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THE GLANS PENIS IN *PROECHIMYS* AND OTHER CAVIOMORPH RODENTS

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THE peculiar morphology of the penis of the guinea pig, porcupines and other hystricomorph and caviomorph rodents (sensu Wood, 1955) has been described by several authors. For example, Cole (1897) outlined the structure of the glans of the guinea pig (Cavia) and gave special attention to the morphology and function of the eversible part which he termed the "intromittent sac." Tullberg (1899), in his synopsis of rodents, noted the presence of this cul-de-sac in species of Hystrix, Cavia, Dasyprocta, Chinchilla, and Echimys. He named it the "sacculus urethralis" and considered it to be a characteristic of the tribe Hystricognathi. Pocock (1922) described and figured the glans in a number of species, and prepared a key, based on the glans and prepuce, to the following genera: Acanthion, Coendu, Cavia, Galea, Dolichotis, Dasyprocta, (Cuniculus=Agouti), Lagostomus, Chinchilla, Capromys, Myocaster, Octodon, and Ctenomys. Dathe (1937) studied species of 10 genera, mostly those seen by Pocock. By the use of serial sections as well as gross specimens, and supplemented by observations of live animals, Dathe was able to delineate details of structure and function of various parts of the glans. Angulo and Alvarez (1948) described the male genital tract in Capromys, and Mirand and Shadle (1953) figured the tract in Erethizon. Landry (1957) referred to features of the hystricomorph glans and indicated that the organ is taxonomically important. And most recently, Layne (1960) studied Dactylomys and found that it, like Lagostomus (Pocock, 1922), may be dissimilar to other caviomorph rodents. Other reports on the subject are listed by Dathe (1937).

My purpose in dissecting representative caviomorphs was to observe, first hand, the phallic architecture in that group and especially to compare it with the basic structural plans that are present in

myomorph rodents, the Cricetidae in particular. For systematic reasons, for example, it was important to know in what manner the more or less capacious terminal crater observed in some cricetids (Hooper, 1959, 1960) is comparable to the cul-de-sac in caviomorphs. As a result of these studies it is now feasible to figure the heretofore undescribed glans of *Proechimys* and, for four other genera, to focus on details that are inadequately illustrated in the literature.

I am indebted to Philip Hershkovitz and William J. Schaldach for specimens from, respectively, Colombia and México, and to the National Science Foundation for financial support. Figures 1–5, rendered from camera lucida tracings, are the work of Donna Snyder. The specimens, all processed and studied by conventional means (Hooper, op. cit.), are as follows: (Erethizontidae) Erethizon dorsatum, Michigan, 2. (Caviidae) Cavia tschudii, Peru, 1. (Dasyproctidae) Dasyprocta aguti, Colombia, 3. D. mexicana, México, 1. Cuniculus (= Agouti) paca, Colombia, 2. (Capromyidae) Geocapromys ingrahami, Bahama Islands, 1. (Echimyidae) Proechimys sp., Colombia, 9. The following descriptions are based on adult animals.

DESCRIPTIONS OF SPECIMENS

PROECHIMYS

In the three adult specimens at hand the glans is subcylindrical and elongate, its length being approximately three times its greatest diameter; the largest specimen measures 16.3 mm. in length and 5.3 mm. in diameter. About midway in its length there are dorsal and lateral constrictions, the lateral ones of which continue distad on the ventral surface as a pair of sinusoidal troughs that set off an ampulla-shaped ventral mass (Fig. 1); the narrow neck of the ampulla terminates at the crescentic ventral rim of the intromittent sac. Dorsal to the opening of this sac is a distally projecting mass which contains the meatus urinarius, its ventral lip a moulded, distinct process.

