Penises as Variable-Volume Hydrostatic Skeletons

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ABSTRACT: Penises are inflatable intromittent organs that transfer sperm to a female during copulation. Most of the time, males store their penises in a flexible detumesced state, but they can rapidly inflate them with blood when an opportunity for reproductive behavior arises. In mammals, the primary erectile tissue is called the corpus cavernosum; its anatomy is a close match to a model hydroskeleton reinforced by an axial orthogonal fiber array. The wall of the corpus cavernosum contains layers of highly organized collagen fibers arranged at 0° and 90° to the penile long axis. Flaccid wall tissue is folded. Collagen fiber straightening during erection expands the tunica albuginea and increases both its stiffness and its second moment of area. These changes make the entire penis larger and harder to bend. Axial orthogonal fiber reinforcement affects the mechanical behavior of the erect corpus cavernosum, making it resistant to tensile, compressive, and bending forces.

KEYWORDS: penis; hydroskeleton; hydrostat; mammal

INTRODUCTION

All male mammals have a penis. Penises are inflatable intromittent organs that transfer sperm to a female during copulation. Most of the time, males store their penises in a flexible detumesced state, but they can rapidly inflate them with blood when an opportunity for reproductive behavior arises. During inflation, or erection, the structural properties of the penis change: the flexible structure gets larger and becomes much harder to bend.

Because reproduction is a critical stage in a mammal's life, the behavior of the penis during erection and copulation has important implications for the study of mating systems and sexual selection, as well as for human and veterinary medicine. Most studies of penile function have been reductive in nature, focused on understanding its anatomy, hemodynamics, neurology, or its physiological effect on females. But penile mechanics also fits into a larger

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context of skeletal mechanics. In this review I will demonstrate how the behavior of hydrostatic skeletons can inform our understanding of the anatomy and functional morphology of mammalian penises during both erection and copulation.

HYDROSTATIC SKELETONS

From a functional standpoint, a skeleton is a structure that supports tissues and transmits force from one part of an organism to another.[1] The most familiar skeletons are built of stiff materials like the bone in the vertebrae endoskeleton or the chitin in the arthropod exoskeleton. But skeletal systems based around an internal volume of fluid are far more widespread among organisms, forming the main support system in organisms as diverse as cnidarians,[2] nematode worms,[3] and plants,[4] and playing functional roles in organisms with hard skeletons like echninoderms,[5] vertebrates,[6–9] and arthropods.[10,11] Fluid-filled skeletons are variously referred to as hydrostats, hydroskeletons, or hydrostatic skeletons.

Composition of Hydrostatic Skeletons

A hydrostatic skeleton is a balloon-like structure made up of a volume of fluid surrounded by a membrane in tension.[12] The fluid is typically water—depending on the taxa, it can be found in the form of blood, extra- or intracellular fluid, or seawater. Water is functionally incompressible. As long as it is constrained in some way, it effectively resists compressive forces.[13] The membrane surrounding the fluid is not strong in compression; its function is to limit fluid movement when forces are placed on the skeleton. Both components of the hydrostatic skeleton must interact to produce support. Unconstrained fluids flow when they are stressed,[13] and an empty membrane folds and collapses under compression.

When the fluid in a hydrostatic skeleton is placed in compression by either the addition of fluid to the central space or deformations of the entire structure, the membrane resists fluid movement and is placed in tension. If the hydrostat is cylindrical, the tensile stresses inside its membrane are twice as great around its circumference as the stresses along its length.[12] If the membrane were made of a homogeneous material, this imbalance of forces would tend to make the skeleton bulge out in an aneurysm. To prevent this type of failure, hydrostatic skeletons are reinforced with relatively inextensible fibers that redistribute the forces in the hydrostat wall. The fibers are made of biomaterials that are strong in tension, like collagen or cellulose.[12]

There are two ways to arrange the reinforcing fibers around the long axis of a cylindrical hydrostatic skeleton. They can be arranged in left- and right-handed helices around the structure's long axis, a pattern called a crossed-helical array. Or they can be arranged at 0° and 90° to the structure's long axis,[1] a pattern called an axial orthogonal array.[14] Fiber arrangement has a profound effect on the structural behavior of the hydroskeleton.

