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THE GLANS PENIS IN *NEOTOMA* (RODENTIA) AND ALLIED GENERA

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THIS report, the third of a series describing male phalli of cricetid rodents, deals with the genera *Neotoma, Xenomys, Ototylomys, Tylomys,* and *Scotinomys.* In these and other genera treated to date (Hooper, 1958, 1959) the glans is comparatively simple, with few or no processes or adornments, and its baculum consists of no more than two parts, a proximal osseous segment and a terminal, usually conical, mass of cartilage. With few exceptions, other genera of New World cricetids possess more elaborate glandes that are embellished with an assortment of soft and spinous adornments, and the baculum in each is comprised of a proximal unit and three distal segments, the four parts typically osseous or cartilaginous. Phalli with those characteristics will be described in detail in subsequent reports.

MATERIALS AND METHODS

The phalli described here are in the Museum of Zoology, University of Michigan (UMMZ); Natural History Museum, University of Kansas (KU); Museum of Vertebrate Zoology, University of California (MVZ); Los Angeles County Museum (LAM); and U. S. National Museum (US). I am indebted to the custodians of those collections and to other colleagues and students who graciously made special effort to provide me with formalin-fixed adult specimens. Those persons are : J. S. Findley, N. L. Ford, E. R. Hall, C. O. Handley, Jr., R. S. Hoffmann, C. J. Jones, J. K. Jones, W. Z. Lidicker, Jr., C. A. McLaughlin, A. P. Olson, R. R. Patterson, W. B. Quay, W. J. Schaldach, and A. Starrett. The illustrations (Pls. I–XI) are the work of W. L. Brudon, expert staff artist of the Museum of Zoology. These studies receive financial support from the National Science Foundation.

The specimens represent species and geographic areas as follows: *Neotoma albigula*: Arizona, Coconino Co., 1; New Mexico, Valencia Co., 1, Bernalillo Co., 2; México, Aguascalientes, 1, Zacatecas, 2. *N. alleni*: México, Nayarit, 3. *N. cinerea*: Montana, Carbon Co., 3, Missoula Co., 1. *N. floridana*: Florida, Monroe Co., 1; Kansas, Douglas Co., 2. *N. fuscipes*: California, Monterey Co., 2, San Diego Co., 1. *N. lepida*: California, Los Angeles Co., 2. *N. mexicana*: México, Chiapas, 2, Durango, 1, Guerrero, 2. *N. micropus*: New Mexico, Eddy Co., 2; Oklahoma, Cimarron Co., 1. *N. phenax*: México, Sonora, 2. *N. stephensi*: Arizona, Coconino Co., 1. *Xenomys nelsoni*: México, Colima, 1. *Ototylomys phyllotis*: El Salvador, 1; Guatemala, 1; Nicaragua, 2. *Tylomys fulviventer*: Panamá, 2. *T. nudicaudatus*: México, Chiapas, 2. *Scotinomys teguina*: Costa Rica, 1; El Salvador, 1.

Procedures are described in detail elsewhere (Hooper, 1958, 1959). The phalli were processed through solutions of KOH and alizarin and transferred to glycerine for permanent storage. Camera lucida tracings were made of selected examples and all specimens were measured by means of an ocular micrometer. The measurements (Table 1) are as follows:

Length of hind foot: Conventional heel to claw-tip length of the right hind foot.

Length of distal tract: Length of that part of penis extending beyond its ventral flexure; measured from tip of glans to a plane touching the proximal face of the flexure (Hooper, 1958:fig. 1).

Length of glans: Greatest length of glans on mid-longitudinal plane; measured from its base, where it joins the prepuce, to its distal limits (Hooper, *loc. cit.*).

Length of os penis: Chord length of basal, osseous segment of the baculum.

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

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

Plates I–XI are scale models of translucent specimens. They are rendered directly from camera lucida tracings from which most artifacts have been deleted. The baculum, situated deep within the glans, is indicated by dense stippling (osseous part) and sparse stippling (cartilaginous segment). Broken lines extending proximad from the bone's base mark positions of the corpora cavernosa penis; and less distinct broken lines outline the terminal and internal craters and other parts within the glans. Faint horizontal bars, situated ventral to the corpora and baculum, indicate the urethra. Spine-bearing areas on the surface of the glans are delimited by bold dashed lines; and a few of the spines, highly magnified, are shown in insets on the plates. Since the specimens are drawn to different scales, vertical bars are provided to indicate relative sizes of glans and baculum with respect to length of hind foot. Absolute sizes as well as ratios are stated in Table 1.

A few anatomical terms (bold face type below) require definition and amplification: From the musculus bulbocavernosus the penis courses craniad and ventrad and then, when at rest, it flexes sharply caudad and shortly thereafter is enveloped by the prepuce. That part of the penis that lies beyond this **ventral flexure** is the **distal tract.** In most cricetids, two-thirds or more of the tract is glans, but in some species, *Neotoma phenax* and *N. fuscipes* for example, the glans constitutes no more than one-half of the tract and, thus, it is situated some distance from the ventral flexure.

The surface of the glans typically is armed with low conical **tubercles** or, more often, with sharply pointed, proximally directed **spines,** each usually projecting from a depression in the epidermis. Characteristics of these surface spines vary among the species. They may be conical or keeled, longitudinally curved or straight, broadly spaced or closely packed and overlapping, and narrowly or widely distributed on the glans. When they occur throughout the length of the glans they are typically graded in size, the largest being near the base of the glans and the smallest situated distally. The extreme basal part of the glans, at its junction with the prepuce, is non-spinous. So is the low, mid-ventral ridge, the ventral **raphe.**

The urethra courses along the ventral face of the baculum and terminates as the **meatus urinarius** somewhere near the tip of the glans. In all species treated here, except *Ototylomys phyllotis,* the urethra is confluent distally with a chamber, the **internal** or **terminal crater.** These craters contain the distal part of the baculum (including its enveloping tissues) and usually a urethral flap and other structures. Configuration of the crater and its contents vary specifically and generically. The **urethral process** or **urethral flap** is an extension of the mid-ventral lip of the meatus urinarius. It is situated either at the confluence of the urethra and the crater or at the external opening of the crater. At either location it apparently acts as a flutter valve at the terminus of the urogenital canal, typically abutting against some part of the cartilaginous spine of the baculum.

The **dorsal papilla** is an elongate cone of soft tissue situated mid-dorsally on the floor of a terminal crater between the crater wall and the mound of tissue that houses the tip of the baculum. It contains a vascular sinus and is erectile. Typical of species that have a compound, three-pronged baculum, it is usually absent in species with comparatively simple bacula and glandes. Of the species treated here, it occurs only in *Xenomys nelsoni* and *Neotoma alleni*.

The **baculum** approximates the median longitudinal axis and, in most species, is the structural core of the glans. When fully grown it typically consists of at least two parts: a bone and, attached distally to the bone, a cap or spine of cartilage. The expanded proximal part of the bone, referred to as the **base**, tapers distad into a narrower **shaft** which may bear a terminal enlargement or **head.** The proximal face of the bone, where the corpora cavernosa insert, is usually enlarged laterally as a pair of **condyles;** these are directed dorsolaterad. The baculum may be completely imbedded in dorsal tissues of the glans, as it is in *Tylomys,* or various parts of it may be free in the terminal crater, as in the other species treated here. Any free part is enclosed in an envelope of soft tissue.

DESCRIPTION OF PHALLI

NEOTOMA

There is considerable diversity in *Neotoma* in regard to morphology of the phallus. Some of the species are closely similar while others contrast markedly in many features of glans and baculum. In the following accounts the species are arranged approximately according to degree of resemblance of their phalli; any other systematic arrangement is disregarded.

Neotoma albigula and Allies

In morphology of phallus, *albigula, floridana, micropus,* and *mexicana* are much alike. In each the glans is robust and oblong, its length twice the greatest diameter and approximately 2/5 the hind foot length. It is almost as large as the prepuce and it constitutes most of the distal tract (Table 1). Almost all of the surface is spinous, the spines moderate in size. A smooth-walled, internal crater opens to the exterior between a dorsal hood and a ventral urethral flap; the flap either is entire or it is divided distally into two processes. There is no urethral process at the confluence of the urethra and the floor of the crater. The baculum is comparatively gross (its length approximately 1/3 that of the foot) and most or all of its cartilaginous tip and envelope of soft tissue lie within the internal crater and are entirely free of its walls. The remainder of the baculum is buried in tissues of the dorsal sector of the glans.

Of the four species, *mexicana* is the most distinctive. The other three, *albigula, floridana,* and *micropus,* are so similar as to suggest that they are conspecific or are sibling species. The samples of the species are compared below.

N. albigula.—Glans oblong and corpulent (Pl. I), almost as large as its prepuce and constituting 3/4 the extent of the distal tract; its length twice the greatest diameter and 2/5 the hind foot length. Basal 3/4 topographically plain, covered densely with moderate-sized, curved, sharp spines, but without lobes or ridges other than a low mid-ventral raphe. Distal 1/4 sculptured, its wrinkled, mostly nonspinous, and undulating ventral sector sloping distad and dorsad to the urogenital opening and to a large hood overhanging that opening (Pl. I *a, b*). Ventral lip of the opening equipped with a pair of attenuate urethral processes. Internal crater smooth and spineless, without processes at its confluence with the urethra. Head of the os penis and all of its terminal cartilaginous spine contained within the crater and free of its walls; remainder of baculum imbedded.

Baculum composed of a bone capped by a long cartilaginous spine (Table 1), their combined lengths 3/4 that of glans and 1/3 the hind foot length. Base of bone much wider than deep and with lateral facets and condyles, the dorsal face between them slightly concave and the ventral face deeply and broadly concave. The base tapered gradually into a cylindrical shaft, this slightly enlarged distad and terminating in a broadly rounded head. Terminal cartilage consolidated in a symmetrical cone, its length 2/5 that of the bone.

N. floridana.—Glans and baculum closely similar to those of *albigula* but for slight differences as follows: Glans larger (Table 1); its terminal hood relatively smaller and faintly cleft (not entire) distally; urethral processes shorter and wider; crater shallower, occupying terminal 1/4 (rather than 1/3) of glans; a shorter segment of baculum (distal 3/4 of cartilaginous spine) free in crater. Os penis slightly shorter and cartilaginous spine larger, relative to lengths of glans and foot (Table 1), *floridana* being between *albigula* and *micropus* in these characters; the bone also slightly different in configuration. (Pl. I *g*), with a wider and more angular base which usually bears lateral flanges that join the sides of the shaft somewhat abruptly, rather than gradually; a small knob projects distad from the head of the bone.

There are fewer distinctions between *floridana* and *micropus*; *floridana* has shorter urethral processes, a shallower crater with less exposure of baculum, and a slightly different os penis, in which characters it differs equally from both *micropus* and *albigula*.

N. micropus.—Glans and baculum like those of *albigula* (Pl. I *a–c*) except for slight differences as follows: glans larger (Table 1), its terminal hood relatively smaller and slightly cleft distally (not entire); osseous part of baculum shorter and its spine longer, relative to both glans and foot length (Table 1).