Most of the vestiture is spinous. A middorsal stripe (situated external to the dorsal suspensory ligament) and a narrow band at the glansprepuce junction are smooth and spineless, but the remainder of the epidermis, including that of the intromittent sac, is studded with small, sharp, barely recurved spines. These are of two types: Those of the ventral and basal sectors (that part of the glans ventral to the sinusoidal troughs and proximal to the lateral constrictions) are narrow and typically single-pointed, although some bear slight serrations

on the single, long, sharp shaft. Those occurring on the dorsal lobes (distal to lateral constrictions and dorsal to troughs) and on the walls of the intromittent sac are multitoothed serrate ridges (Fig. 1) which are arranged in well-defined longitudinal rows. The spines within the sac are directed distad, such that when the sac is everted those, like the others of the vestiture, point proximad. There are no spikes on the floor of the sac, neither are there large dorsolateral combs or plates as in *Cavia*, *Agouti*, or *Dasyprocta*.

The involuted part—the intromittent sac or sacculus urethralis, of authors—comprises slightly more than the ventral and distal halves of the contracted glans; its dorsal wall abuts against the urethra and its floor is situated within the basal half of the glans. The walls of the sac consist of a series of longitudinal folds (about 10 of them) which are closely appressed to each other and almost obliterate the lumen of the sac. Immediately basal to them are two cords of tissue, termed "tendons" by Cole (1897) and "elastic bands" by Dathe (1937), which have to do with erection and retraction of the sac. Distally, where they join the sac and appear to connect with a spongy layer that lines the walls, they are highly vascular and cavernous. But proximally, as they course along the ventral face of the corpus cavernosum urethra, they gradually lose their vascularity and become tendonous. In the ventral flexure of the penis they merge with the fibrous tunic of the corpus cavernosum penis.

The urethra courses along the ventral faces of the corpus cavernosum penis and baculum and opens between smooth non-spinuous lips in the dorsal mound at the tip of the glans. The thick cavernous layer surrounding the urethral tube appears to branch approximately at the level of the base of the baculum, giving off large right and left ovate vascular lobes which grid the ventral and lateral sectors of the intromittent sac. These lobes lie dorsal and lateral to the "tendons" and are separate from them, at least in the basal part of the sac. Whether, farther distad, the lobes and tendons join each other or the cavernous urethra can not be determined in the specimens at hand.

The corpus cavernosum penis is convex dorsally and deeply concave ventrally, partly enclosing the urethra. It is bordered middorsally by the dorsal vein and more superficially by the suspensory ligament which inserts on the middorsal face of the os penis, the insertion terminating just short of the tip of that bone. The fibrous and vascularized part of the corpus cavernosum penis inserts on the base of the baculum and, thus, terminates there. However, dense cartilage-like tissue, spread as a veneer on the bone, continues on distad and at the

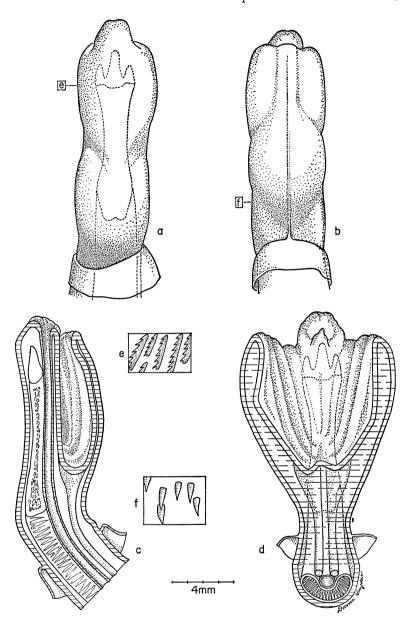


Fig. 1. Glans penis in *Proechimys sp.* as viewed: a, dorsally; b, ventrally; c, in medial sagittal section; and d, when incised mid-ventrally exposing the intromittent sac and retractor cords and, dorsal to them, the urethra and baculum. Insets e and f show spines which invest the glans and its intromittent sac. UMMZ P-3991, Colombia.

tip of the bone merges with, or expands into, a trilobed cartilaginous distal process, which is part of the baculum.

