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Anatomy of the Baculum–Corpus Cavernosum Interface in the Norway Rat (*Rattus norvegicus*), and Implications for Force Transfer During Copulation

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ABSTRACT The baculum is a nonappendicular bone found in the glans tissue of members of five orders of mammals. Its function during copulation is unknown. Anatomical examination of the baculum and corpus cavernosum in the Norway rat (*Rattus norvegicus*) shows that the two structures are connected by a layer of fibrocartilage, and that the distal tip of the corpus cavernosum swells during erection to surround the proximal end of the baculum. Microradiographs of bacula from sexually experienced males show that regions of the bone may be remodeling; these data suggest that the baculum is load-bearing. On the basis of this anatomy, I propose that the baculum increases the overall flexural stiffness of the penis during copulation by transferring bending and compressive forces from the distal end of the glans to the tensile wall of the corpus cavernosum. Forces on the distal end of the penis during copulation press the baculum against the corpus cavernosum, reducing its internal volume and increasing intracavernosal pressure and corpus cavernosum wall strains. Because the wall of the erect corpus cavernosum is reinforced with inextensible collagen fibers, an increase in wall strain will also increase wall tissue stiffness, and thereby increase the flexural stiffness of the corpus cavernosum. J. Morphol. 244:69–77, 2000.

KEY WORDS: penis; baculum; copulation

The penises of all male therian mammals are supported during copulation by a pair of hydrostatic skeletal elements: the corpus cavernosum and the corpus spongiosum. The corpus cavernosum is a high-pressure system (Beckett et al., 1972, 1974; Purohit and Beckett, 1976; Hanyu et al., 1987) designed to increase the flexural stiffness of the penis during erection (Kelly, 1999) and to maintain its shape during copulation (Kelly, 1997). The corpus spongiosum is a low-pressure system (Purohit and Beckett, 1976) that inflates the glans during erection and supports its tissue during copulation (Schummer et al., 1979; Williams-Ashman and Reddi, 1991; Holmes et al., 1991). But some mammals (specifically, some carnivores, insectivores, rodents, bats, and primates) have an additional skeletal element in their penises (Romer, 1970; Williams-Ashman, 1990). The baculum, or *os penis,* is a bone found in the glans tissue at the distal end of the penis, dorsal to the urethra, with its proximal end abutting the distal end of the corpus cavernosum (Vilmann and Vilmann, 1979; Williams-Ashman, 1990). Although the species-specific shape of the baculum has long been used as a diagnostic taxonomic character (see, for example, Burt, 1936; Wade and Gilbert, 1940; Hooper and Hart, 1962; Long, 1969; Patterson, 1980; Mondolphi, 1983; Thorington et al., 1996), little is known about either its detailed anatomical relationship to other penile elements or its functional significance.

Some authors have suggested that the baculum is an ossification of the distal end of the corpus cavernosum (Schummer et al., 1979; Smith and Madkour, 1980; Evans, 1993), but recent work on rodents has shown that the bone has a more complex origin. The baculum and the corpus cavernosum originate from the same mesenchymal mass in the embryonic penis in both mice (Glucksmann et al., 1976) and rats (Murakami and Mizuno, 1984; Vilmann and Vilmann, 1986), but the two structures develop separately. The rat (*Rattus norvegicus*) baculum has three developmentally distinct parts: a proximal portion derived from cartilage, a central portion derived from membranous bone, and a distal portion made up of nonlamellar bone. The proximal and central portions fuse and begin to ossify within five days of birth, but the distal portion does not ossify until puberty (Ruth, 1934; Murakami and Mizuno, 1984, 1986; Williams-Ashman and Reddi, 1991). Increases in baculum length at puberty are derived from an endochondral growth plate located at the proximal end of the bone, against the distal end of

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the corpus cavernosum (Ruth, 1934; Vilmann and Vilmann, 1986). Postnatal baculum growth and ossification are highly androgen-dependent; the bone does not develop its adult form without induction by testosterone (Lyons et al., 1950; Glucksmann et al., 1976; Murakami, 1986). For a more complete review of baculum development, see Edwards (1997).