Its phallus is also similar to that of *floridana* but for slight distinctions as follows: urethral processes longer and narrower, crater deeper (occupying terminal 1/3 rather than 1/4 of glans); a longer segment of the baculum—head of os penis and all of cartilaginous spine—free of crater walls; configuration of the os slightly different, the base narrower and more evenly tapered distad and the terminal head without, or with, a smaller, distally projecting knob.

N. mexicana.—Glans (Pl. II) robust, oblong, and spinous. Generally similar in shape, surface armature, dimensions, and most proportions to the glandes of *albigula*, *floridana*, and *micropus*, but differing from them as follows: Internal crater deeper, its floor situated below tip of os penis; distal part of bone and all of its terminal cartilaginous spine, thus, contained within the crater and free of its walls. Urethral flap shorter (not protruding outside mouth of crater), blunt, and entire (not divided distally into two processes). Osseous part of baculum different (Pls. II and I). The bone is described below: Slightly sinuous in lateral view and paddle- or violin-like in ventral aspect, its shape different in each specimen at hand, all of them from adult animals. Basal 1/2 spatulate and angular; its ventral surface essentially flat in one specimen, shallowly concave in two, and more deeply concave between lateral flanges in a fourth specimen; its dorsal surface narrowly concave between angular, lateral condyles. Distal 1/2 club-like, smallest proximally, largest subapically, and constricted just proximal to a terminal enlargement, this lightly cleft distally (Pl. II *b*).

Neotoma stephensi

In a classification based on morphology of glans and baculum, *N. stephensi* should be placed between *N. mexicana* and *N. phenax*, as suggested by Hoffmeister and de la Toore (1959), for its characters are in various degrees shared with those two species. Its glans is smaller than that of *mexicana* and *phenax*, but the exterior proportions and spiny coats of the three are similar. In length of glans and baculum with respect to foot length (Table 1), and in shape of the os penis, *stephensi* is nearer *phenax*. It is between those two species in regard to length of glans with respect to length of distal tract. It is like *mexicana* alone in configuration of the tip of the glans: there is a terminal hood above the urogenital opening, rather than a proboscis through which the urogenital canal passes to the exterior; the baculum lacks the long, terminal, soft process that is present in *phenax;* and the urethral process is stubby and is situated at the mouth of the internal crater, rather than being longer, distally cleft, and located at the floor of the crater. Finally, *stephensi* is unlike both *mexicana* and *phenax* and like *Ototylomys* in that the cartilaginous spine of the baculum is short (about 1/4 length of bone) and only its tip is free of the crater walls. Thus, *N. stephensi* is unique, but principally because of intermediacy and recombinations of traits of other species. Its glans and baculum are described below.

Glans oblong and comparatively small, its length twice its greatest diameter, 2/3 the extent of the distal tract, and 1/4 the hind foot length. Ventral surface with a mid-ventral raphe, this terminating distally at a slight shelf situated at the junction of the spinous and (the more distal) non-spinous areas. Terminal and basal parts of the glans spineless (Pl. III), the remainder armed with sharp, curved, non-overlapping spines, each emerging from a circular pit. Urogenital opening bounded dorsally by a protractile, globular hood and bordered ventrally by folds of soft tissue bearing a few minute spines. Urethral process a short, wafer-like flap (thin dorso-ventrally and conical in ventral aspect) situated mid-ventrally just below the urogenital opening (Pl. III *e*). Urethra confluent with a shallow, smooth-walled internal crater, the confluence without a urethral process. Terminal half of cartilaginous spine of baculum free of crater walls, the remainder of the baculum imbedded.

Baculum comprised of a bone and a terminal cartilaginous spine; its total length 3/4 that of glans and 1/6 that of hind foot. The bone unevenly tapered and paddle-like (Pl. III), wider than deep throughout its length; both dorsal and ventral faces almost flat, but part of dorsal face of base of bone concave between angular lateral condyles; terminating in a slight head. Cartilaginous cone symmetrical and short, its length 1/4 that of bone.

Neotoma phenax

In shape and proportions of glans and baculum, *N. phenax* resembles *N. stephensi* and, to a lesser extent, *N. alleni* and *N. mexicana*, but it differs from those and all other species of *Neotoma* in several characters, of which the following are examples: The glans constitutes only about 1/2 of the distal tract, it being separated from the ventral flexure by a comparatively long expanse of the stalk of the penis. It terminates distally in a protractile proboscis within which is the urogenital canal that leads from an internal crater and opens at the tip of the proboscis. The crater contains a long urethral process and the distal 1/2 of the cartilaginous spine of the baculum together with a long attenuate process (of softer tissues) that caps that spine. A description of the glans and baculum follows.

Glans, comprising terminal 1/2 of distal tract, oblong and somewhat swayback, terminating in a dorsal proboscis which when at rest is flexed ventrad over the truncate ventral sector of the glans (Pl. IV *a*); its length (proboscis in flexed position) approximately twice the greatest diameter and 1/4 the hind foot length. Its surface indented mid-dorsally by a shallow longitudinal trough and relieved mid-ventrally by a full-length raphe, and most of it armed with sharp, keeled, non-overlapping spines; these absent at extreme base and tip of glans. Proboscis wider than deep, attenuate and clearly protractile, its distal and dorsal sectors filled with erectile tissue. Urethra confluent with a small internal chamber, this containing a part of the baculum (distal 1/2 of cartilaginous cone and its attenuate soft tip) and a bifurcate urethral flap (Pl. IV *e*). This flap opposes the cartilaginous cone of the baculum, and both the flap and the distal part of the baculum are free of the chamber walls; the remainder of the baculum is imbedded.

Baculum composed of a bone and a long cartilaginous cone, the latter tipped with an attenuate process of softer tissue; length of the two (excluding terminal soft spine) 4/5 that of glans and 1/6 the hind foot length. The bone shaped like a violin (Pl. IV *b*), wider than deep throughout most of its length; its length 1/10 that of foot; in its basal 1/3, the dorsal face concave and ventral face almost flat; in distal 2/3, the ventral face concave between ventrally directed lateral ridges, these ridges and the trough between them diminishing distad and terminating on the rounded head of the bone. Cartilaginous cone 1/2 the length of the bone, its rounded tip capped by an attenuate process (1/2 the length of the cone) composed of fairly dense, but apparently not cartilaginous, tissue; this spine curled in one specimen (Pl. IV *c*) and extended within the proboscis in another example.

Neotoma fuscipes

The glans of *N. fuscipes* is an elegant, flower-like structure (Pl. V) unlike that of any other woodrat. Moreover, whereas in most other neotomines (Merriam, 1894) the glans constitutes most of the distal tract and is almost as large as the prepuce, in *fuscipes* the glans constitutes only the terminal one-half of the tract and it occupies a minor part of the prepuce cavity. Following are features of the glans that set *fuscipes* apart from other species of the genus: Its peculiar, squat, lobate body from which there extends a flexible, tapered tube, the external surface mostly smooth and non-spinous; the baculum is entirely imbedded, no part of it extending into the urethra or into an interal chamber; a short, peculiarly shaped, urethral flap (Pl. V *g*) opposes an attenuate middorsal process that extends distad into the flexible tube. And finally, both the glans and the baculum are stubby (Table 1). They are described below.

Glans a small flower-like structure comprised of a graceful lobate body and a distal tube (Pl. V), its total length 1/6 that of the hind foot. Its body short and thickset (length 3/4 to 4/5 the greatest diameter and about 1/8 the foot length), cylindrical basally and flared and lobate distally, the lobes as follows: a ventral pair separated midventrally by a distal, longitudinal groove and a full-length raphe; a dorso-lateral pair, these concave distally, forming a basin from which extends the tubular process. This smooth, pliable tube slightly expanded and flexed about midway in its length, the structure apparently slightly protractile. Surface of glans comparatively smooth, the weak armature consisting of small, sparse tubercles that occur only on dorsal and lateral parts of the glans. Meatus urinarius situated at the tip of the distal tube, contractile tissue around the canal apparently giving rigidity to the tube. Two structures present within the urethra, namely, a short mid-ventral flap equipped with a pair of minute processes (Pl. V *g*) and, opposing this flap, a long attenuate cone of soft tissue that emerges from the middorsal wall of the urethral canal and extends into the distal tube.

Baculum composed of a small bone capped by an oblong mass of cartilage, its total length slightly less than that of body of glans (excluding tube) and 1/20 the hind foot length. Bone shorter than cartilaginous segment; its basal part much broader than deep, the dorsal and ventral faces concave between lateral condyles; its distal part short and cylindrical. The entire baculum imbedded in dense tissue of dorsal sector of glans and apparently essentially immobile.

Neotoma lepida

The glans of *Neotoma lepida* also is unique among woodrats. It is a long, slender, gently curved and structurally simple cylinder (Pl. VI). Its finely annulated surface, resembling that of an earthworm, suggests that the glans is highly protractile. Its surface armature consists of small tubercles, these occurring only on the basal part of the glans. The urethra is enlarged distally, forming an elongate crater which surrounds a part of the long baculum and which terminates apically between a bifurcate dorsal lip and an attenuate ventral process. These and additional characters set *lepida* apart from other species of *Neotoma,* and they lend support to the suggestion of Burt and Barkalow (1942:290) that *lepida* perhaps should be segregated subgenerically. Its glans and baculum are described below.

Glans constituting almost all of distal tract (Table 1), the base of the baculum situated within the ventral flexure. Its shape that of a slender, gently bowed cylinder (Pl. VI); its length 10 times its greatest diameter and 3/5 the hind foot length. Basal 1/4 armed with short tubercles, each recessed in a circular pit. Distal 3/4 without armature, but finely rugose, encircled by numerous accordian-like folds which apparently allow for considerable protractility of the glans. Urogenital opening guarded mid-ventrally by a conical process and bounded dorsally by the bifurcate tip of the glans, the ventral surface of this tip concave, forming a channel leading from the urogenital opening and the internal crater. Crater narrow and deep, almost completely filled with distal 1/3 of os penis and its cartilaginous spine; basal 2/3 of the bone imbedded in tissue below the crater floor. Urethra confluent with crater at crater floor.

Baculum a curved, osseous rod capped by a cartilaginous spine, the length of the two slightly less than that of the glans and 1/2 the hind foot length. Osseous segment 3/4 the length of the glans; basal part emarginate proximally and but slightly expanded laterad, its dorsal and ventral faces slightly concave; the shaft cylindrical and gently bowed ventrad, its bluntly rounded tip covered by an attenuate, cartilaginous spine; in the two specimens at hand, length of spine, respectively, 1/3 and 1/6 that of the bone.

Neotoma cinerea

Neotoma cinerea differs markedly from other woodrats not only in morphology of skin and skull (Goldman, 1910) but also in structure of the phallus. The glans is slender, awl-shaped, and essentially spineless (Pl. VII). It is much smaller than its prepuce. The urogenital opening is situated at the end of the glans' slender, flexible tip, and the short rod-like os is capped by an attenuate cartilaginous spine that equals the bone in length. There is an undivided urethral process situated at the confluence of the urethra and the tubular internal crater. This distinctive glans, seen only in *N. cinerea,* is described in detail below.