In total length the baculum comprises two-thirds that of the glans, while the bone alone is slightly more than one-half the glans length; in the largest specimen the bone and the cartilage tip measure 9.0 and 2.8 mm., respectively. Although the bone is wider than deep throughout its length, it is widest apically where there are two lateral platforms separated by a crescentic cavity; thus, the tip is slightly bilobed (Fig. 1). The paddle-shaped and emarginate basal part is essentially plane ventrally and slightly convex dorsally. In its distal two-thirds the bone is strongly convex dorsally and deeply concave ventrally.

GEOCAPROMYS

Unfortunately the specimen of Geocapromys at hand is misshapen and excessively cleared by KOH, consequently few details of the soft anatomy remain for comparison with descriptions of Capromys by Angulo and Alvarez (1948), Dathe (1937), and others. Features which can be seen in the example are as follows: There is an intromittent sac of approximately the same size, relative to total volume of glans, as in Proechimys and Agouti. The sac has no spikes on its floor, but its longitudinally folded walls and most of the exterior epidermis apparently were spinous, the spines in the sac at least tending to be in longitudinal, and probably multi-toothed, rows. (Almost all sheaths of the spines are now lacking, but the bases on which they were mounted are still evident.) The urethra opens terminally, just dorsal to the sac. Most of the corpus cavernosum penis inserts on the basal one-fourth of the os penis. Situated dorsally just below the epidermis, this bone is an elongate dorso-ventrally thin plaque that is shaped somewhat like a long finger nail, its dorsal face gently convex and the ventral surface shallowly concave. As seen dorsally, it is broadest subterminally (its width there 5.3 mm.), slightly constricted in the middle third of its length, and broad again proximally (4.8 mm.) before tapering gently to its proximal limits within the corpus cavernosum penis.

AGOUTI

The two available specimens of Cuniculus (= Agouti) paca fit published descriptions of the species, the best of which is by Dathe (1937) who presents cross-sectional sketches of the glans and a clear view of its dorsal surface with its median longitudinal ridges, sharp

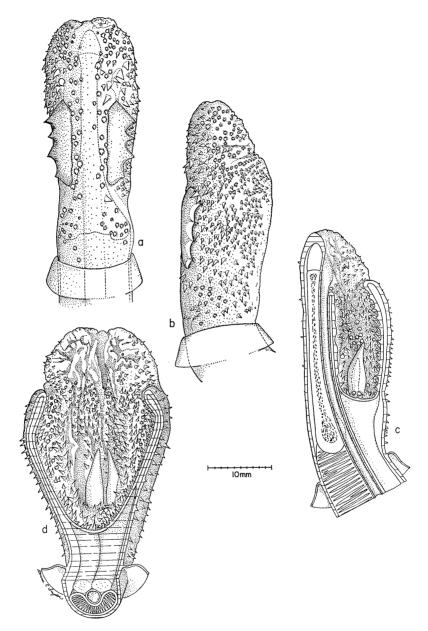


Fig. 2. Glans penis in $Agouti\ paca$ as viewed: a, dorsally; b, laterally; c, in medial sagittal section; and d, when incised mid-ventrally exposing the two spikes on the floor of the intromittent sac. UMMZ P-3993, Colombia.

spines, pair of large rasps, and other structures. Surface and internal details which he and others did not illustrate adequately are shown in Figure 2.

The two examples are closely similar in structure and proportions. The largest one measures 67.5 mm. in tip-to-prepuce length and 15.7 mm. in greatest diameter. In its current retracted state, well over half of the glans consists of intromittent sac. Its walls are longitudinally folded and heavily spinous and from its floor arise two long spikes, each of which consists of a hard sheath mounted on a similarly shaped softer base. While the pair of large dorsolateral rasps (Fig. 2) are multi-toothed as in *Cavia* and some other forms, all other epidermal tubercles on the glans are single sharp-pointed cones. A pair of large retractor cords extend proximad from the sac; in shape, structure, and course they appear to match comparable cords in other caviomorphs.

