder (Pl. I), its length 4 or 5 times its greatest diameter and $1/3$ the hind foot length (Table I). Body of glans evenly cylindrical, without raphae or other folds or grooves except distally where it invaginates to merge with the protractile tip. Surface of its basal portion comparatively smooth, that of the remainder of the body armored with sharp, proximally directed spines (Pl. I), these smaller and more closely spaced distally than proximally. Distal border of body of glans crenate ventrally and entire dorsally, without dorsal or ventral processes. Terminal segment of glans comprised of an elongate capsule of soft, non-spinous tissues covering the tip of the baculum, the surface of the capsule evenly convex dorsally and laterally, and concave ventrally, forming a gradually narrowed channel for urinogenital products. Urethra, situated in ventral sector of glans, courses along ventral face of the baculum and terminates at the ventral base of the protractile tip.

The baculum is a simple, gently arched, osseous rod, largest and spatulate basally, and comparatively blunt terminally; its length much greater than that of the glans and approximately $1/2$ the hind foot length.

R. humulis.—The only specimen of *humulis* at hand is a young adult. Although the phallus is not fully grown it closely resembles the glans of *megalotis*, differing from it in minor features as follows: shorter and larger in diameter with respect to length, its diameter $1/4$ the length, and the length $1/4$ that of the hind foot; basal non-spinous area larger; distal, dorsal border of glans body less deeply cleft, forming two short, blunt, dorsal processes; and baculum shorter, its length $1/3$ the hind foot length.

R. sumichrasti.—Glans more stubby than that of *megalotis*, its

diameter almost $1/3$ (rather than $1/4$) its length and its length actually and relatively less than in that species (Table I). The difference in length attributable mostly to the non-spinous tip, this segment being shorter and more closely confined to the glans body in *sumichrasti*. Non-spinous area at the base of the glans slightly smaller. Baculum similar in the two species, perhaps larger basally and more strongly curved distally in *sumichrasti*.

R. fulvescens.—Glans and baculum much as in *megalotis*; the bone, however, slightly larger in diameter, the distal border of the glans body deeply cleft middorsally—forming two, long, dorsal processes—and the distal $1/4$, as well as the basal $1/4$, of the body spineless.

R. mexicanus.—Glans and baculum larger in all dimensions in *mexicanus* than in *megalotis*, but the two species similar in proportions of parts and in length with respect to that of the hind foot. Spines longer and thicker and the spineless basal area larger in *mexicanus* (Pl. I).

NEOTOMODON

The glans of *N. alstoni*, the only species of the genus *Neotomodon* (Miller and Kellogg, Bull. U. S. Natl. Mus., 205, 1955), is a minute, awl-shaped structure with a dense coat of spines over much of its surface, a terminally situated meatus urinarius, and a slender osseous baculum capped by a cartilaginous cone. In size, shape, and position of urethral opening it resembles the glandes of *Peromyscus banderanus* and *P. floridanus*; however, it is by no means identical with the phallus of either of those species.

N. alstoni.—Glans small, its length 4 times the greatest diameter and $1/5$ the hind foot length; awl-shaped and subcylindrical; largest basally and tapered gradually distad, but abruptly reduced in diameter at a subapical collar (Pl. II) formed by a simple infolding of the surface layers. This collar topographically divides the glans into two parts; a cylindrical, spine-covered body and an attenuate, nonspinous tip. The body composed of dense, resilient tissues, its even contours interrupted midventrally by a low raphe extending from the base of the glans to the subapical collar. Surface armature comprised of sharp, proximally directed spines, each seated in a circular pit; these spines larger and more closely spaced proximally than distally, but these entirely absent in three areas, namely, a narrow strip bordering the raphe, a band girdling the base of the glans, and the subapical collar. Distal segment of glans (beyond collar) laterally compressed and blade-like, the dorsally situated heel of the blade supported by the distal part of the baculum; the thinner ventral part, consisting of

soft tissues, arranged as a triangular funnel and trough leading distad from the urethra, and opening at the tip of the glans.

The baculum is a simple osseous rod approximately as long as the glans and $1/6$ the hind foot length. Its basal part, situated in the ventral flexure of the penis, wider than deep, somewhat triangular in dorsal or ventral view. Its shaft cylindrical, slightly bowed, tapered gradually distad, and terminating in a slight enlargement capped by a cartilaginous cone 0.1–0.2 mm. in height.