Glans a delicate, elongate, awl-shaped structure constituting most of the distal tract (Table 1), its length 4 times its greatest diameter and 1/4 the hind foot length. Slightly sinuous and gradually tapered throughout most of its length (Pl. VII), but rather abruptly constricted in two areas: (1) about half-way in its length, just beyond a pair of slight, longitudinal, ventral ridges bordering a mid-ventral trough and (2) immediately distal to a subapical, dorsal swelling. A few, narrow, long spines scattered in a small area near its base, the surface otherwise smooth, without tubercles or rugae. Urethra confluent with a long, smooth, tubular crater that surrounds the cartilaginous spine of the baculum and that opens between two triangular lips at the tip of the glans. An attenuate, mid-ventral, urethral process present at the confluence of urethra and crater, the process opposing the base of the bacular spine.

Baculum composed of a bone capped by a cartilaginous spine, the two approximately equal in length and their total extent almost as long as the glans and 1/4 the hind foot length. The bone a slightly contorted rod, its length 1/8 that of the foot; its basal part expanded laterad, wider than deep, concave dorsally, and essentially plane ventrally; remainder of bone cylindrical, the distal part slightly enlarged.

In two specimens the distal part of the glans is flexed, partially so in one and more completely in the other (Pl. VII *f*). Since the glans occupies only a small part of the prepuce cavity, there is adequate room within the cavity for flexion and extension of its tip.

Neotoma alleni

The available phalli of *Neotoma alleni* may be suspect, because all of them were obtained from dried study skins. After receiving special treatment, however, they have become pliable and tumescent and very probably they have largely regained their true shapes. In basic plan and structure they are clear and reliable, but their proportions may remain slightly distorted, and they should be checked against those of fluid-preserved specimens when such become available.

Of the fifteen species treated here, *N. alleni* is perhaps nearest *Xenomys nelsoni* in regard to morphology of glans. The resemblance is not as close as that between *albigula* and *floridana* or, even, between *phenax* and *stephensi*, but there are important traits in both *N. alleni* and *X. nelsoni* that are not seen in the other species. For example, in these two only there is a dorsal papilla, situated middorsally on the floor of the terminal crater (Pl. VIII *a*, a^1); the cartilaginous part of the baculum is broad and rather diffuse distally, and it is enclosed in a large bulbous mass of softer tissue that largely fills the crater; and a long, distally divided urethral process is present at the confluence of the urethra and the crater. The aforementioned arrangement (of crater, dorsal papilla, bacular mound, and urethral process) resembles the plan that is seen in microtines and other rodents that have a three-pronged baculum. Nothwithstanding these similarities, *N. alleni* is phallically distinguishable from *X. nelsoni* and from all other species studied to date. Characteristics of its glans and baculum follow.

Glans oblong, somewhat swayback, and slightly constricted about midway in its length (Pl. VIII *a, b*). Its surface indented by shallow middorsal and mid-ventral troughs, the latter bearing a raphe. Its length approximately twice the greatest diameter and 1/4 the hind foot length. Epidermis armed with spines, each minute, sharp, and almost entirely recessed within its pit. The spineless, shallow terminal crater almost completely filled with a bulbous mass of soft tissue covering the tip of the baculum; this mass entirely free of crater walls. A short, conical, soft papilla present middorsally at the base of the bulbous mass. Urethra terminating on floor of crater, the mid-ventral lip of its meatus prolonged distad as a pair of thick, obtuse, urethral processes (Pl. VIII *d*).

Baculum comprised of a bone capped by a mass of cartilage, its overall length somewhat less than that of glans and 1/5 the hind foot length. The bone rather angular, and wider than deep throughout, its length 1/6 that of foot; basal part expanded laterad, the dorsal face deeply concave between lateral condyles and the ventral face with a shallow, longitudinal trough on each side of a pronounced mid-ventral keel which decreases in height distad on the shaft of the bone; the dorso-ventrally flattened shaft terminates in a bilobed head, its two dorsally directed lobes separated by a median groove. This head capped by a comparatively large mass of tissue of various densities, the fan-shaped, cartilaginous, basal part blending distally with less dense tissue, the outermost clearly non-cartilaginous.

XENOMYS

The glans of *Xenomys nelsoni* is thickset, truncate, and minutely spinous, spines being present not only on most of the exterior surface, but also occurring on the lateral walls of its shallow terminal crater. The crater contains a comparatively long dorsal papilla, a large bulbous mound that houses the tip of the baculum, and a four-pronged urethral process (Pl. VIII *d'*) which is situated mid-ventrally where the urethra opens onto the crater floor. In morphology of glans, *Xenomys* is distinctive, but some of its traits are essentially matched in other neotomines, especially in *Neotoma alleni* (for which see the account of that species). The lone phallus at hand was obtained from a dry study skin. Now pliable and tumescent, it likely has regained its true shape; its length and diameter, however, may remain slightly distorted. It is described below.

Glans stubby and barrel-shaped (Pl. VIII a^1, b^1), the greatest diameter approximately 3/4 the length, and the length approximately 1/5 that of hind foot. A full-length raphe present mid-ventrally, and all of exterior of glans, except a narrow band at its base, armed densely with small spines, each contained in a pit. Lateral walls of the comparatively shallow terminal crater also spinous, the spines occurring in rows running from floor to rim. Other contents of crater as follows: (1) A large bulbous mound of soft tissue housing tip of baculum. (2) An elongate dorsal papilla, arising from middorsal base of the bulbous mound and extending distad almost to crater rim; its tissues soft and spineless. (3) Meatus urinarius, situated at crater floor immediately ventral to bacular mound. (4) The meatus guarded mid-ventrally by a thick urethral flap, its distal part comprised of 4 short processes, the medial pair smaller than the lateral ones (Pl. VIII d^1).

Baculum consisting of a bone capped by a mass of cartilage, their total lengths approximately equal to that of glans, and 1/5 the hind foot length. Osseous part 1/6 the length of the foot; its basal 2/3 wider than deep, the ventral face broadly scooped between prominent lateral flanges, and the dorsal face narrowly and deeply concave between lateral condyles; its distal 1/3 wider than deep and with a middorsal longitudinal groove that terminates just short of the gently rounded tip of the bone. Cartilaginous mass mushroom-shaped in ventral view (Pl. VIII c^1) and triangular in lateral aspect, the mass enclosed in non-cartilaginous tissue.

OTOTYLOMYS

In *Ototylomys* the glans is fusiform and heavily spinous. The urethra empties into a smooth-walled internal crater which opens at the tip of the laterally compressed, somewhat blade-like, distal part of the glans (Pl. IX). The crater contains a part of the baculum, but only the tip of the cartilaginous spine is completely free of the chamber walls. There is no urethral process or dorsal papilla, In shape, and in a few other traits, the glans of *Ototylomys* is unique, but its strongly spinous coat is like that of *Tylomys*, and other characters are essentially matched in glandes of species of *Neotoma*. A description of the glans and baculum of *O. phyllotis* follows.

Glans constituting most of distal tract, and almost as large as its prepuce; its total length 1/3 to 2/5 that of hind foot and its greatest diameter approximately 2/5 its length. Basal 2/3 cylindrical and without lobes, but with a full-length mid-ventral raphe and a shallow middorsal trough. Distal 1/3 tapered and compressed (dorso-ventral diameter exceeding the transverse one), its ventral sector with numerous folds, most of these trending toward the terminally situated urogenital opening (Pl. IX *b*). Most of surface, excepting areas at tip and base of glans, densely armed with long, sharp spines, these spaced such that they do not overlap one another. Urethra enlarged distally, forming a smooth-walled internal chamber containing the cartilaginous spine of the baculum; tip of the spine free of chamber walls, the remainder attached by a septum to the dorsal wall. All of osseous portion of baculum imbedded in dense tissues of dorsal sector of glans.

Baculum consisting of a bone capped with a spine of cartilage, their total lengths 4/5 that of glans and slightly less than 1/3 the hind foot length. Base of bone much wider than deep, the dorsal face narrowly concave between lateral condyles and the ventral face shallowly concave between lateral flanges. The wide base tapered into a narrower shaft, this also wider than deep, but becoming cylindrical near its rounded tip. Length of cartilaginous spine 1/5 to 1/8 that of bone; the core of the spine partly osseous in one of the four available specimens.

TYLOMYS

Although the glans in *Tylomys* resembles that of *Neotoma floridana* and allies in absolute size and in some proportions, it differs markedly from any species of *Neotoma* in many features. Among these are its exceptionally bristling coat of apparently hollow spines, completely buried baculum, and its peculiar distal portion which lacks a terminal crater (Pl. X). Details of its structure are given below.

Tylomys fulviventer.—Glans comprising most of distal tract (Table 1) and almost as large as its enveloping prepuce, its length 1/3 that of hind foot. Oblong, largest subapically, the diameter there 1/3 the total length. Basal 2/3 plain, without grooves or ridges other than a full-length mid-ventral raphe. Distal 1/3 with several grooves and elevations, including a low middorsal mound that covers the tip of the baculum and a larger mid-ventral prominence. Meatus urinarius unusually wide, extending across most of distal face of glans; this opening guarded dorsolaterally by a pair of small, soft, spine-tipped papillae; and its mid-ventral lip set off as a thin, elongate plate, only the lateral and distal margins of which are free. All of exterior of glans, except for small areas at its base and tip (Pl. X), densely armed with unusually long spines (those on proximal half of glans as much as 1 mm. in length), each overlapping its neighbor and each apparently hollow basally. Baculum completely imbedded in dense tissue, no part of it projecting into urogenital canal, and that canal approximately the same diameter throughout length of glans, there being no terminal or internal crater.

Baculum composed of a bone capped by a cone of cartilage, its total length 2/3 that of glans and 1/5 the hind foot length. The bone short and broad, its length slightly less than 1/2 that of glans and 1/6 the foot length; its base wider than deep, essentially flat dorsally, and concave ventrally between angular, lateral condyles; its distal 2/3 subcylindrical and slightly keeled ventrally, the tip broadly rounded, but not differentiated as a distinct head. Proximolateral parts of terminal cartilage somewhat less dense than the medial core, but all of it consolidated into a symmetrical cone, its length 1/3 or 2/5 that of bone.

T. nudicaudatus.—The single adult specimen at hand closely resembles the two available adults of *T. fulviventer*. The two samples differ slightly, but the distinctions may not be truly interspecific. In the specimen of *nudicaudatus*, both the ventral prominence and the pair of papillae on the dorsal lip of the meatus urinarius are absent. The baculum is longer relative to glans length and it is somewhat more ornate distally (bearing several small projections, and strongly constricted subapically) than in the examples of *fulviventer*.

SCOTINOMYS

The glans of *Scotinomys* is quite similar to that of *Baiomys* (Hooper, 1959); the resemblance of the two exceeds that of some pairs of species of either *Neotoma or Peromyscus* (Hooper, 1958). Principal differences between *Scotinomys* and *Baiomys* are in proportions of soft parts and in configuration of the baculum. The glans of *Scotinomys*, occupying most of the distal tract (Table 1), is an elongate, spinous cylinder with a small terminal crater that contains the meatus urinarius and a mound which incloses the tip of the baculum (Pl XI). There is no dorsal papilla or urethral process. The baculum is comparatively simple. Specimens of *S. teguina* are described below.