In adult rodents, the baculum is embedded in the glans tissue, and seems to be anchored to the distal end of the corpus cavernosum (Vilmann and Vilmann, 1979; Sportono, 1992). But although several small ligaments attach the baculum to folds in the glans tissue surrounding the urethra (Sportono, 1992), no muscles or ligaments connecting the proximal end of the baculum to the corpus cavernosum have been described. The corpus spongiosum and corpus cavernosum are held together by a thin layer of connective tissue and skin, but these tissues are highly elastic and mobile and do not provide much mechanical support during erection. At present, the anatomical position of the baculum in relation to the erect corpus cavernosum and the nature of its attachment are unknown.

The functional relevance of a free-floating bone in the penis has been debated for some time. The possibility that the bone is a pleiotrophic artifact of penile development is disputed by Patterson and Thaeler's (1982) morphometric analysis of baculum variability; their data suggest that the baculum is subject to direct selection and therefore has an adaptive, functional role in copulation. This hypothesis is supported by anatomical data from studies of mutant *Hoxd-13* mice: *Hoxd-13* is expressed in the developing penis but not in germ cells or gonads, and *Hoxd-13* mutant males have anatomically normal corpora cavernosa but malformed bacula. Mutant females are fertile, but mutant males cannot father offspring, although they copulate normally (Dollé et al., 1993). These data suggest that the successful impregnation of a female requires either a specific bacular shape or specific bacular movements during copulation.

Despite evidence that the baculum has a functional role during copulation, the identity of that role remains a mystery. The baculum's bony nature has led some authors to suggest that it provides additional support to the ancestral hydrostatic skeletons in the penis by bracing the corpus spongiosum and urethral tissue in the glans (Romer, 1970; Dixson, 1987, 1995). It has also been suggested that the baculum facilitates penetration, acting as a wedge to open the female's vaginal tract (Ruth, 1934; Long and Frank, 1968), or that it stimulates the female during copulation, eliciting a neuroendocrine response that could either enhance sperm transport, induce ovulation, or prepare the uterus for implantation (Patterson and Thaeler, 1982; Eberhard, 1985, 1996). None of these hypotheses has been biomechanically tested, and the baculum's true function could be any one or a combination of those proposed.

A detailed knowledge of the baculum's anatomical relationship to other penile structures is required to test hypotheses of baculum function during copulation. As the first part of a biomechanical study of baculum–corpus cavernosum interaction during copulation, I performed a morphological study of the interfaces of the baculum with the corpus cavernosum and corpus spongiosum in the penis of the Norway rat (*Rattus norvegicus*).

MATERIALS AND METHODS

Twenty-one fresh-frozen sexually mature male Norway rats (*Rattus norvegicus*) were obtained from a supplier (Southwest Rodents, Tucson, AZ). Rats ranged in mass from 181–603 g; each rat was thawed for 4 h before its penis was used for study.

The length, dorsoventral diameter, and lateral diameter of each penis and its baculum were measured with a pair of digital calipers (Mitutoyo) to a precision of 0.01 mm. For each measurement, the penis was first removed from the rat by dissecting proximally to the penis' ischial attachments and carefully separating the penile crurae from the bone. The intact, isolated penis was placed on a flat surface and the calipers were closed on either side of a pair of landmarks until they just touched the tissue. External penile length was defined as the distance between the distal opening of the urethra and the proximal split of the crura of the corpus cavernosum. External dorsoventral and lateral diameters of the soft portion of the penis were measured near the midpoint of the corpus cavernosum, approximately 5 mm proximal to the bacular attachment. External baculum length was defined as the distance between the distal and proximal ends of the baculum, both of which can be felt through the surrounding tissue; external dorsoventral and lateral diameters of the baculum were measured approximately 2 mm distal to the flared proximal end of the bone. Three repeated measurements of these variables were within 0.05 mm in all cases. External flaccid corpus cavernosum length was estimated by subtracting mean baculum length from mean total penile length.

Gross Morphology

Gross dissections of thawed penises from four individuals were used to examine the spatial relationship of the baculum and corpus cavernosum and to try to identify muscular or ligamentous attachments between them. Penile tissue distal to the ischial attachment of the corpus cavernosum was removed from each individual and examined under a dissecting microscope. Two penises were dissected whole, while two were first cut into 5-mm thick serial transverse sections. All tissue was kept moist with physiological saline (Kiernan, 1990) during dissection.