The urethra and corpus cavernosum penis are described in fair detail by Dathe. The meatus urinarius lies distal to the retracted intromittent sac and its ventral lip is simple, not formed into or bordered by a lappet such as is seen in *Proechimys*. Distally, much of the corpus cavernosum penis inserts on the base of the baculum, but some of it appears to branch laterally and a medial part apparently continues distad to the tip of the glans, enclosing the bone and providing the dense base to which the two dorsal rasps are attached. The baculum is a subcylindrical osseous rod capped by a mass of cartilage; the longer of the two specimens measures 37.2 mm., of which 4.1 mm. is the length of the cartilaginous tip. Its laterally expanded basal one-fourth is deeply concave ventrally and convex dorsally; the tip of the bone is truncate and angular. The bone and part of the adjoining corpus are visible externally as a middorsal ridge.

DASYPROCTA

Both the retracted and everted states are represented in the four specimens of *Dasyprocta* at hand. In the erected example (*D. mexicana*), which grossly resembles Pocock's sketch (1922: fig. 23 I) of the glans of *Agouti paca*, the erected intromittent sac is a formidable bell-shaped object, its densly spinous surface bearing at its tip a pair of long spikes which extend distad well beyond the remainder of the glans. These would seem to pose copulatory problems, but, according to Dathe (1937), full eversion of the spike-bearing sac normally occurs late in copulation—only after the glans is within the vagina.

The three retracted examples, all of D. aguti and closely similar to

one another, are the basis for the following description. Elongate and subcylindrical, each is largest terminally where a long dorso-ventral slit separates right and left lobes. Within this slit-like opening are, in dorsal to ventral order: a dorsal mound containing the tip of the baculum, the meatus urinarius, and the mouth of the intromittent sac. The dorsal surface bears three longitudinal crests: a middorsal keel, situated dorsal to the baculum and bordered on each side by a trough, terminates distally on the bacular mound; a pair of spine-tipped lateral crests or blade-like lamina span about two-thirds of the length of the glans, or almost the full extent of the bone. The hard, dense core of each lamina possibly is part of the corpus cavernosum penis since proximal to the bone each appears to join the dorsal part of that corpus. The ventral surface of the glans, particularly the lateral parts, consists of a series of transverse rugae, the crests bearing rows of spines.

The largest specimen (Fig. 3) measures 8.9 mm. in greatest diameter and 28.7 mm. in tip-to-prepuce length. The os penis spans approximately two-thirds that distance (its length 18.3 mm.); its terminal cartilaginous cap is 2.0 mm. in height. In a few small areas—such as around the meatus urinarius, bordering the prepuce-glans junction, and along the mid-ventral raphe—the epidermis is comparatively smooth and spineless. But for the most part, it is spinous and the spines are of several types. They are finely and sharply multi-toothed within the intromittent sac, on each dorsolateral blade where they form a continuous serrate line, and on the rugose ventral surface of the glans where their rows are transversely oriented and most of them crest the rugae. Those situated dorsal to the blades are simpler, most of them being single cones but a few having two or three points. Each spine is comprised of a tough sheath mounted on a softer, similarly shaped core.

The intromittent sac and its retractor tendons (Fig. 3) are like those in other forms. The spinous, longitudinally folded walls enclose a pair of sharp spikes; these are longer (relative to glans size) and sharper than in the other specimens examined. Dorsal to the sac, and at the base of the bacular mound, is the urethral opening; its thick ventral lip appears as a gentle convex arc when seen ventrally.