ONYCHOMYS

In *Onychomys* the glans is a comparatively simple, yet distinctive, organ comprised externally of a globular or elongate body that merges, by way of a subapical collar, with a bud-like tip. Its armament is impressive. Almost all of the glans is covered with curved, sharp, overlapping, proximally directed spines. Small on the subapical collar and on the sides of the terminal bud, these spines are progressively larger toward the base of the glans where they attain a length as much as 0.6 mm. The baculum, laterally compressed for most of its length, is much shorter than the glans and is confined to it, no part of it extending proximal to the glans-prepuce junction.

The phalli of the two known species of *Onychomys* are basically similar, nevertheless the glans of each kind apparently is unique in several features, as indicated below.

O. torridus.—Glans constituting almost all of the distal tract (Hooper, *op. cit.*), the glans-prepuce junction situated at the ventral flexure (the base of that tract). Longest dorsally, that length about twice the greatest diameter and $2/5$ the hind foot length. Comprised of two topographic divisions, namely, an oval body and a bud-like tip, the two regions separated by a shallow groove (Pl. III). The oval body compressed dorso-ventrally, that diameter clearly less than the transverse one. The bud-like tip tapered distad, terminating in a small, triangular dorsal lip and a longer funnel-shaped structure situated laterally and ventrally, these two parts bordering the urethral opening. The glans heavily armored with sharp, curved, overlapping spines; these largest on the basal half of the glans (their maximum length there exceeding 0.5 mm.) and smallest on the sides of the terminal bud; these absent, however, at the tip of the bud and at the extreme base of the glans.

Baculum consisting of a single blade-shaped bone confined to, and much shorter than, the glans, its length slightly less than $1/3$ that of the hind foot (Table I). Its extreme proximal part inflated, slightly

wider than deep. This small bulbous base tapered sharply into the laterally compressed shaft, its depth as much as twice its breadth. The shaft gradually diminishing in depth distad, terminating in a slight head capped by a thin layer of cartilage.

O. leucogaster.—Glans impressively spinous and topographically similar to that of *O. torridus*, but slimmer in appearance, the body more nearly circular in cross-section, and distinct in other details. Glans longer dorsally than ventrally, its greatest length about $2/5$ that of the hind foot, as in *torridus*. A wider, more distinct collar or ledge present at the junction of the bud-like tip and the main body of the glans, however, and the body almost circular in cross section, the transverse diameter but slightly exceeding the dorsoventral one and amounting to no more than $1/3$ the greatest length of the glans. The oval tip terminating in four flaps of soft tissue, a lateral pair and smaller ones dorsally and ventrally, these encircling the meatus urinarius. The spiny outer coat present over all of glans except its extreme base and part of the tip, and the spines largest on the basal half of the glans, as in *torridus*.

The baculum is an osseous blade, its length $1/4$ that of the hind foot and no more than $3/4$ the length of the glans. The basal part inflated, its breadth and depth about equal. Remainder of the bone thin and deep and tapered, knife-like, to an obtuse tip covered with a thin layer of cartilage.

BAIOMYS

The glans in the two known species of *Baiomys* is a bell- or urn-shaped structure terminating in a shallow crater that is largely filled by a mound of soft tissue. Superficially it resembles the glans of *Ochrotomys nuttalli* (Hooper, *op. cit.*), but that similarity does not carry over to details in structure of the phalli of the two genera. The two species of *Baiomys* are distinguishable on the basis of absolute size of glans, but in proportion of parts and in fundamentals of that organ the two species are closely similar.

The architecture of the glans is shown in Plate IV. The baculum, situated near the center of the cylinder, serves as the structural core. Attached basally to the corpora cavernosa penis, it extends distad for most of the length of the glans, its cartilaginous cap joined to, and covered by, soft tissues within the terminal crater. Immediately ventral to the baculum, and closely bound to it, is the urethra; its lumen and muscular walls are viewed longitudinally in Plate IVc. For much of its length the central column composed of baculum and

urethra is rather loosely joined laterally, by filamentous tissue, to a thick, spongy layer which is riddled with sinuses. These spaces seem to be part of the circulatory system, apparently draining into the deep dorsal vein. Lateral to this thick layer is the epidermis in which the spines are seated. The positions and relative thicknesses of the several layers as indicated in Plate IVc are approximately correct with the exception of the filamentous area. In an undissected specimen that area is a narrow sleeve of tissue between the muscular urethra and the spongy layer, the two lying in close juxtaposition; they separate when the specimen is stretched, as the one is in Plate IVc.