Vascular casts of six penises were produced by severing one crus of the corpus cavernosum at its ischial attachment and injecting liquid colored latex into the exposed vascular space. Latex was injected until the corpus cavernosum was erect, and the exposed vascular opening was clamped shut with a hemostat to maintain the erection until the latex hardened. When the latex had hardened, the penile tissue was removed from the rat and digested in a KOH bath for 14 days. Digested tissue was carefully pulled away from the latex cast with forceps so the baculum would remain in place. Vascular casts with the baculum in situ were examined under a dissecting microscope.

Microanatomy

Whole flaccid penises were removed from eight individuals and fixed in 10% buffered formalin (Kier, 1992). The penises were transferred into 70% ethanol after 48 h. Penises were embedded in paraffin or glycol methacrylate plastic, sectioned, and examined with brightfield and polarized light microscopy.

For paraffin embedding, whole penises were dehydrated in ethanol, cleared in Hemo-De (Fisher Scientific, Fair Lawn, NJ), and embedded in Ameraffin (Baxter Scientific, McGaw Park, IL). Blocks were sectioned at 4 μm with a rotary microtome in three mutually perpendicular planes and stained for collagen and elastin with Masson trichrome stain (Humason, 1972). For glycol methacrylate embedding, penises were cut into 5 mm thick transverse sections, dehydrated in ethanol, and embedded in glycol methacrylate plastic (Polysciences, Warrington, PA). These blocks were sectioned at 4 μm with glass knives on a rotary JB4 microtome in three mutually perpendicular planes and either stained with Lee's methylene blue-basic fuschin stain (Bennett et al., 1976) or examined unstained under polarized light.

Dorsoventral and lateral diameters of the corpus cavernosum and the thickness of penile tissues were measured by capturing images of randomly selected transverse and parasagittal sections through a video camera (MTI CCD72S) attached to a compound microscope (Olympus BS2). Images were analyzed with NIH Image 1.61 (National Institutes of Health, Bethesda, MD) running on a Macintosh Quadra 840AV computer. Distances were measured to a precision of ±0.001 mm (repeated measurements were within ±0.001 mm).

Baculum microanatomy was also examined with microradiography. Whole bacula were removed from the flaccid penises of three rats and fixed in 100% EtOH for 1 week. Bacula were embedded in methyl methacrylate, cut into 1-mm thick segments, and ground with increasingly fine sandpaper mounted on a horizontal grinder to a thickness of approximately 60 μm. Polished sections were radiographed on a custom micrographic unit (Westenskow Co.).

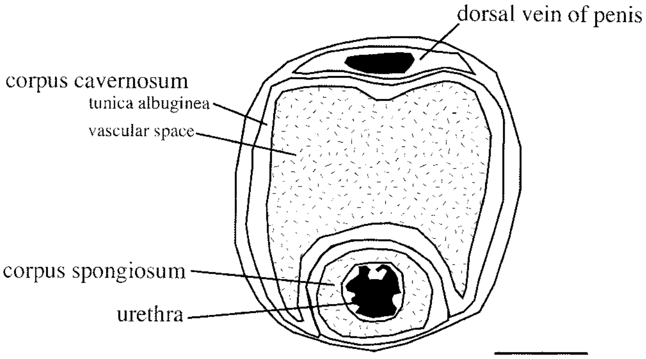

Fig. 1. Tracing from a photomicrograph of a transverse section through a *Rattus norvegicus* penis at the level of the corpus cavernosum. Erectile tissue in the vascular space of the corpus cavernosum is stippled. The corpus cavernosum has a thick tunica albuginea and a noncircular cross-section. Its cross section approximates an ellipse oriented with its major axis pointing dorsoventrally, but is somewhat flattened dorsally and has a deep horseshoe-shaped indentation ventrally where it surrounds the corpus spongiosum. Scale bar = 1.0 mm.

Where appropriate, results are expressed as means with standard error shown in parentheses.

RESULTS

Corpus Cavernosum Anatomy

The *Rattus norvegicus* corpus cavernosum is composed of a single vascular space with a noncircular cross section surrounded by a relatively thick wall (the tunica albuginea) (Fig. 1). Its vascular space approximates an ellipse, oriented with its major axis pointing dorsoventrally, but it is somewhat flattened dorsally and has a deep horseshoe-shaped indentation on its ventral side where it surrounds the corpus spongiosum. Its mean flaccid length is 18.99 (0.67) mm, mean dorsoventral diameter is 1.60 (0.02) mm, mean lateral diameter is 2.47 (0.01) mm, and mean tunica albuginea thickness is 0.295 (0.070) mm (Table 1).