Behavior of Hydrostatic Skeletons

Hydrostats that are reinforced with crossed-helical arrays of fibers can change their length and bend smoothly without kinking.[1] Because their fibers are arranged at an angle to the long axis of the skeleton, they can reorient in response to stresses on the tissue.[15–16] Thus, if one of these hydroskeletons has a constant volume, forces on its ends will make it shorter and fatter, and forces that squeeze its circumference will make it longer and thinner.[17] When paired with either muscles in antagonistic pairs or muscles and energy-storing materials, crossed-helical hydroskeletons become an effective locomotory system.[3,18]

In contrast, hydroskeletons that are reinforced with axial orthogonal fiber arrays resist deformation. Forces that would tend to make the skeleton shorter and fatter are resisted by the circumferential fibers; forces that would tend to make the skeleton longer and thinner are resisted by the longitudinal fibers. Longitudinal fibers also directly resist forces that bend the skeleton, giving axial orthogonal arrays the highest flexural stiffness of any fiber-reinforced system.[19] Hydroskeletons with axial orthogonal reinforcement seem so far to be limited to reproductive structures that require high stiffness and stable shapes, such as penises[14,20] and octopus ligulae.[21]

Although many hydroskeletons are constant-volume structures, variable-volume hydroskeletons that can inflate smoothly in response to increases in internal volume also exist. Some of these hydroskeletons are reinforced by crossed-helical arrays of fibers: examples include developing vertebrate notochords,[16] inflating pufferfish,[22] fin whale throats,[23] and sea anemones.[12] Others are axial orthogonally reinforced reproductive structures.[14,20,21] In all cases, hydroskeleton expansion is possible because the tensile fibers are folded and unstressed in the deflated skeleton. Folding gives the wall tissue nonlinear material properties. Unstressed folded tissue is compliant, but as the tissue is stretched and its integral fibers straighten its stiffness increases. Ultimately, the stiff fibers are loaded in tension and resist further extension of the tissue.

THE PENIS AS A HYDROSTATIC SKELETON

In this context, penises are variable-volume hydroskeletons that inflate and increase their flexural stiffness during erection. Inflatable penises are widespread in amniotes, where they are found in turtles,[24,25] snakes and lizards,[26,27] crocodilians,[28] some birds,[28–30] and mammals.[31] This article will focus on the structural behavior of the penile hydroskeleton in mammals.

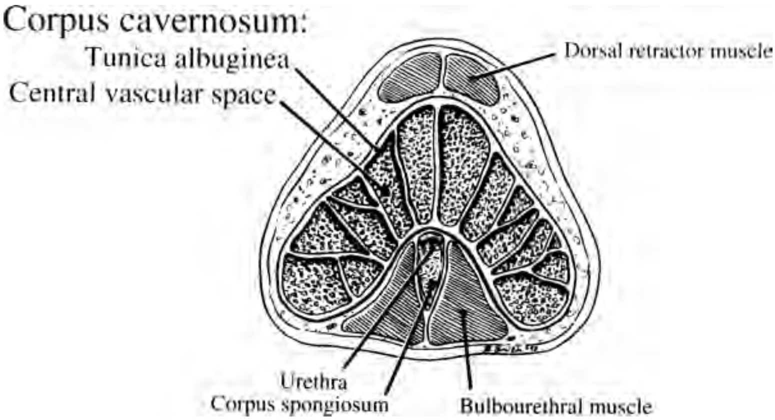

FIGURE 1. Cross-section of an erect armadillo (*Dasypus novencinctus*) penis. Most of the penile volume is comprised of the corpus cavernosum, which contains the vascular space and surrounding tensile membrane that characterizes hydrostatic skeletons. Scale bar = 1 mm. (Reprinted from Kelly,[14] with permission from Wiley-Liss, Inc.)

Mammalian penises contain a pair of hydrostatic erectile structures, the corpus cavernosum and the corpus spongiosum (FIG. 1). The corpus cavernosum is found on the dorsal side of the penis, and is a high-pressure system responsible for increasing penile size and flexural stiffness during erection.[32] The smaller corpus spongiosum contains the urethra, and in many species expands distally to form the glans. Although it also undergoes vasodilation during erection, it is not responsible for penile rigidity.[33]

Gross Anatomy of the Corpus Cavernosum

The corpus cavernosum is made up of a central endothelium-lined vascular space surrounded by a thick wall of collagenous tissue called the tunica albuginea.[34] Its distal end is often covered by an expanded section of corpus spongiosum tissue called the glans. Proximally, the corpus cavermosum splits into a pair of crurae; each one is anchored to an ischium and is surrounded by an ischiocavernosus muscle.[35] In cross-section, the corpus cavernosum is noncircular, and its vascular space contains collagenous cords called trabeculae that originate in the tunica albuginea and connect the internal dorsal and ventral surfaces of the corpus cavernosum. In some mammals, including humans, a concentration of trabeculae at the midline of the vascular space form a septum that divides the space into two distinct sections. However, the septum contains many fenestrations that permit blood to flow between the two chambers,[36] making it functionally a single vascular space. The pressure inside both sections of the corpus cavernosum is therefore the same, and pressure changes will place the same force on all parts of the corpus cavernosum's wall.