B. musculus.—Glans stubby, its greatest length less than twice its greatest diameter (Table I) and $1/4$ the hind foot length; rather evenly cylindrical, but slightly constricted in the middle of its length, and with a short, mid-ventral raphe at its base; terminating in a shallow crater surrounding a mound of soft, wrinkled, non-spinous tissue (Plate IV). Its surface, except that of the crater and of a narrow band girdling the base of the glans, densely covered with small, proximally directed spines, these longer and more widely spaced proximally than distally. Rim of crater finely striated, the small ridges and grooves spiraling downward into the crater and upward onto the medial mound that houses both the tip of the baculum and, in a depression within the mound, the meatus urinarius.

The baculum is a single somewhat ornate bone, its length approximately equal to the ventral extent of the glans and $1/5$ the hind foot length. Its basal portion angular, concave ventrally, and with a broad, rounded, proximally directed process and two lateral flanges, the latter two extending laterad and ventrad; lateral border of each flange prolonged distad as an attenuate process, this projection apparently increasing in length with age. Shaft of the bone broader than deep, slightly to deeply concave ventrally and, in old animals, constricted subapically. Distal portion again enlarged, medially cleft, convex dorsally, concave ventrally, and crowned with a thick layer of cartilage.

B. taylori.—Glans like that of *B. musculus*, but smaller in all dimensions except length of baculum (Table I) and thickness of the cartilage layer capping that bone.

NELSONIA

The glans of the monotypic genus *Nelsonia* is a rigid, elongate organ, simple in form externally, but somewhat elaborate internally. Of the numerous phalli studied to date, representing 37 genera of

muroid rodents; the glans of *Nelsonia* is perhaps most similar to types seen in *Neotoma*; nevertheless it is distinct from any of those.

Nelsonia neotomodon.—Glans externally simple in form, finger-like, largest basally, tapered distally, and blunt terminally; its length less than 3 times its greatest diameter (Table I) and $1/3$ the hind foot length. Its tissues comparatively hard and rigid, much less pliable than in other species discussed here. Subterminal $1/6$ of its surface bare and smooth, the remaining proximal $2/3$ and terminal $1/6$ dotted with short, conical tubercles, each set in a circular depression; distal tubercles as much as twice the size of those situated near the base of the glans. Those also present on the lips of the terminal orifice and on the walls of the internal crater, a large segment of the walls being elevated as a wide, internal, armored plate divided midventrally by a smooth, longitudinal groove. Internal crater unusually deep, extending $4/5$ the length of the glans, its outer walls thick, resilient and rugose (proximal $2/3$) or tuberculate (distal $1/3$), these walls surrounding a central column composed of the baculum and, ventral to it, the urethra (Pl. V). Urethra terminates slightly proximal to the tip of the bone, its ventral lip prolonged as a conical process, and its lateral walls continued distad as ridges along the ventral face of the bone forming a trough for the conduction of fluids to the mouth of the crater.

Baculum consisting of a bone capped with a long cartilaginous spine, its overall length $1/3$ that of the hind foot. The bone simple, extending approximately from ventral flexure just into the distal third of the glans, its length $1/4$ the hind foot length. Its angular, broad, and dorsoventrally flattened basal part tapered gradually into a cylindrical shaft, this terminating in a rounded head capped by a long cartilaginous cone; length of the cone almost $1/2$ that of the bone.

DISCUSSION

To date, in this initial phase of a comprehensive survey of the glans penis in cricetid rodents, 98 species representing 37 genera have been examined and figured. Although the survey is still far from complete, there are now sufficient data at hand to indicate that the glans is rich in systematic characters and that these very likely will provide significant clues to the interrelationships of cricetids, particularly at generic and higher levels. Several basic phallic patterns are evident in the 98 species, and each may indicate a phyletic line within the Muroidea. These patterns and their possible significance will be dis-

cussed in subsequent reports when the data are more nearly complete and when generalizations are then warranted.