Sections of tunica albuginea stained with Masson trichrome show that the tissue is composed primarily of fibers with the staining characteristics of collagen arranged in regular parallel bundles. The collagen fibers in the flaccid tunica albuginea are highly crimped, and are arranged in two layers. In the outer layer, collagen fibers appear to be arranged parallel to the long axis of the penis; in the inner layer, fibers appear to be arranged circumferentially around the corpus cavernosum, perpendicular to the long axis of the penis. There is a sharp transition between the two layers (Fig. 2).

Baculum Anatomy

The *Rattus norvegicus* baculum is found immediately distal to the corpus cavernosum; it is a simple rod that is flared proximally and pointed at its distal

TABLE 1. Mean dimensions of Rattus norvegicus *penises**

		Diameter		
	Length	Dorsoventral	Lateral	Thickness
Penis	26.34 (0.72)	2.68 (0.14)	2.87 (0.14)	—
Baculum	7.35 (0.15)	1.02 (0.05)	0.96 (0.04)	—
Corpus cavernosum	18.99 (0.67)	1.60 (0.02)	2.47 (0.01)	—
Tunica albuginea	—	—	—	0.295 (0.070)
Fibrocartilage	—	—	—	0.051 (0.001)

*Measurements are in millimeters with standard error in parentheses. Gross external measurements of the penis and baculum, as well as corpus cavernosum length, are the mean of 21 specimens. Corpus cavernosum diameters and penile tissue thickness are the mean of 15 measurements of randomly selected sections taken from eight individuals.

end. It is approximately circular in cross section over most of its length. Mean baculum length is 7.35 (0.15) mm, mean dorsoventral diameter is 1.02 (0.05) mm, mean lateral diameter is 0.96 (0.04) mm (Table 1). The baculum is entirely surrounded by corpus spongiosum tissue; the urethra runs ventral to and parallel to the bone (Fig. 3).

Microradiography shows that the baculum is composed largely of dense vascularized lamellar bone (Fig. 4); all bacula contained regions where darker areas characteristic of demineralization (Jee, 1983) were visible.

Baculum–Corpus Cavernosum Interface

In the flaccid *Rattus norvegicus* penis the flared proximal end of the baculum fits into a small three-dimensional depression found at the distal end of the corpus cavernosum. The depression in the tunica albuginea does not cover the proximal end of the baculum, and the two structures are not connected by either muscles or large ligaments. Sections of the interface of the baculum and the corpus cavernosum stained with Masson trichrome show that the two structures are separated by a tissue layer with the staining characteristics of fibrocartilage and a mean thickness of 0.051 (0.001) mm (Fig. 5A). Collagen fibers originating in both the baculum and the corpus cavernosum enter the fibrocartilage layer. Sections from the interface of the corpus spongiosum and the baculum do not show anything similar: collagen fibers in the wall of the corpus spongiosum are immediately adjacent to the bacular bone (Fig. 5B).

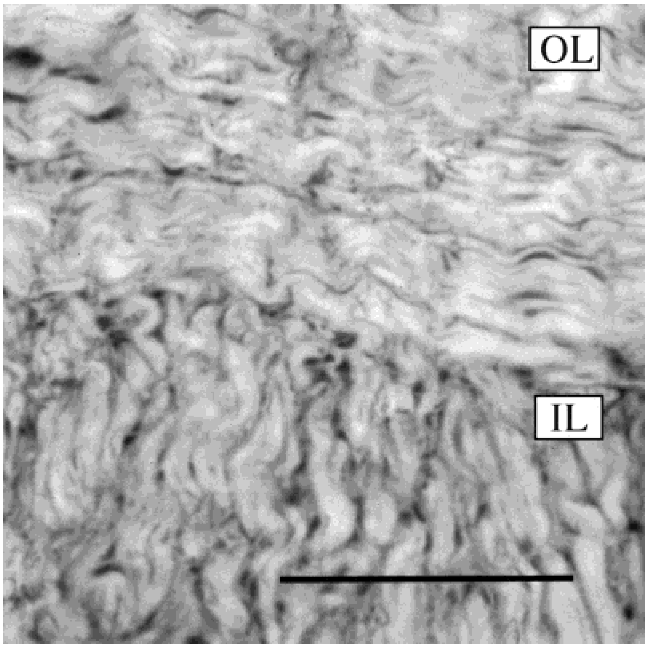

Fig. 2. Photomicrograph of a parasagittal grazing section of flaccid tunica albuginea from *Rattus norvegicus* viewed under brightfield microscopy. Note that the collagen fibers are highly crimped, and that this section shows collagen fibers in two layers: an outer layer (OL) oriented at 0° and an inner layer (IL) oriented at 90° to the penile long axis. IL, inner layer of tunica albuginea; OL, outer layer of tunica albuginea. Scale bar = 0.1 mm and denotes the direction of the long axis of the corpus cavernosum.