Glans oblong, slightly expanded subapically (Pl. XI), its length twice the greatest diameter and approximately 1/5 the hind foot length. Exteriorly without lobes or grooves, other than a shallow, middorsal, longitudinal trough and a full-length mid-ventral raphe, but densely armed with short, sharp spines; these absent, however, at extreme base of glans and within its terminal crater. The crenate crater rim surrounds a bilobed mound of soft tissue; the larger dorsal lobe houses the tip of the baculum, and the ventral part contains the meatus urinarius, its obtuse ventral lip opposed dorsally by a keel on ventral face of the dorsal lobe. Thus, the urethra opens terminally, not onto the crater floor, and that part of it distal to the floor (within the bilobed mound) is completely free of the crater walls.

Baculum a comparatively simple bone capped by cartilage, its length somewhat less than that of glans and approximately 1/5 the hind foot length. Its base expanded laterad and scoop-like, the ventral face broadly concave and the dorsal face narrowly concave between lateral condyles. The broad, thin base tapered into a delicate cylindrical shaft that terminates in a medially cleft head covered with cartilage. This cartilage occurs as a thin and rather indistinct layer in one specimen (Pl. XI) and as a distinct cone in another.

DISCUSSION

A glans that contains a four-part baculum is dissimilar, in the positions and shapes of soft parts, to one in which the baculum consists of no more than two segments. They represent two different architectural schemes, one simple, the other comparatively complex. In the complex type, the baculum is comprised of a proximal bone and three distal units which are composed of bone, cartilage, or soft non-connective tissue. The glans, typically stubby and frequently lobate, terminates in a crater in which there are several mounds, papillae, and other processes of various shapes and sizes. These structures are erectile, and their movements apparently are governed, in part at least, by sets of large, sac-like, vascular sinuses that are present below the floor of the crater.

In the simple type of phallus the baculum consists of no more than two parts; the bony proximal part typically is capped by a segment of cartilage, but this apical unit is absent in some species. The glans is not divided externally into paired lobes, and usually there is no terminal crater. It never has both the array of processes and embellishments within the crater and the sac-like circulatory sinuses below the crater that are seen in the complex type of glans. This basic architectural plan is simpler than that centered on the three-pronged baculum, and it apparently also is more plastic, more amenable to modification; for among species with the simple type there is a wide variety of shapes and sizes of the glans and of its component parts, an array that is not matched in kind or magnitude in the complex glans. Seemingly, the three-pronged baculum does not allow for major differences in external form of glans, while the simple baculum imposes no such close restrictions.

All of the cricetid glandes that are now known, representing several hundred species of approximately 50 genera, are constructed according to one of these two basic plans. The complex plan is the common and geographically widespread one. It is predominant in cricetids (*sensu* Simpson, 1945) in both the Old and New worlds, and likely it is typical of murids. It occurs in *Mus, Rattus, Apodemus, Micromys, Acomys, Arvicanthis, Nesokia, Meriones, Rhambomys, Cricetus, Cricetulus, Mesocricetus,* most if not all microtines, and most if not all South American cricetines.

While the complex plan is widespread, both taxonomically and geographically, the simple type is restricted to a few North American kinds. Of the 50 or more genera studied to date, the following twelve are characterized by simple glandes and bacula: *Peromyscus, Reithrodontomys, Neotomodon, Ochrotomys, Onychomys, Baiomys, Scotinomys, Nelsonia, Neotoma, Xenomys, Ototylomys,* and *Tylomys.*

Grouping of the 12 Genera.—These twelve genera are distinguishable from other New World rodents on the basis of fundamental design of the male phallus. They differ from each other in various modifications or elaborations of that fundamental design; those modifications are described in detail in this report and elsewhere (Hooper, 1958, 1959). Following is a summary of resemblances and differences of the genera as indicated solely by the glans and its baculum.

Reithrodontomys is similar to *Peromyscus,* particularly to the *maniculatus* division (Hooper, *ibid.*) of that genus. The resemblance between those two exceeds that between some pairs of species of *Peromyscus—banderanus* and *californicus,* for example. The two genera are unequal in regard to differentiation of the phallus, but they clearly belong together in a morphological group.

Neotomodon and *Ochrotomys* also fit with *Peromyscus* and *Reithrodontomys,* closest resemblance of *N. alstoni* perhaps being with *P. floridanus* or *P. banderanus* (Hooper, *ibid.*). *Onychomys* also may be included in this group, but peculiarities of its glans and baculum suggest that it be set apart slightly from the other genera.

Baiomys and *Scotinomys* constitute a second group which is not far removed from the preceding one. These two genera are morphologically close. They differ from each other about as much as do *Reithrodontomys* and *Peromyscus* (*maniculatus* division).

A third group includes the wood rats, *Nelsonia, Neotoma,* and *Xenomys.* The degree of difference between these genera is highly unequal, and largely because of the diversity within *Neotoma.* That genus, as now constituted (Hall and Kelson, 1959), is like *Peromyscus* in that several of its species are closely similar while others are strongly differentiated from one another; all, however, are morphologically interrelated, and for this reason it makes sense to retain them in a single genus. If this be done, then the species (*Xenomys*) *nelsoni* should be added to *Neotoma,* because it is no more distinct from *N. alleni* and *N. phenax* than some other species of *Neotoma* are from each other. Affinities of the woodrat species, as indicated by the glans, are approximately as indicated below.

Nelsonia neotomodon is set apart slightly. Its glans is woodrat-like in form and size (Hooper, 1959), but it is well differentiated from the glandes of the other species. Based on glans and baculum there is no major argument against placing *Neotomodon* in *Neotoma,* but there is much more justification for adding *X. nelsoni* to that genus if *N. alleni* is retained in it.

Neotoma albigula, N. micropus, N floridana, and *N. mexicana* are all basically similar. *N. mexicana* is the most distinctive, but it is not strongly demarked from the other three species. The four clearly belong together, in contrast to a second subgroup composed of *N. stephensi* and *N. phenax*. The phalli of those two species are readily distinguishable, but they are constructed according to the same plan and proportions. Through *mexicana* they connect with the *albigula* subgroup, the resemblance being particularly evident in the shape of the baculum and of the distal part of the glans.

N. alleni and *X. nelsoni* share characters which suggest that the two species have close affinities. The stubby glans with its terminal crater, dorsal papilla, and large mound of soft tissue that encloses the wedge-shaped cartilaginous segment of the baculum are examples in point. Of these two species, *nelsoni* is farther removed morphologically from other woodrats. Its affinities with them appear to be through *alleni* and *mexicana*.

The species *fuscipes, cinerea,* and *lepida* are markedly distinct from other species of *Neotoma*. In a morphological series extending from a robust, spinous glans equipped with a gross baculum (as seen in *floridana)* to a long, tubular, essentially spineless glans and rod-like baculum (as seen in *lepida*), the sequence of species would be as follows: *floridana, fuscipes, cinerea,* and, finally, *lepida*. The sequence may or may not be meaningful from the point of view of evolution of the phalli, for the three species are highly specialized, each in its own way, and affinities of the three are not apparent. Each must be arranged alone, but placed nearer the *albigula* subgroup rather than the *alleni–nelsoni* subgroup. The distinction between any two of the three species —*fuscipes, cinerea,* and *lepida*—exceeds that between any species within other woodrat subgroups.

Ototylomys and *Tylomys* constitute a fourth group. These are well differentiated from each other and from all other species. The peculiar shape of the glans and the completely buried baculum of *Tylomys* are distinctive, but these and its other characters are approached in *Ototylomys*. *Ototylomys,* thus, morphologically tends to connect *Tylomys* with *Neotoma,* but the connection is not complete.

In summary, the aforementioned 12 genera, or 11 if *Xenomys nelsoni* be assigned to *Neotoma,* are phallically diverse; nevertheless they constitute an assemblage that is distinct from other cricetid rodents in characters of the penis. Certainly neither the assemblage nor any part of it fits with akodont, sigmodont, oryzomyine, *Rhipidomys–Thomasomys,* or other Neotropical groups with which authors have associated it on the basis of cranial characters. Instead it has the aspect of a distinct natural unit, of subfamily or family rank, which like the Heteromyidae and Geomyidae is endemic to the New World. The possibility that it is a natural group now requires intensive investigation, utilizing all pertinent anatomical data.

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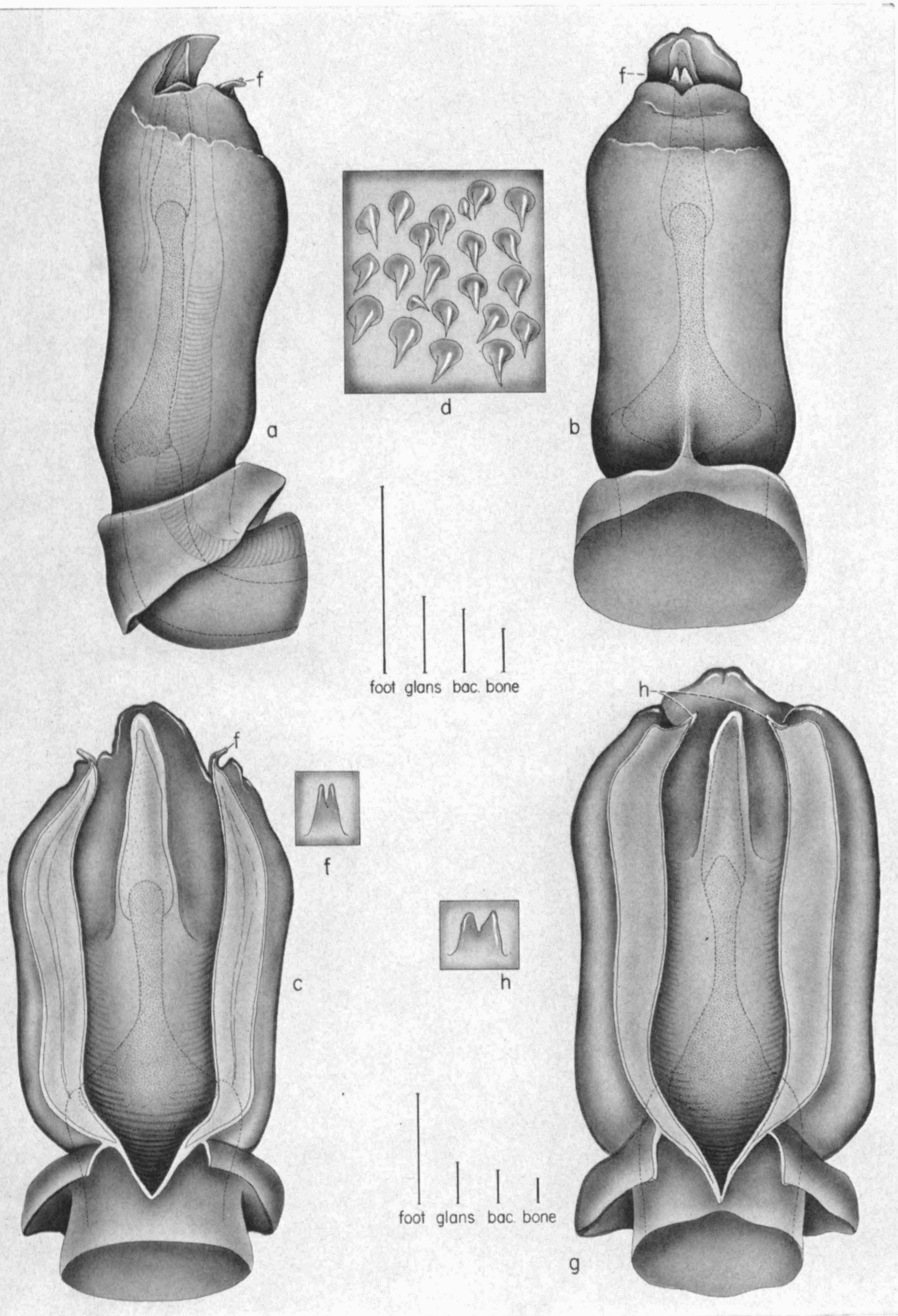
TABLE 1