Suffice it to say now that the five genera discussed here, namely *Reithrodontomys*, *Neotomodon*, *Onychomys*, *Baiomys*, and *Nelsonia*, all of which are cricetines in current classifications, have the same fundamental type of phallus. It is a comparatively plain structure with a simple baculum and few or no external or internal adornments. The same simple type is also seen in *Peromyscus*, *Neotoma*, *Tylomys*, and *Scotinomys*.

Those nine genera, and undoubtedly others not yet studied, stand in strong contrast to groups that include *Sigmodon*, *Oryzomys*, *Oecomys*, *Nectomys*, *Akodon*, *Phyllotis*, and *Hesperomys*. In these seven genera, also supposedly cricetines, the glans is an elaborate organ equipped with internal processes and a compound baculum. It has much in common with the phallus of microtines and that of some murid genera, as for example *Apodemus*, *Acomys*, and *Meriones*.

Thus, preliminary data on the male phallus suggest that the subfamily Cricetinae is polyphyletic. They indicate further that a classification based on anatomy of the phallus may not jibe with current classifications which are founded largely on cranial, especially dental, characters. It remains to be seen which of the two schemes most likely reflects the true relationships of muroid rodents.

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TABLE I
MEASUREMENTS AND PROPORTIONS OF THE GLANS AND BACULUM IN ADULT SPECIMENS
OF 5 GENERA OF RODENTS

Genus and species	Specimens	Mean Measurements (in mm.)					Ratios (in percent)			
		hind foot	lengths			diameter of glans	lengths		glans diameter length	
			glans	os penis	cartilage tip		glans foot	os foot		
<i>Reithrodontomys</i>										
<i>megalotis</i>	2	17	6.0	7.8	0	1.3	35	46	22	
<i>sumichrasti</i>	2	19	5.4	7.9	0	1.6	28	42	30	
<i>fulvescens</i>	1	19	6.5	8.0	0	1.4	34	42	21	
<i>mexicanus</i>	2	19	7.0	8.4	0	1.7	37	44	24	
<i>Neotomodon</i>										
<i>alstoni</i>	6	26	4.9	4.7	0.2	1.3	19	18	27	
<i>Onychomys</i>										
<i>torridus</i>	2	20	8.7	5.8	0	4.1	43	29	47	
<i>leucogaster</i>	2	21	8.1	5.2	0	2.5	39	25	31	
<i>Baiomys</i>										
<i>musculus</i>	5	15	3.9	3.2	0.4	2.3	26	21	59	
<i>taylori</i>	2	13	3.7	3.2	0.1	1.9	28	25	51	
<i>Nelsonia</i>										
<i>neotomodon</i>	1	26	7.9	5.9	2.7	2.9	30	23	37	