Vascular casts of the erect corpus cavernosum with the baculum in situ show that when the corpus cavernosum inflates during erection, the tunica albuginea at its distal end expands and surrounds the flared proximal end of the baculum (Fig. 6).

DISCUSSION

The Corpus Cavernosum–Baculum Complex

In adult Norway rats, the corpus cavernosum makes up most of the penis' length; the baculum

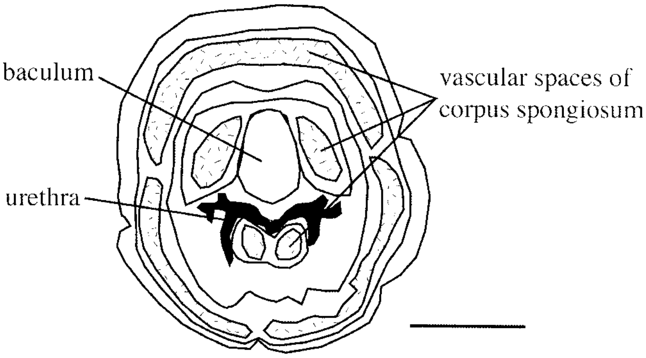

Fig. 3. Tracing from a photomicrograph of a transverse section through a *Rattus norvegicus* penis at the level of the baculum and corpus spongiosum. Erectile tissue in the vascular space of the corpus spongiosum is stippled. Toward the distal end of the penis, the corpus spongiosum expands and splits into several cavities that completely surround both the baculum and the urethra. Scale bar = 1.0 mm.

Fig. 4. Microradiograph of a mid-shaft transverse section of *Rattus norvegicus* baculum. This section of the baculum is made up of dense lamellar bone and is approximately circular in cross section. A dark region characteristic of bone demineralization is visible immediately dorsal to the midline of the bone. Scale bar = 0.5 mm.

occupies only the distal 28% of the penis (Table 1). The mature bone is a single fused unit surrounded by the vascular spaces of the corpus spongiosum, and its proximal end is attached to the distal end of the corpus cavernosum by a layer of well-organized fibrocartilage, rather than the "zone of scattered cells" described by Vilmann and Vilmann (1979). There are neither muscular nor ligamentous connections between the baculum and the corpus cavernosum, and there is very little overlap of the corpus cavernosum onto the external surface of the baculum in flaccid penises. But vascular casts of erect *Rattus norvegicus* penises show for the first time that the tissue at the distal end of the corpus cavernosum expands during erection to cover the flared proximal end of the baculum.

Force Transfer and Corpus Cavernosum Stiffening: The "Plunger" Model

Given the relative sizes of the baculum and the corpus cavernosum in rats, it seems unlikely that the baculum plays a large role in directly stiffening the penis as a whole during erection; the stiffness of most of the penile tissue during erection is therefore produced by the inflation of the hydrostatic corpus cavernosum. But it is possible that the baculum can indirectly increase the overall flexural stiffness of the penis during copulation by transferring bending and compressive forces from the distal end of the glans to the tensile wall of the corpus cavernosum.

Because the distal end of the erect corpus cavernosum surrounds the proximal end of the baculum, any compressive or bending force on the distal end of the baculum during copulation will press the proximal end of the bone directly into the corpus cavernosum (Fig. 7), thereby reducing the internal volume of the corpus cavernosum and increasing its intracavernosal pressure. Because wall tension is proportional to internal pressure in a pressurized cylinder (Wainwright et al., 1976), any increase in intracavernosal pressure will increase the tension in the wall of the corpus cavernosum and strain its tissue.