MEASUREMENTS AND PROPORTIONS OF THE GLANS PENIS IN ADULT SPECIMENS OF FIVE GENERA OF RODENTS

Genus and species	Specimens	Mean Measurements (in mm.)							Ratios (in per cent)				
		lengths							glans	lengths			
		hind foot	distal tract	glans	os penis	cartilage tip	total length baculum	diameter of glans	diameter / length	glans / distal tract	glans / foot	os / foot	baculum / foot
Neotoma													
albigula	3	32	17.2	13.1	6.8	3.0	9.8	6.1	47	76	41	21	31
floridana	1	39	19.7	14.6	7.4	3.7	11.1	7.8	53	74	37	19	28
micropus	3	38	17.7	14.7	6.6	4.4	11.0	6.8	46	83	39	17	29
mexicana	2	34	15.3	12.0	7.6	3.4	11.0	6.0	50	78	35	22	32
stephensi	1	28	9.9	6.4	3.9	1.0	4.9	3.3	52	65	23	14	18
phenax	1	35	15.0	8.1	4.0	2.1	6.1	3.7	46	54	23	11	17
alleni	3	42	. . .	9.8	6.4	1.4	7.8	5.3	54	. . .	23	15	19
fuscipes	2	39	13.1	6.7	0.8	1.2	2.0	5.3	79	51	17	2	5
lepida	2	33	22.5	19.4	14.4	3.2	17.6	2.1	11	86	59	44	53
cinerea	3	42	14.4	11.3	5.0	5.1	10.1	2.6	23	79	27	12	24
Xenomys													
nelsoni	1	30	. . .	6.6	5.2	1.1	6.3	5.1	77	. . .	22	17	21
Ototylomys													
phyllotis	2	28	. . .	10.4	7.5	1.3	8.8	4.2	40	. . .	37	27	31
Tylomys													
fulviventer	2	41	19.6	14.5	6.6	2.4	9.0	5.3	37	74	35	16	22
Scotinomys													
teguina	1	17	4.9	3.8	3.1	0.1	3.2	1.7	52	78	22	18	19

PLATE I

Glans penis in *Neotoma albigula* (*a–d*, *f*) and *N. floridana* (*g*, *h*) as seen: *a*, laterally; *b*, ventrally; *c*, *g*, in longitudinal section, the specimen incised mid-ventrally exposing lumen of urethra, crater, and baculum. *d*, enlargement of spines which cover most of surface of glans. *f*, *h*, urethral processes. *N. albigula,* UMMZ No. 110380, Bernalillo Co., New Mexico. *N. floridana,* UMMZ No. 110379, Douglas Co., Kansas.


f
a
d
b
f
foot glans bac. bone
h
f
f
c
h
foot glans bac. bone
g

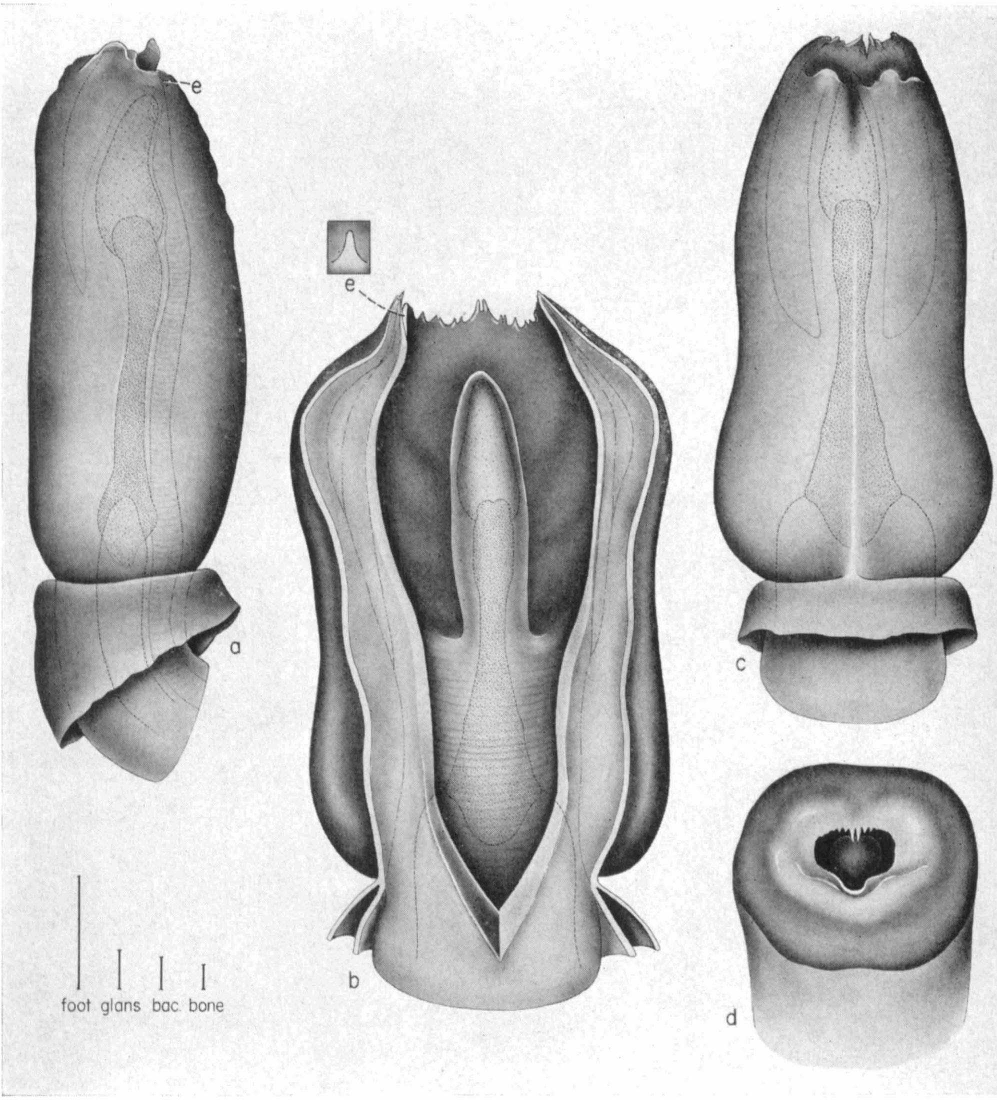


PLATE II

Glans penis in *Neotoma mexicana* as viewed: *a*, laterally; *b*, in longitudinal section, the specimen incised mid-ventrally exposing lumen of urethra, crater, baculum; *c*, ventrally; and *d*, apically. *e*, urethral process. External spines are as in *N. albigula* (Pl. I, d). UMMZ No. 109669, near San Cristobal, Chiapas, México.

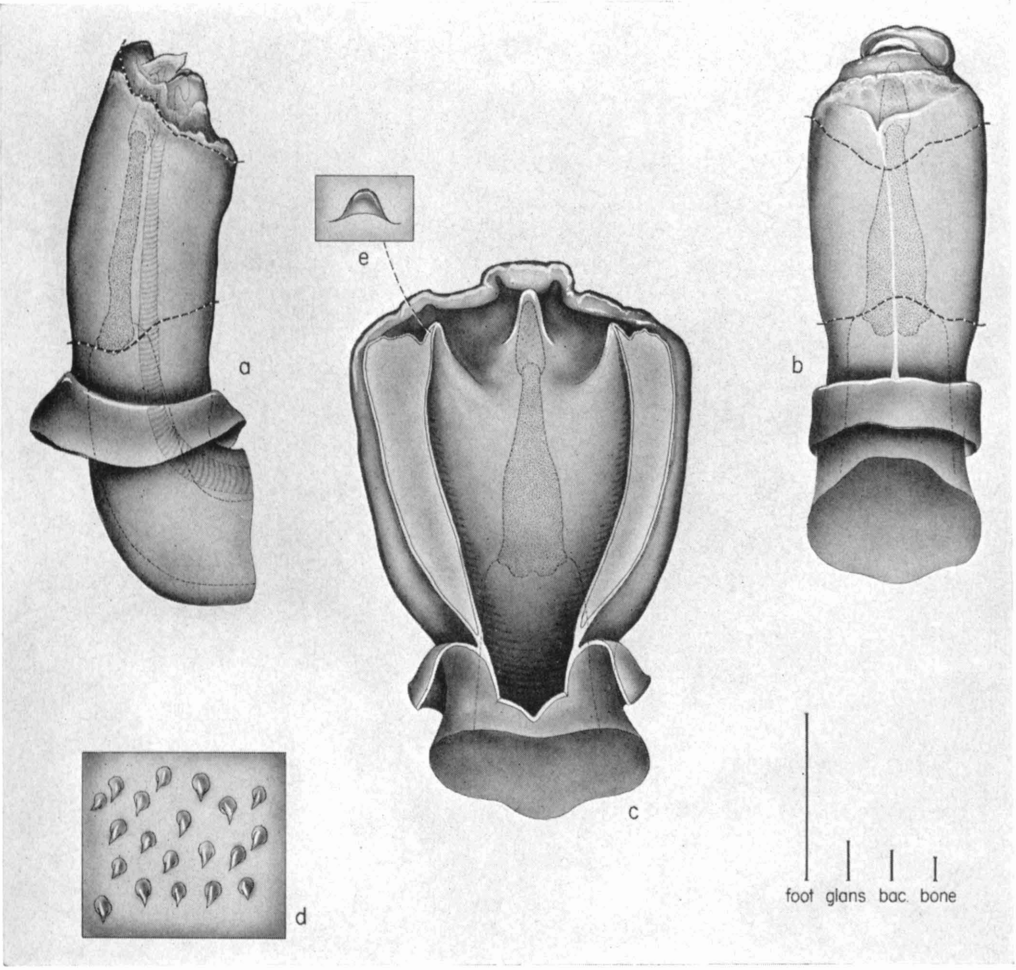


PLATE III

Glans penis in *Neotoma stephensi* as seen: *a*, laterally; *b*, ventrally; c, in longitudinal section exposing lumen of urethra, crater, and baculum. *d*, enlargement of spines which occur on most of surface of glans (those areas between bold dashed lines in *a* and *b*). *e*, urethral process. UMMZ No. 110384, Coconino Co., Arizona.