The os penis is a dorso-ventrally flattened rod which is largest basally and truncate and somewhat angular at both ends. Its dorsal surface is gently convex and the ventral face is concave. Its enveloping tissues and those comprising the partly bifurate mass at its tip may be part of the corpus cavernosum penis, but most if not all of that corpus termi-

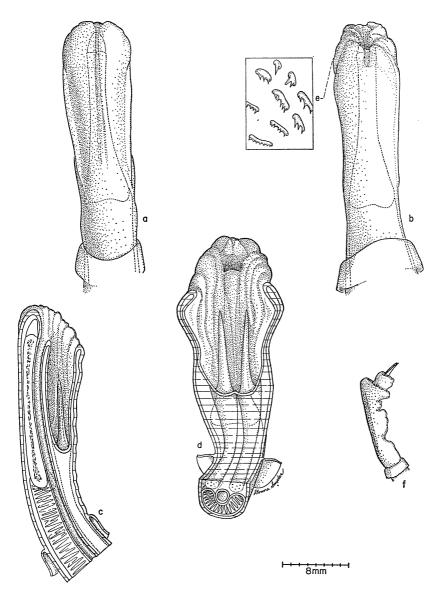


Fig. 3. Glans penis in Dasyprocta as seen: a, dorsally; b, ventrally; c, in medial sagittal section; d, when incised mid-ventrally exposing the two spikes on the floor of the intromittent sac; and f, with intromittent sac everted. Spines, inset e, stud the epidermis both within and outside the sac. a-d, D. aguti, UMMZ P-3992, Colombia. f, D. mexicana, UMMZ P-3994, Oaxaca, Mexico.

nates on the base of the bone. The dorsal suspensory ligament inserts on the base of the bone and on adjoining parts of the corpus.

CAVIA

The specimen of Cavia tschudii (Fig. 4) closely resembles those of $C.\ cobaya$ (= porcellus) as described and figured by Cole (1897) and Dathe (1937). The small glans constitutes no more than the terminal half of the distal tract (that part of the penis beyond the ventral flexure); its length (7.5 mm.) is not quite twice its greatest diameter and is one-fifth the hind foot length. The baculum is as long as the glans and is confined to it; the length of bone alone (6.4 mm.) is 85 per cent of the glans length.

The spiny armature is similar to that shown by Dathe, but there are more comb-like rows, particularly within the intromittent sac. The shape and distribution of the spines vary. There are none in three areas: near the glans-prepuce junction, in a middorsal band extending from prepuce to tip, and around the meatus urinarius. Elsewhere on the glans they are rather sparsely distributed, occurring singly or in groups, each separated from the other by spineless areas of the epidermis. Those on the ventral half of the glans, excluding the intromittent sac, are mostly single- double- or triple-pointed cones and a few of these simple types are also present on the back of the glans and within its intromittent sac. In those latter two regions, however, most of the spines are consolidated into multi-toothed plates or long serrate ridges, these more or less paralleling the longitudinal axis of the glans. Each spine, plate, or ridge consists of a tough, hard sheath mounted on a similarly shaped but softer epidermal base. While the exterior spines point proximad, those lining the sac are directed distad.

The intromittent sac is about maximally retracted; its floor is situated several millimeters proximal to the glans-prepuce junction (Fig. 4). Its longitudinally folded walls are lined by long rows of spines. Two dorsal folds, bedecked with few spines, continue distad out of the sac where, enlarged, they form a yoke-shaped structure which surrounds the meatus urinarius. Arising from the floor is a pair of small spikes which resemble the spikes in *Erethizon*, each consisting of a hard sheath mounted on a softer papilla. Extending proximad from the floor is a pair of large retractor cords which appear to have the same structure and position as in *Erethizon*, *Agouti*, and other forms which have a well-developed intromittent sac.

The urethra, corpus cavernosum penis, and baculum are essentially

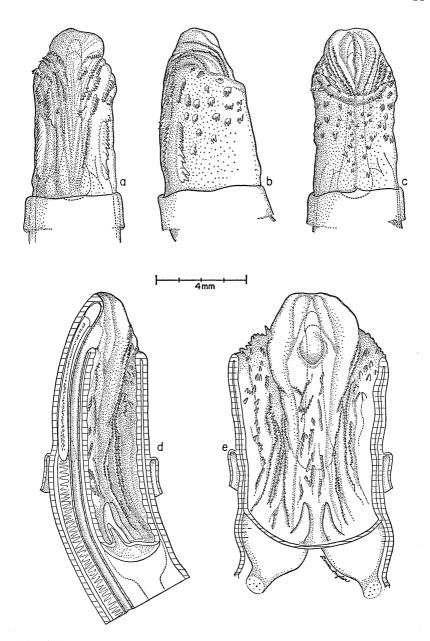


Fig. 4. Glans penis in *Cavia tschudii* as viewed: a, dorsally; b, laterally; c, ventrally; d, in medial sagittal section; and e, when incised mid-ventrally exposing the intromittent sac and retractor cords. UMMZ 80229, Peru.