The wall of the erect corpus cavernosum is reinforced with extended, inextensible collagen fibers, and tissue strains are opposed by the high tensile modulus of the fibers (Kelly, 1997). Erect tunica

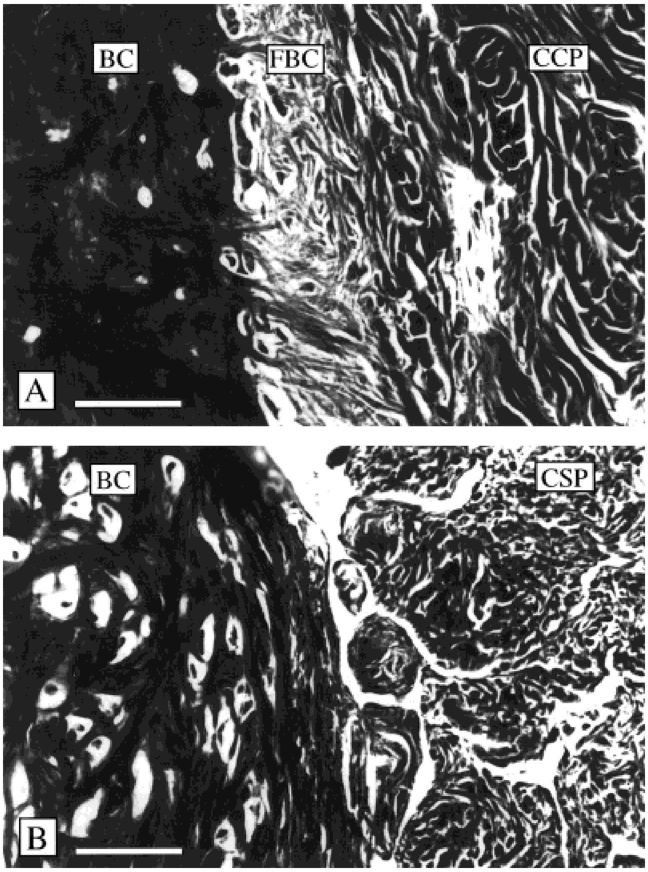

Fig. 5. Photomicrographs illustrating the interfaces between the baculum and the penile erectile tissues. **A:** Photomicrograph of a midline sagittal section at the interface of the corpus cavernosum and baculum in *Rattus norvegicus.* The dense collagen of the corpus cavernosum is on the right (CCP), bacular bone is on the left (BC). There is a thin layer of fibrocartilage (FBC) between these two tissues, and collagen fibers are visible entering the fibrocartilage from both the bone and the tunica albuginea. Scale bar = 0.05 mm. **B:** Photomicrograph of a midline sagittal section at the interface of the corpus spongiosum and baculum in *Rattus norvegicus.* The dense collagen surrounding the corpus spongiosum (CSP) is on the right, bacular bone (BC) is on the left. There is no fibrocartilage at the baculum–corpus spongiosum interface; collagen fibers from the corpus spongiosum lie directly against the surface of the baculum and do not penetrate into the bone. Scale bar = 0.05 mm. BC, baculum; CCP, corpus cavernosum penis; CSP, corpus spongiosum penis; FBC, fibrocartilage.

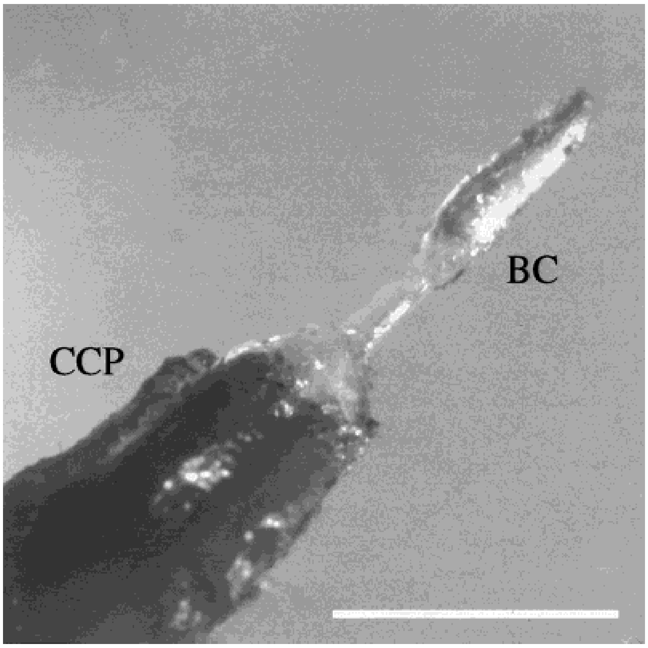

Fig. 6. Vascular cast of erect *Rattus norvegicus* corpus cavernosum with the baculum in situ. The distal tip of the erect corpus cavernosum (CCP) has inflated around the flared proximal end of the baculum (BC). Scale bar = 5.0 mm.

albuginea is already quite stiff, and its nonlinear properties imply that any additional strain on the tissue will further increase its stiffness (Kelly, 1999). Because a material's stiffness is a component of the flexural stiffness of a beam (Roark and Young, 1975), increasing its value will increase the flexural stiffness of the beam as a whole. Therefore, any external force that strains the erect tunica albuginea could increase the flexural stiffness of the entire corpus cavernosum.