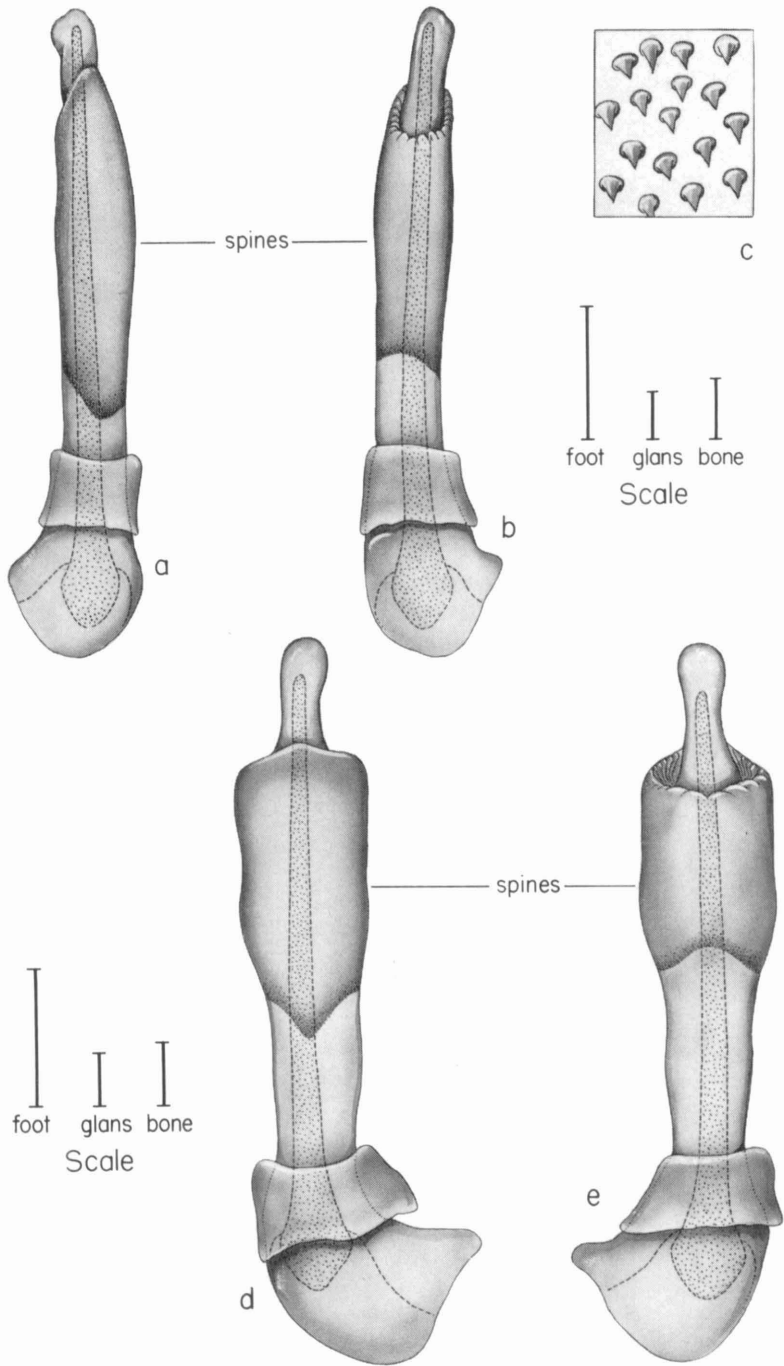


PLATE I

Glans penis in two species of *Reithrodontomys*. *a* and *b*, dorsolateral and ventral views, *R. megalotis*; UMMZ No. 59524, Walla Walla Co., Washington. *d* and *e*, dorsal and ventral views, *R. mexicanus*; UMMZ No. 109186, Pueblo Nuevo, Chiapas, México. *c*, enlargements of spines present in deeply shaded areas of *a*, *b*, *d*, and *e*.