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as in Cavia porcellus (Dathe, 1937). Coursing distad in the ventral trough formed by the corpus cavernosum penis, the urethral tube together with its surrounding cavernous layer terminates subapically within the deep cavity formed by the aforementioned yoke of soft spineless tissue. The ventral lip of the meatus is simply the unadorned rim of a partition which separates the urethra from the intromittent sac. I am unable to determine all limits of the corpus cavernosum penis in the present specimen, but it is clear that most of the corpus terminates on the base of the baculum. Some of it, however, may extend laterad and distad a few millimeters as a pair of thin narrow sheets. The bone is a comparatively simple slightly bowed rod which is enlarged basally and is truncate distally beneath a terminal cone of cartilage; throughout its length the transverse diameter slightly exceeds the dorso-ventral one.

ERETHIZON

The specimen of *Erethizon* which is described below was injected when fresh and then fixed while still distended. Compared with its former contracted state, it is more inflated distally and approximately one-fifth of its intromittent sac is everted (Fig. 5). This sac and several other structures which are present in the specimen are not mentioned by Mirand and Shadle (1953) in their description of nine examples of the same species.

The oblong glans, which measures 19.3 mm. in length and 13.2 mm. in greatest diameter, is simple in form, without external lobes or troughs other than those involving the intromittent sac and the urethral opening. In several small areas-along a low mid-ventral raphe, near the glans-prepuce junction, and surrounding the meatus urinarius-the epidermis is spineless and comparatively smooth or but slightly rugose, but elsewhere it is studded with low spines. Most of these are simple cones but some are two- and three-crested and each consists of a tough sheath which overlies a similarly shaped (single-, double-, or triple-coned) soft base; each is slightly recessed in the epidermis. This spiny exterior coat continues on over the lips of the large terminal opening and down to the floor of the intromittent sac, but leaving those parts of the epidermis which adjoin the urethra (dorsal wall of the sac and area around the meatus urinarius) comparatively smooth and spineless. There are no large external serrate blades or plates as are seen in Cavia, Dasyprocta, and Agouti.

In this partially erected specimen the intromittent sac is necessarily

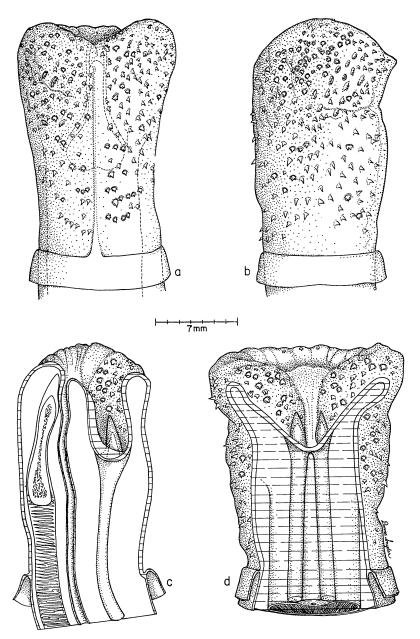


Fig. 5. Partly extended glans penis in $Erethizon\ dorsatum\ as\ seen:\ a,\ ventrally;\ b,\ laterally;\ c,\ in\ medial\ sagittal\ section;\ and\ d,\ when\ incised\ mid-ventrally\ exposing\ the\ intromittent\ sac,\ retractor\ cords,\ urethra,\ and\ corpus\ cavernosum.\ UMMZ\ P-3943,\ Michigan.$