Three things must be true for the baculum to indirectly stiffen the corpus cavernosum during copulation: 1) the baculum must be load-bearing; 2) forces must be transferred between the baculum and the corpus cavernosum; and 3) deformations of the corpus cavernosum must raise intracavernosal pressure and strain the tunica albuginea.

The Baculum as a Load-Bearing Bone

Burt (1936) suggested that, unlike limb bones, the baculum is not subjected to stress and strain because it is not directly attached to the axial or appendicular skeleton. Indeed, the absence of any muscular attachments on the proximal end of the baculum implies that internal muscular forces generated by the animal cannot be directly transferred between the corpus cavernosum and the bone. But this does not mean that external forces cannot produce strains within the baculum. A study by Baum (1979) points out that a male mammal's thrusts against the female during copulation are often sufficiently forceful to push her forward. Most of the force pushing the female forward is generated by the male's limbs and lower body, implying that the baculum is also being pushed against internal vaginal or cervical tissue, placing localized externally generated stresses on the bone.

The microstructure of the rat baculum suggests that it is load-bearing, as it contains localized demineralized regions that may be indicative of bone remodeling (Jee, 1983) (Fig. 4). Regular intensive loading of a bone often leads to the resorption and replacement of the material within it (Curry, 1984; Lieberman and Crompton, 1998). Internal remodeling of the bone may either rearrange its material to align with the direction of the prevailing strains, or remove microfractures induced by those strains (Curry, 1984). Curiously, the zones of remodeling in the rat bacula are not correlated with the regions that would be under the greatest amount of stress, but this agrees well with studies of remodeling in the limb bones of rabbits (Hert et al., 1972), humans (Atkinson and Woodhead, 1973), and macaques (Bouvier and Hylander, 1981).

Because the males used in this study were all sexually experienced "retired breeders," it is not known whether the microscopic bone structure of sexually naive males is different from males with sexual experience. A study by Taylor et al. (1983) found that sexually experienced male rats had significantly heavier penises than their sexually inexperienced counterparts, implying that copulatory experience produces tissue remodeling. Because whole penile weights were compared in this study, it is not clear whether the weight difference is due entirely to bone remodeling or whether soft tissues within the penis are being remodeled as well.

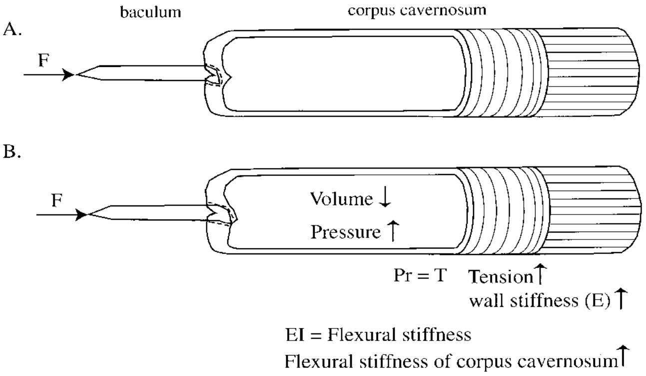

Fig. 7. Schematic diagram of the rat penis in lateral view, illustrating the proposed "plunger" stiffening mechanism. **A:** A compressive force is applied to the distal end of the baculum. **B:** The proximal end of the baculum is pushed into the distal end of the corpus cavernosum, producing a chain of events that increases the flexural stiffness of the entire corpus cavernosum.