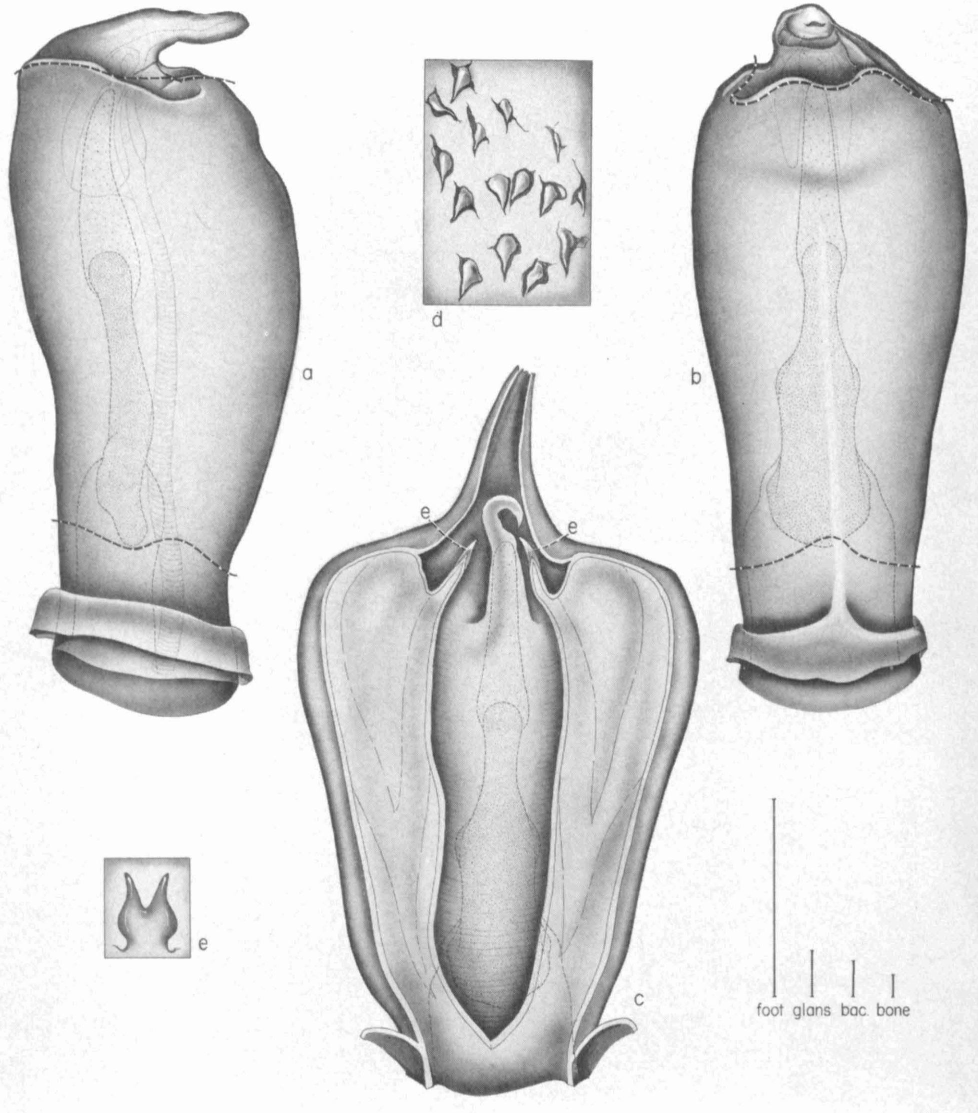


PLATE IV

Glans penis in *Neotoma phenax*, as viewed: *a*, laterally; *b*, ventrally; *c*, in longitudinal section exposing lumen of urethra, baculum, crater, and interior of proboscis. *d*, enlargement of spines which occur on most of surface of glans (those areas between bold dashed lines in *a* and *b*). *e*, urethral processes. MVZ No. 86038, Guasima, Sonora, México.

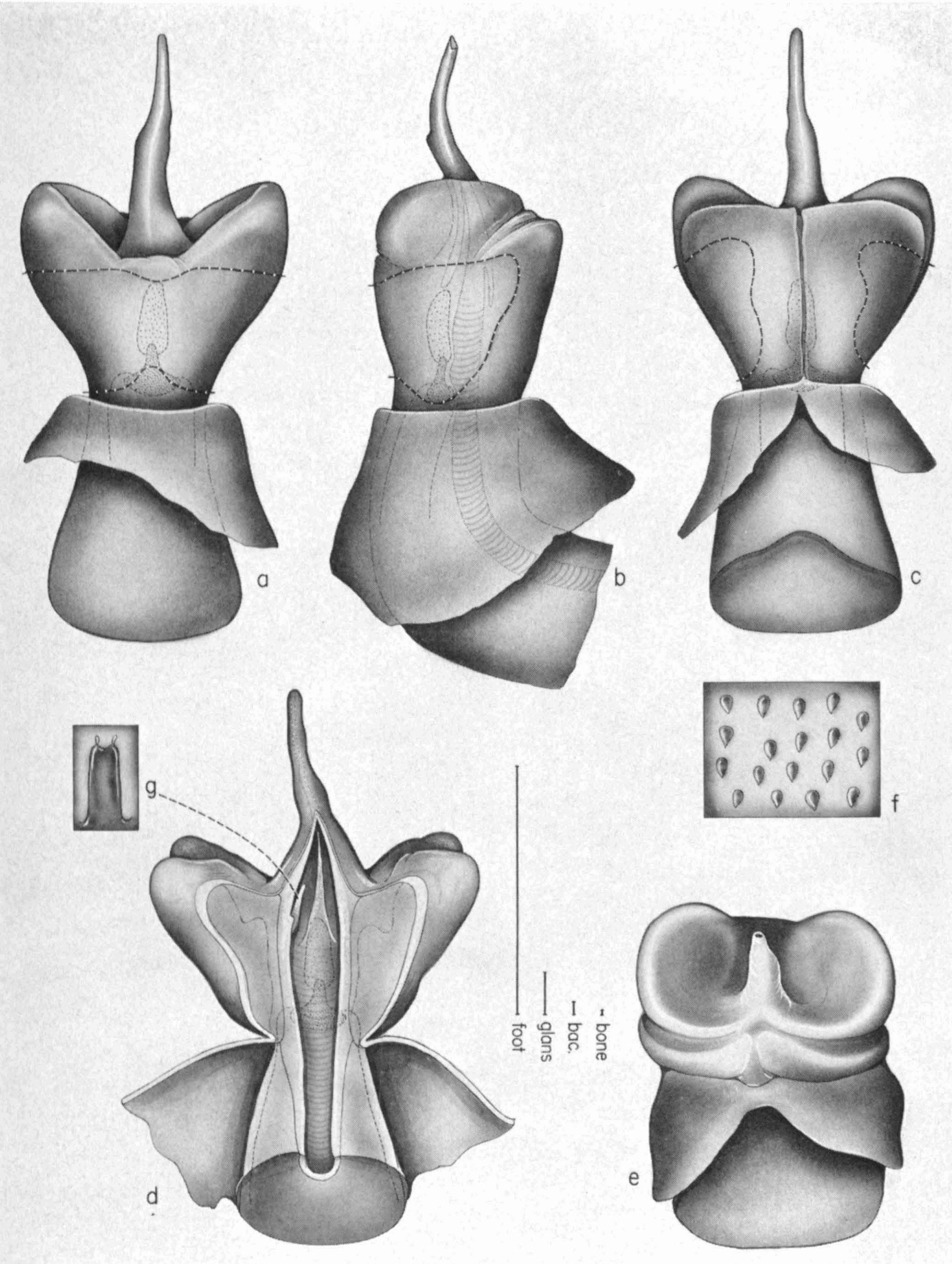


PLATE V

Glans penis in *Neotoma fuscipes* as viewed: *a*, dorsally; *b*, laterally; *c*, ventrally; *d*, in longitudinal section exposing lumen of urethra, baculum, and the attenuate dorsal process; and *e*, apically. *g*, urethral process. Tubercles (shown enlarged in *f*) are limited to areas enclosed by bold dashed lines. UMMZ No. 109700, Monterey Co., California.

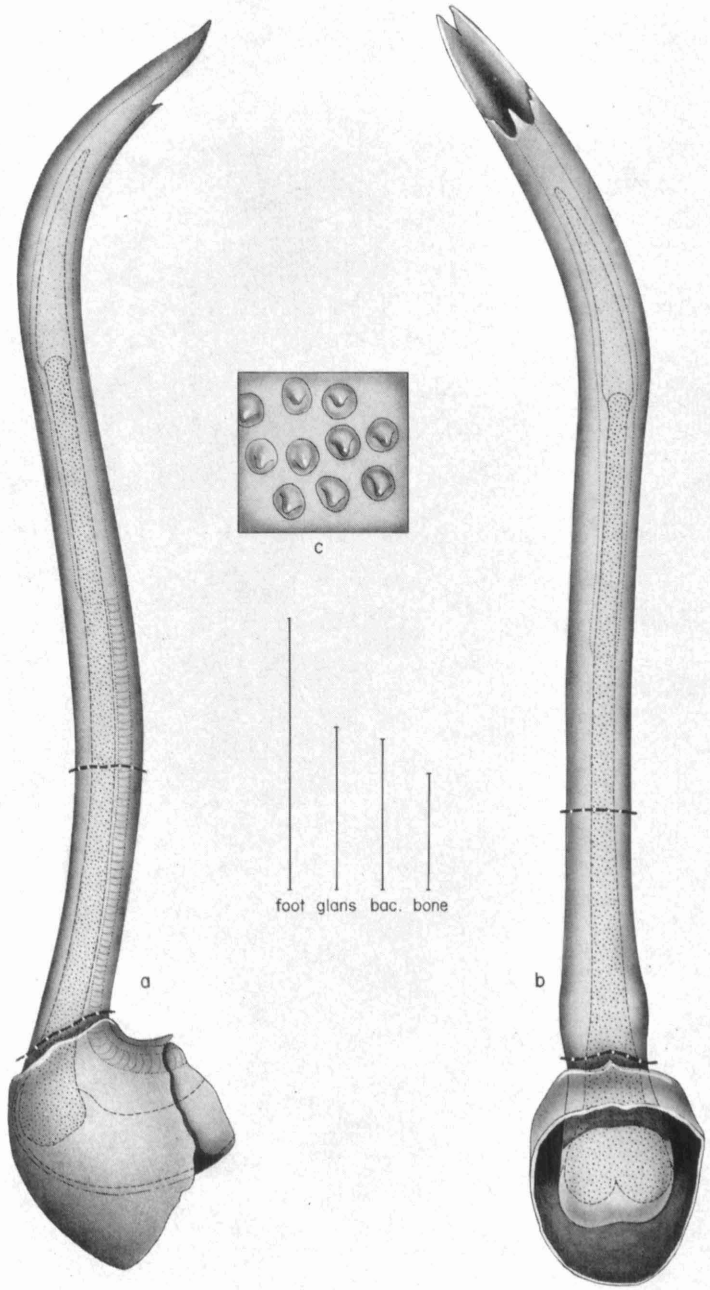


PLATE VI

Glans penis in *Neotoma lepida* as viewed: *a*, laterally; *b*, ventrally. *c*, enlargement of surface tubercles which occur only on basal part of glans (area between bold dashed lines). UMMZ No. 109208, Los Angeles Co., California.