shallow and its turgid walls are unfolded and mostly spinous. The dorsal wall, however, is smooth and spineless; it terminates distally at the gently convex ventral lip of the meatus urinarius. On the floor of the sac is a pair of spikes, each consisting of a tough sheath about 3 mm. long which is mounted on a softer conical papilla approximately 2 mm. in height. Below these spikes are paired masses of spongy tissue which appear to feed into a cavernous layer that surrounds the sac. Proximally, these masses are consolidated as two longitudinal cords of tissue (the "elastic bands" of authors) which course along the ventral face of the corpus cavernosum urethra and eventually join the outer sheath of the corpus cavernosum penis.

The urethra lies in the broad trough formed by the corpus cavernosum penis. The soft lining of its lumen is surrounded by a thick cavernous layer, the dorsal part of which appears to terminate some distance short of the meatus urinarius while the ventral sector continues on into the meatus' thick ventral lip.

The corpus cavernosum penis and baculum in *Erethizon* is described by Mirand and Shadle (1953) and the os penis is figured by Burt (1960). The corpus is a dorsally convex and ventrally concave broad strap which encompasses much of the dorsal and ventral sectors of the basal half of the glans. It is trifurcate distally. Each lateral branch extends laterad and distad to undertermined limits. Most of the medial branch of the corpus inserts on the base of the baculum; but some of it may veneer the remainder of the shaft and form the blunt cartilaginous mass, 1.7 mm. long, which caps the rounded tip of the bone. The bone is wider than deep throughout its 9.6 mm. length and its laterally expanded base is convex dorsally and broadly concave ventrally; its total length is approximately one-half that of the glans. Dorsal to the bone is the dorsal suspensory ligament which inserts both on the base of the bone and on the adjoining corpus cavernosum penis.

DISCUSSION

The glandes of few species of caviomorph rodents have been described, but those few represent 16 genera in 10 of the 12 families and all of the four superfamilies of the Caviomorpha (Wood, 1955). Thus with only two families, Abrocomidae (Octodontoidea) and Dinomyidae (Cavioidea), remaining as unknowns in regard to structure of the glans penis, the relatively few data afford broad systematic coverage and a fair synopsis of phallic characters of caviomorphs. For

most of the forms studied there is information on internal anatomy, as well as gross morphology; however, for *Dactylomys* and *Lagostomus* the published accounts lack critical anatomical details which are necessary for close comparison of those forms with other caviomorphs. Accordingly, *Dactylomys* and *Lagostomus* are excluded from most of the following discussion.

The glandes of all caviomorphs studied to date, possibly excepting the aforementioned two genera, accord with a single fundamental design which in important respects is unlike the structural plans seen in other major groups of rodents, for example the Muroidea and Sciuroidea (Simpson, 1945). Major features of the caviomorph design are briefly outlined below.

In the resting glans there are typically two external openings, both situated near the tip. The dorsal one is the meatus urinarius while the larger ventral one is the mouth of a more or less capacious cul-de-sac which is a distinctive but not unique feature of caviomorphs, as Tullberg (1899), Pocock (1922) and others have pointed out. And in attempting to indicate something of its structure or function, authors have termed it variously the blind sac, glandular pouch, sacculus urethralis, epithelial sac, and intromittent sac. While each of these names is to some extent descriptive, the term intromittent sac seems most appropriate, for morphologically and histologically the sac is simply the invaginated distal part of the glans which is everted during sexual activity (Dathe, 1937).

Its size, thus, depends upon the sexual state of the glans, and in addition it varies with the species. In *Lagostomus* it is said to be absent (Pocock, 1922), and in *Dactylomys* it occurs as a pair of eversible pockets (Layne, 1960). In the other caviomorphs studied to date it is a spacious cavity which may extend the full length of the glans (e.g., in *Cavia*) and together with its appurtenances occupies the ventral two-thirds of that organ. Its walls, being involuted portions of the epidermis which are squeezed into a cavity, are a series of longitudinal ridges and valleys, the folds closely appressed to one another and, thus, almost obliterating the lumen of the cavity.