The Baculum–Corpus Cavernosum Interface: Transferring Forces and Stiffening

The region between the baculum and the erect corpus cavernosum is characterized by both a layer of fibrocartilage attaching the two structures (Fig. 5A) and an expanded region of tunica albuginea that envelops the proximal end of the bone (Fig. 6). Fibrocartilage can tolerate large tensile stresses (Smeathers, 1992), and is commonly found in intervertebral disks, in tendinous attachments to bone, and between epiphyseal plates in the skull and pelvis (Wainwright et al., 1976; Curry, 1984; Wheater et al., 1987). It is also found in the connections between mammalian hyoid elements, where it forms flexible joints that permit the bones to move with six degrees of freedom but with little relative motion to one another (Curry, 1984).

Because the tip of the penis can bend in any direction during copulation but will only rarely bend with a large lateral excursion, the fibrocartilage between the baculum and the corpus cavernosum may serve as a flexible joint similar to the joints in the hyoid. It is an adequate material for transferring compressive forces; because fibrocartilage deforms more readily than bone, it may be able to distribute contact stresses evenly (Smeathers, 1992).

The expanded tunica albuginea ensures that forces displacing the baculum tip away from the central axis of the penis are transferred to the body of the corpus cavernosum. Indeed, the expanded corpora tissue explains how rats can produce glans movements without muscles connecting the corpus cavernosum and the baculum. During erection but before intromission, a rat's glans is depressed ventrally. In order to achieve intromission, the male must be able to flex his glans dorsally in a "flip." Glans dorsiflexions are correlated with contractions of ischiocavernosus muscles at the base of the penis (Holmes et al., 1991). The muscular contractions deform the proximal end of the corpus cavernosum, causing intracavernosal pressure to increase from a mean maximal pressure of 7.81 ± 1.72 kilopascals (kPa) at erection to a mean maximal pressure of 28.7 ± 6.7 kPa during a glans flip (Bernabe et al., 1995). The increase in intracavernosal pressure strains the distal tunica albuginea; because this tissue completely surrounds the proximal end of the baculum, the small change in its dimensions can subsequently displace the baculum in a flip.

If forces on the proximal end of the penis can stiffen the corpus cavernosum enough to displace the baculum for intromission, it is certainly possible that forces transmitted through the baculum during copulation can also stiffen the corpus cavernosum.

Additional Functions for the Baculum

The plunger hypothesis does not rule out the presence of complementary, simultaneous functions for the baculum during copulation. Rat glans tissue is in a position to be stiffened directly by the baculum, although it is also supported by the internal pressure of the erect corpus spongiosum (Purohit and Beckett, 1976). But in some mammals the baculum cannot support all of the glans during copulation; in dogs, for example, erect glans tissue expands beyond the distal end of the baculum (Grandage, 1972).

The plunger model also does not rule out a stimulatory function for the baculum. In rats, the rate at which females become pregnant is correlated to the number of preejaculatory thrusts the male produces during copulation (Adler, 1969; Matthews and Adler, 1977), implying that stimulation of some kind is an important trigger of either sperm transport or implantation in females. Indeed, the sometimes elaborate species-specific morphologies found at the distal tip of the baculum imply that the baculum takes on a stimulatory role in many mammalian species, potentially leading to female selection among mates after sperm deposition (Eberhard, 1985, 1996). It is entirely possible that the proximal and distal ends of the baculum have evolved different functional roles in copulation.

The possibility that the baculum has complementary functions makes it imperative that we examine its biomechanics in a comparative context. Selective pressures on penile anatomy may be different for each mammalian species, affected by factors like penis size, vaginal activity during copulation, and the large-scale copulatory behavior of both males and females. But comparative biomechanical studies could help us determine which selective pressures are most important for a given species—potentially allowing us to determine whether selection favors maintaining the overall integrity of penile structures during copulation, the performance of specific mechanical functions, such as opening the cervix or the indirect stiffening of the corpus cavernosum, or stimulation of the copulating individuals. For example, the mechanics of rat penile anatomy could be compared to the penile mechanics of both closely related rodents with simple, rod-shaped bacula, and more distantly related rodents with more complex bacula. Comparative studies of baculum biomechanics should also take into account species that lack bacula, either plesiomorphically (such as elephants or armadillos) or apomorphically (such as hyenas, which are members of Carnivora that have lost the baculum).

Although the anatomy of the baculum and corpus cavernosum in the Norway rat implies that the baculum is load-bearing, that forces can be transferred between the baculum and the corpus cavernosum, and that deformations of the corpus cavernosum can raise intracavernosal pressure and increase tunica albuginea strains, direct experimental data are still needed to determine whether baculum movement has an effect on corpus cavernosum stiffness.

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