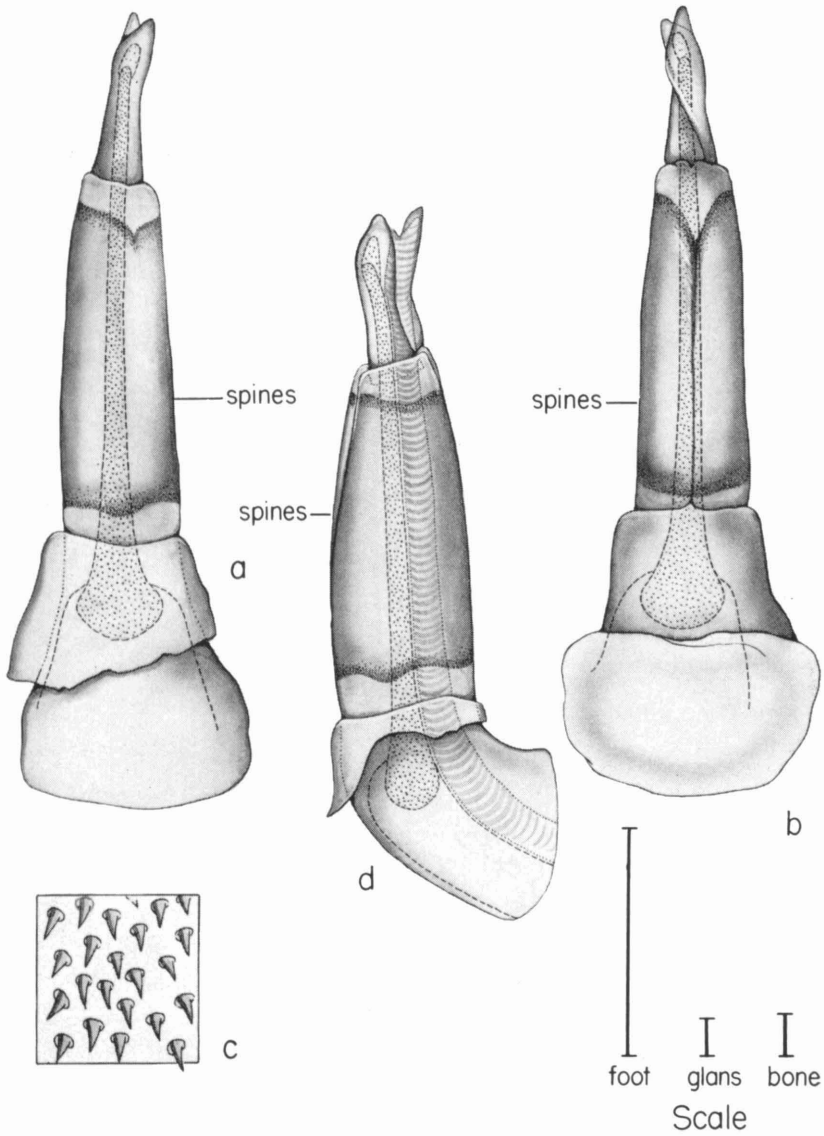


PLATE II

Glans penis in *Neotomodon alstoni*. *a*, *b*, and *d*, dorsal, ventral, and lateral views. *c*, enlarged segment of spinous areas in these views; UMMZ No. 108839, Lengua de Vaca, México.