In all specimens at hand the dorsal part of the sac, particularly that near the urethral opening, is comparatively smooth with few or no spines, while the remainder of the sac is densely spinous. The spines tend to occur in rows, cresting the longitudinal folds, and in form and arrangement they are like those on the outer surface except that they point distad and, thus, are not aligned with the outer armature until the sac is everted. Emerging from the floor of the sac in some speci-

mens is a pair of spikes, each consisting of a conical papilla covered by a much taller conical sheath of hard dense tissue which is like that of the surrounding large and small spines. These spikes are present in the examples of *Erethizon*, *Cavia*, *Dasyprocta*, and *Agouti*, and are absent in those of *Capromys* and *Proechimys*. Pocock (1922) and Dathe (1937) list other genera in this respect and consider these spikes to be taxonomically important, perhaps of familial or superfamilial value, but those authors also suggest that their occurrence may be individually variable in some species.

Extension and contraction of the intromittent sac are controlled by the amount of blood in the spongy layer which surrounds the sac and by a pair of longitudinal cords which at the base of the sac connect with that spongy layer (Cole, 1897; Dathe, 1937). These cords, which in the literature are termed retractor tendons or elastic bands, extend proximad along the ventral face of the corpus cavernosum urethra and are attached by areolar tissue to that and other adjoining bodies. In the ventral flexure of the penis, they merge with the tough outer coat of the corpus cavernosum penis. Near the intromittent sac they are highly vascular, but progressing proximally they gradually lose their cavernous aspect and become bands of tough fibers like those surrounding the corpus cavernosum penis. Histologic cross-sections of these cords show that they consist mostly of dense fibrous connective tissue such as comprises tendons and ligaments. They contain no muscle tissue other than that which girds arterial vessels. These cords are present in all specimens examined and likely they occur in all caviomorph glandes which contain a well-defined intromittent sac. As a systematic character they likely are at least as important as the sac and their presence or absence in forms which are reported to have a vestigial sac (e. g. Dactylomys) or none at all (e. g. Lagostomus) should be investigated.

The urethra in caviomorphs appears to be similar to that of other rodents. The lumen and its lining is surrounded by a thick cavernous layer and the entire structure courses along the concave ventral face of the corpus cavernosum penis and baculum. The location and shape of its mouth vary both among the species and in individuals with regard to degree of protraction of the intromittent sac.

The corpus cavernosum penis, a broad body with a deep ventral channel for the urethra, inserts on the basal part of the os penis. Whether it engulfs the os penis and sends branches laterad is unclear; its detailed configuration in the caviomorph glans is not known. It is said to be trifurcate in *Erethizon* (Mirand and Shadle, 1953). The

os penis is a dorsoventrally flattened, cartilage-capped rod of varying sizes and shapes. In the specimens of *Proechimys* it is broadest terminally; in the other examples it is largest basally. It is confined to the glans. The dorsal suspensory ligament inserts on its dorsal face and on adjoining parts of the corpus.

In summary, the caviomorph genera and families listed herein differ in regard to structure of the glans penis. Intergeneric differences are seen in: size and shape of the glans and baculum; size, shape, and distribution of epidermal spines which invest the glans and its intromittent sac; location of the meatus urinarius and configuration of the parts which surround it; size and shape of the intromittent sac and of large spines which may be present on its floor; and characteristics of retractor cords which engulf the base of the sac. All of these differences, whether intergeneric or interfamilial, appear to be variations on a single basic structural design which characterizes all of these caviomorphs excepting possible Lagostomus and Dactylomys, both of which are inadequately known. In many respects this caviomorph design is unlike the schemes seen in the Muroidea. Whether, as reported in the literature, it is shared by Old World hystricomorphs or other supposedly closely related rodent groups must continue to be questioned until adequate anatomical evidence from Old World forms is avalible.

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