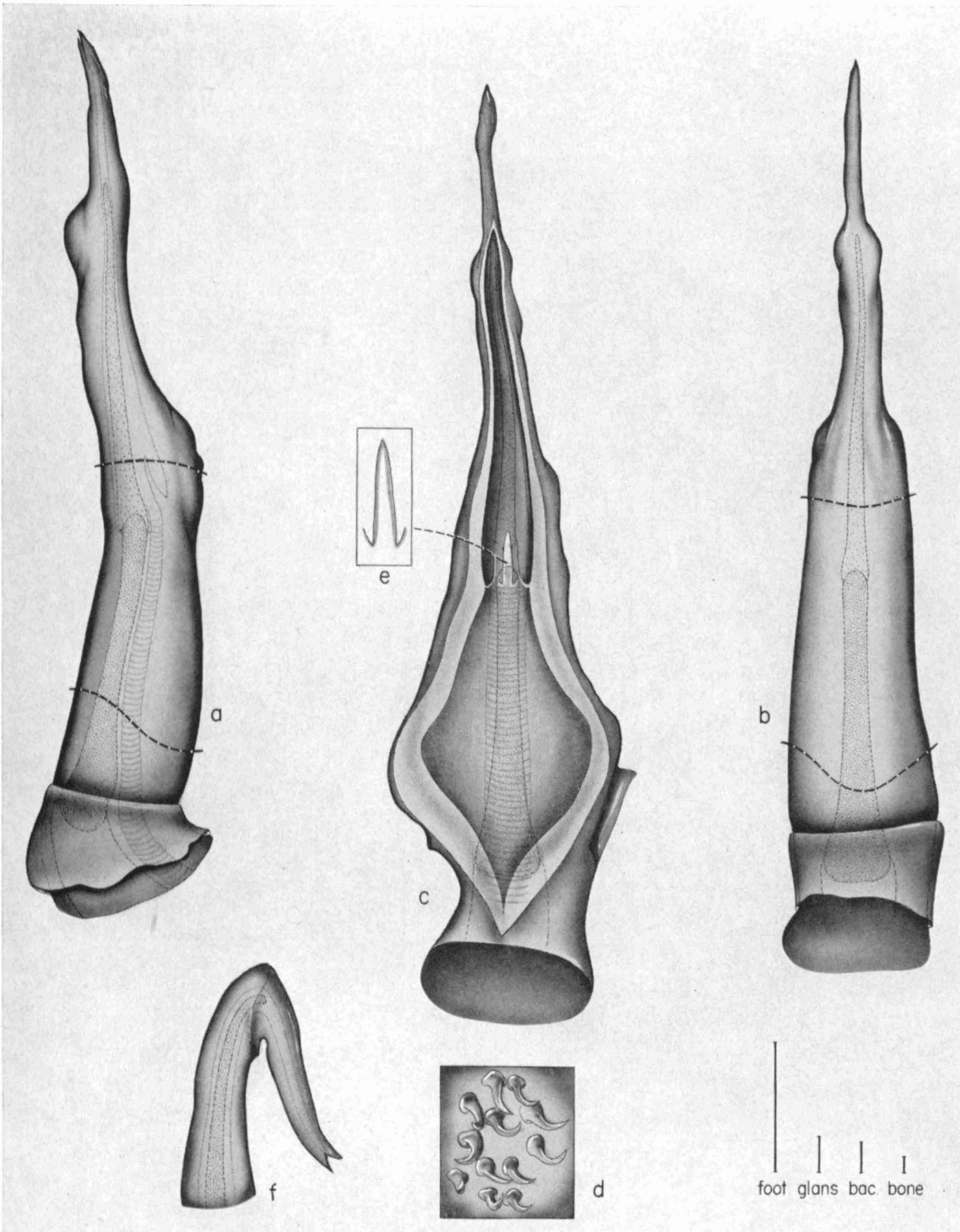


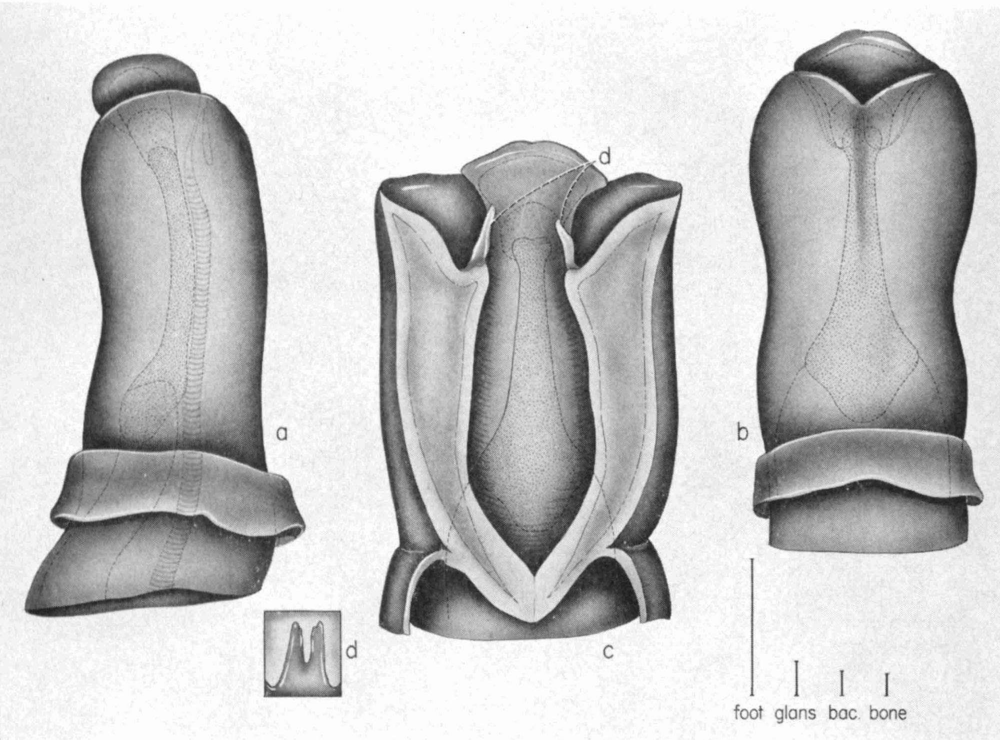
PLATE VII

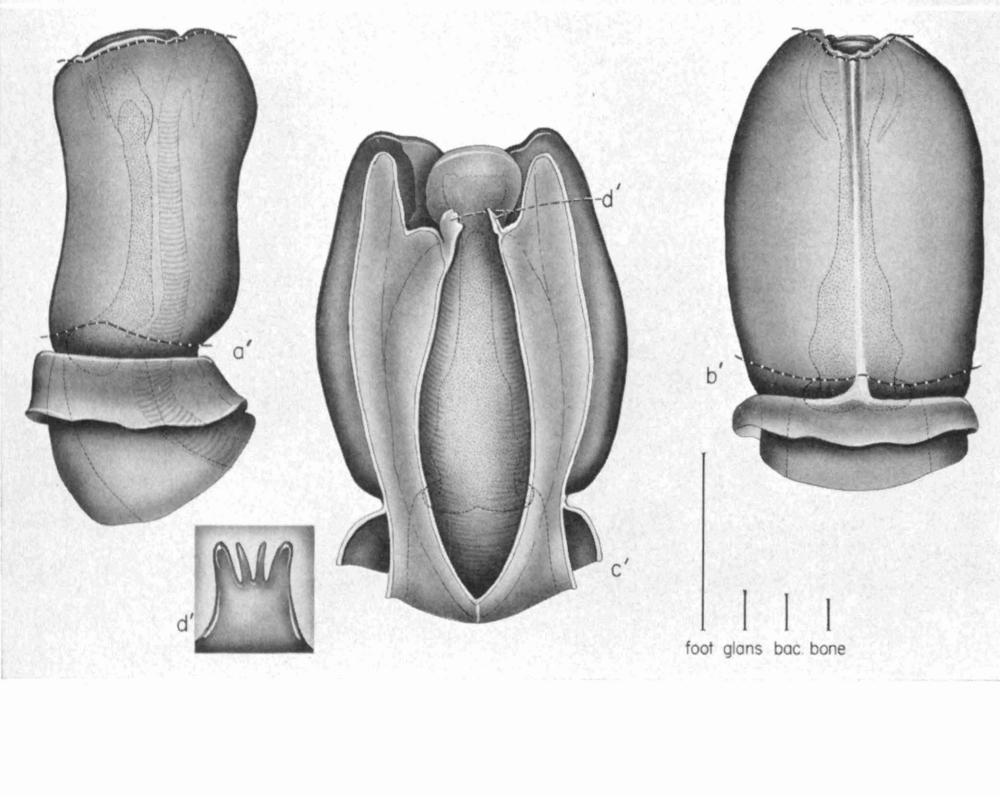
Glans penis in *Neotoma cinerea* as seen: *a*, laterally; *b*, ventrally; *c*, in longitudinal section exposing lumen of urethra, crater, and baculum. *d*, enlargement of surface spines which occur in areas between bold dashed lines in *a* and *b*. *e*, urethral process. *f*, enlarged lateral view of flexed distal part of glans. UMMZ Nos. 110197 (*a–c, e*), 110205 (*d, f*), Carbon Co., Montana.

PLATE VIII

Glans penis in *Neotoma alleni* (*a–d*) as viewed: *a*, laterally; *b*, dorsally; *c*, in longitudinal section exposing lumen of urethra, crater, and baculum. *d*, urethral processes. KU No. 64544, Banderas, Nayarit, México.