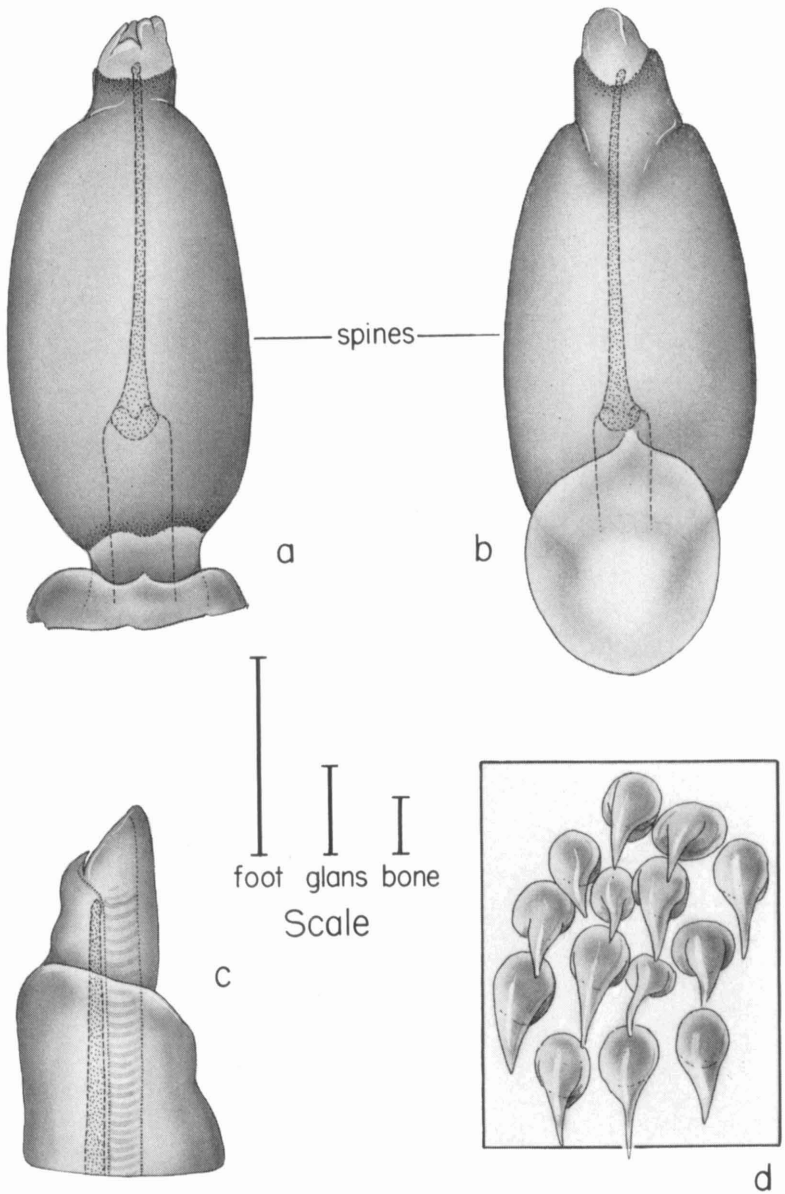


PLATE III

Glans penis in *Onychomys torridus*. *a* and *b*, dorsal and ventral aspect. *c*, enlarged lateral view of distal part of glans showing position of urethra and baculum. *d*, magnified segment of spinous areas (deeply shaded) of glans; UMMZ No. 101614, Brewster Co., Texas

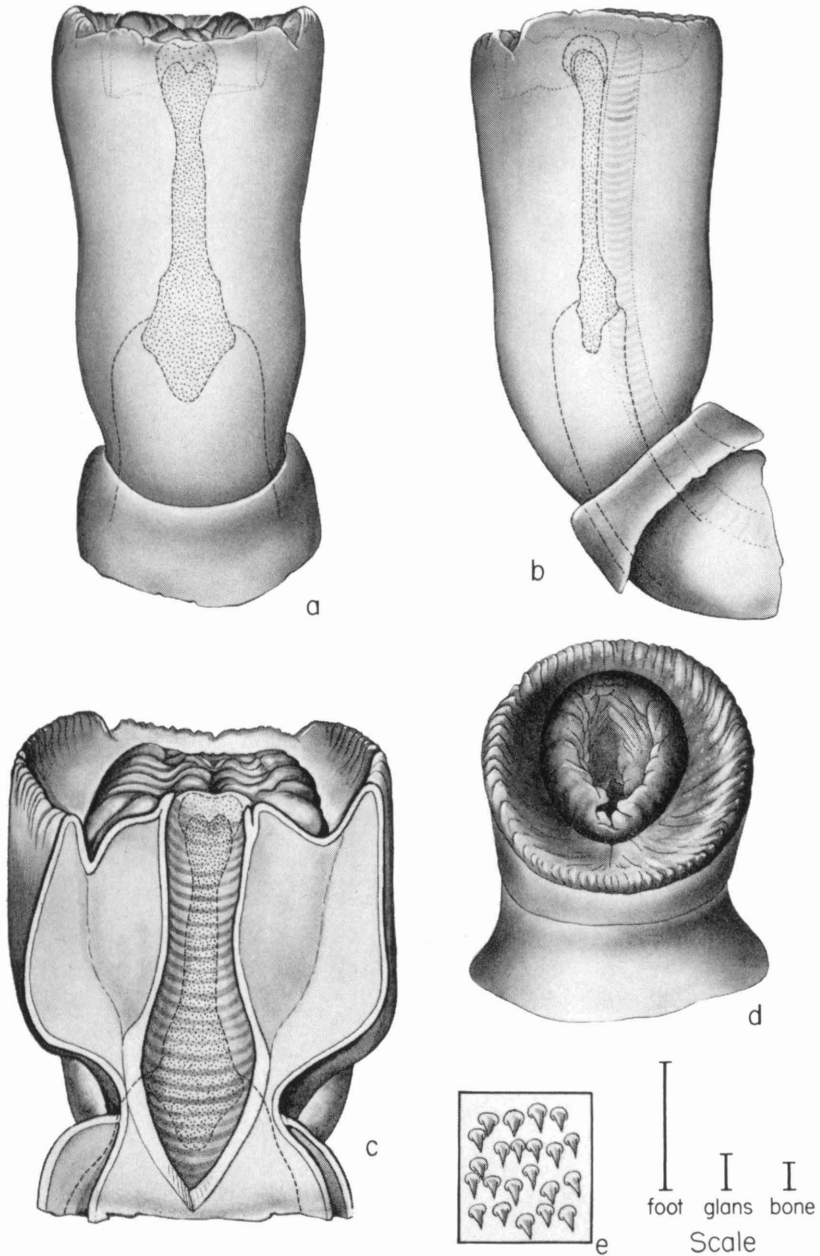


PLATE IV

Glans penis in *Baiomys musculus* as seen: *a*, dorsally; *b*, laterally; *d*, apically; and *c*, in longitudinal section; specimen incised midventrally to expose lumen of urethra and, dorsal to it, outline of baculum. *e*, enlarged segment of spiny coat of glans. UMMZ No 108712, near Oaxaca, México.

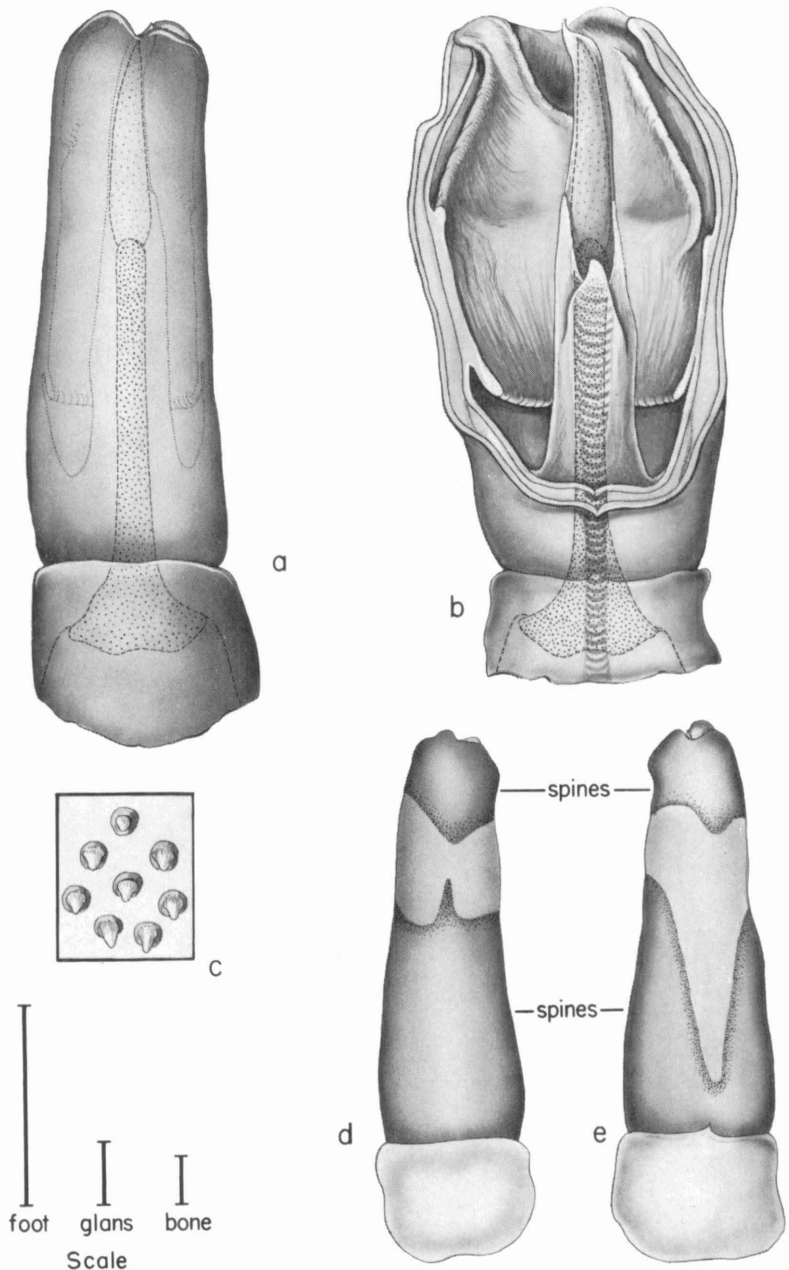


PLATE V

Glans penis in *Nelsonia neotomodon* as viewed: *a*, *d*, dorsally; *e*, ventrally; and *b*, in midventral longitudinal section through outer layers into the deep internal crater. *c*, enlargement of tubercles present both externally (deeply shaded areas in *d*, *e*) and internally, on distal third of the crater walls. Mich. State Univ. No. 3004, near San Luis, Durango, México.