Glans penis in *Xenomys nelsoni* (a^1–d^1) as seen: a^1, laterally; b^1, ventrally; c^1, in longitudinal section exposing lumen of urethra, crater, and baculum. d^1, urethral processes. LAM (UMMZ No. P–3914), Pueblo Juárez, Colima, México.


a
b
c
d
d
foot glans bac. bone


a′
b′
c′
d′
d′
foot glans bac. bone

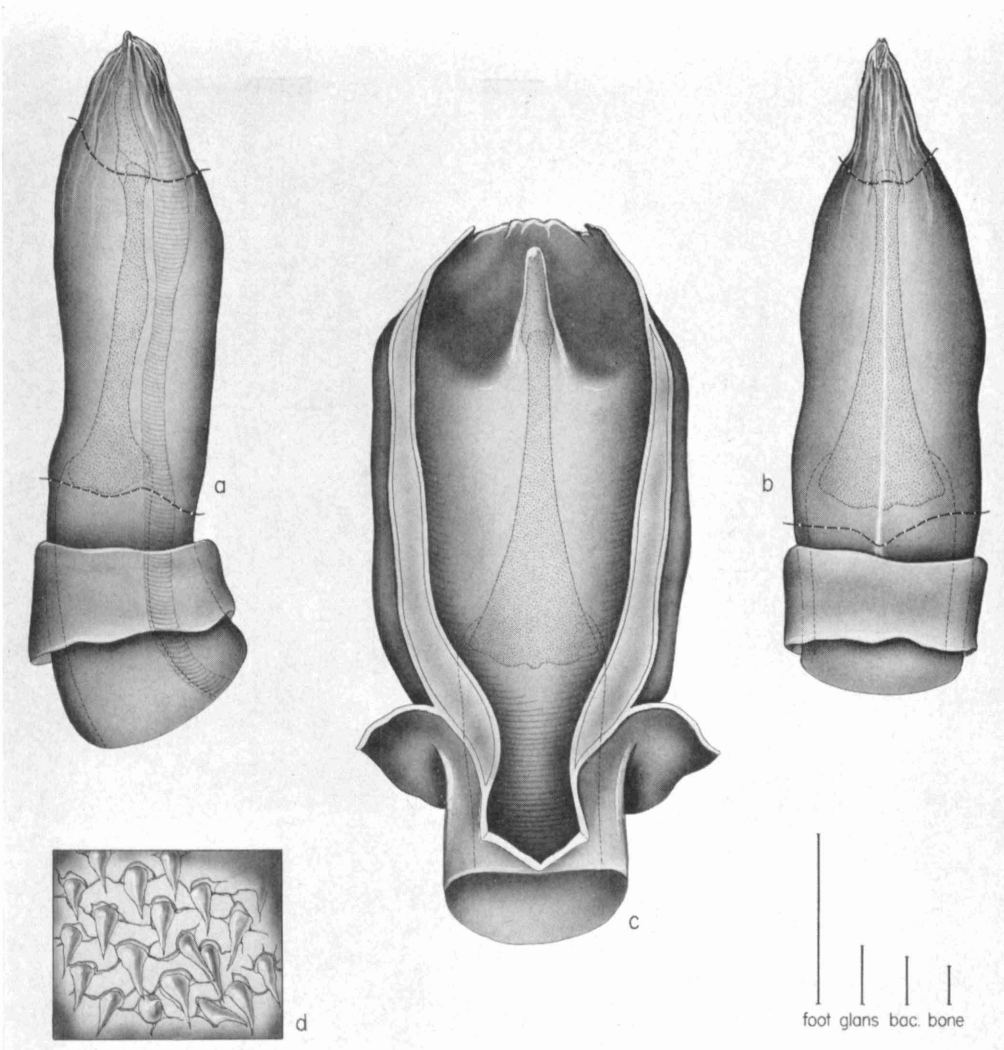


PLATE IX

Glans penis in *Ototylomys phyllotis* as viewed: *a*, laterally; *b*, ventrally; *c*, in longitudinal section exposing lumen of urethra, crater and baculum. *d*, enlarged segment of spiny coat, which occurs on those areas between bold dashed lines in *a* and *b*. MVZ No. 98796, Hacienda Chalata, El Salvador.

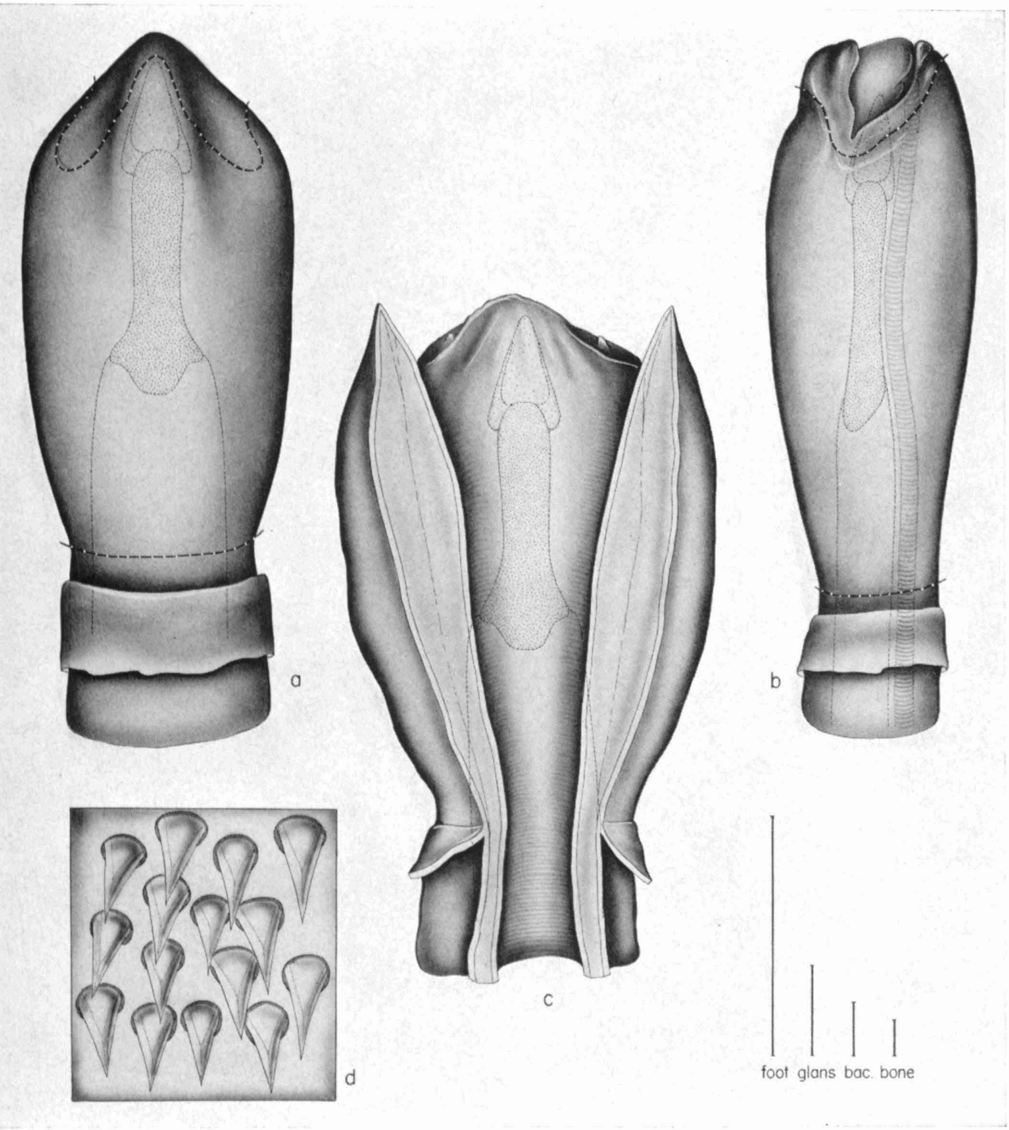


PLATE X

Glans penis in *Tylomys fulviventer* as viewed: *a*, dorsally; *b*, laterally; *c*, in longitudinal section exposing lumen of urethra and underlying baculum. *d*, enlargement of spines which occur in areas between bold dashed lines in *a* and *b*. US (UMMZ No. P–3902), Darien Prov., Panamá.

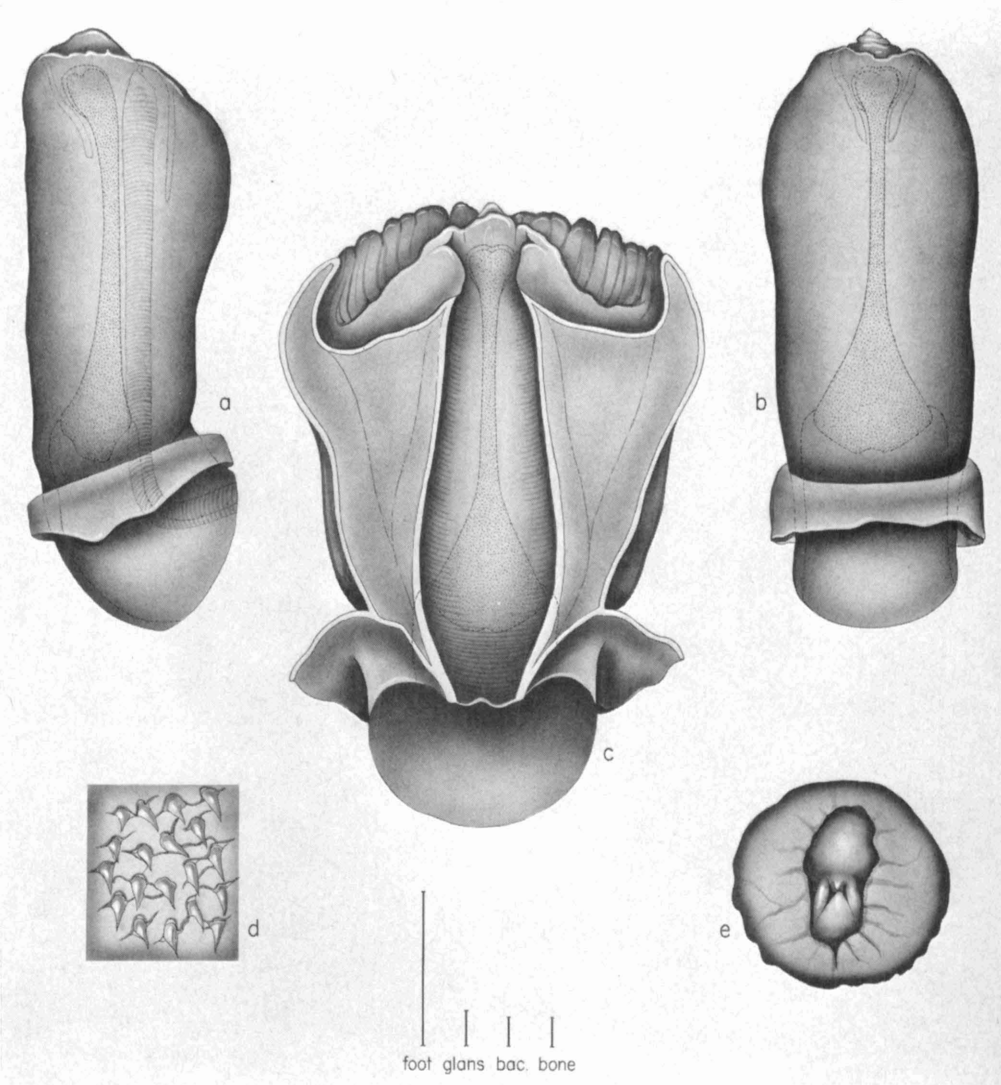


PLATE XI

Glans penis in *Scotinomys teguina* as seen: *a*, laterally; *b*, dorsally; *c*, in longitudinal section into lumen of urethra; *e*, apically. *d*, enlargement of spines which occur on outer surface except at extreme base of glans and within its crater. MVZ No. 98839, Los Esesmiles, El Salvador.