Blood enters the corpus cavernosum through the cavernosal arteries. These arteries enter the corpus cavernosum at its proximal end and run distally through the center of each vascular space. They give rise to clumps of helicine arteries that regulate blood flow into the vascular spaces of the corpus cavernosum.[36] The corpus is drained by the deep veins of the penis, which exit the corpus from its proximal end.[37]

Erection starts when smooth muscle in the vascular space of the corpus cavernosum relaxes[34] and the helicine branches of the deep arteries dilate and straighten[38] in response to signals from the pelvic nerve.[39] Vasodilation increases blood flow into the vascular space of the corpus cavernosum. As the intracavernosal volume of blood increases, the tunica albuginea expands under tension.[40,41] Its expansion compresses the veins leaving the vascular space, reducing venous outflow and allowing the corpus to remain engorged with blood.[42] The pressurized blood inside the vascular space forms the compressive element of the penile hydrostatic skeleton; the wall of the tunica albuginea forms its tensile element.

Microanatomy of the Tunica Albuginea

The mammalian tunica albuginea is comprised primarily of thick bundles of type I collagen fibers[42,43] arranged in two layers.[14,34] Its outer layer contains fibers arranged parallel to the long axis of the penis. Its inner layer contains fibers arranged around the circumference of the corpus cavernosum. Measurements of collagen fiber orientation relative to the long axis of the penis have shown that the fiber angle in the outer layer is not significantly different from 0°, and the fiber angle in the inner layer is not significantly different from 90°.[14,44]

When the corpus cavernosum is flaccid, the collagen fibers in the tunica albuginea are highly crimped, and the tissue is thrown into folds. After erection, most of the tissue folding and collagen fiber crimping is lost as the tunica albuginea expands.[14,42,45]

Behavior of the Penile Hydroskeleton during Erection

A penis built around an inflatable hydrostatic skeleton permits a male mammal to unobtrusively store the deflated organ when he is not actively engaged in reproductive displays or copulation. This ability may convey some advantages: a recent study of poeciliid fish that copulate with modified anal fins supported by bone correlated long reproductive fins with higher rates of predation.[46] When deflated penises are inflated for intromission and copulation, they can undergo dramatic changes in size, shape, and flexural stiffness.

During penile erection, the vascular space in the corpus cavernosum becomes engorged with blood, the tunica albuginea expands, and the entire structure becomes harder to bend—in engineering terms, its flexural stiffness increases. The process is mediated by folded collagenous tissue in the tunica albuginea.

Collagen fibers in the tunica albuginea redistribute tensile forces when a fully inflated skeleton is under load. Collagen is a hierarchically organized fibrillar protein that can bear tensile loads on the order of 100 MPa.[12] Each fiber crimps with a typical period of 100 μm; the crimped fibers straighten under tensile loads to produce the characteristic J-shaped collagen stress–strain curve. But crimping in individual collagen fibers only permits tissue extension to strains of 3%.[47] Corpus cavernosum tissue extension is far greater than this during erection—in the nine-banded armadillo, inflating tunica albuginea reaches strains of 17–30%.[48] The difference is due to the larger scale collagen fiber folding inside the tissue and the three-dimensional folding of flaccid wall tissue.[40,49]

As the central vascular space of the corpus cavernosum fills with blood the tunica albuginea expands longitudinally and circumferentially and its flexural stiffness increases. Flexural stiffness is derived from the product of a structure's second moment of area (I) and the Young's modulus of elasticity (E) of its tissues.[50]

$$\text{Flexural Stiffness} = EI$$

Second moment of area (I) describes the distribution of tissue around a central plane. It is proportional to a cylinder's radius raised to the fourth power, so is very sensitive to small changes in diameter; small changes in a hydroskeleton's diameters can produce relatively large changes in second moments of area.[12] Young's modulus of elasticity (E) describes the stiffness of the material in a structure.[12] Increasing the value of either variable increases the flexural stiffness of a structure. During erection, corpus cavernosum unfolding increases the values of both.

Changes in Second Moment of Area (I)

Circumferential expansion of the tunica albuginea produces larger diameters in the corpus cavernosum (FIG. 2). In nine-banded armadillos, the second moments of area of the corpus cavernosum approximately double both dorsoventrally and laterally during inflation, and could become even larger if the trabeculae did not restrict tissue expansion.[48] As mammalian corpora cavernosa expand radially, their trabeculae are placed in tension and preserve the structure's noncircular cross-sectional shape.[48,51] Hollow, fluid-filled, cylindrical hydrostats should become more circular in cross-section as their internal volume increases, because the pressure on the wall of the structure is equally distributed over its internal surface.[1] Retaining a noncircular cross-sectional shape limits the maximum flexural stiffness of the erect corpus cavernosum, but it also protects the low-pressure corpus spongiosum from compression.[48]

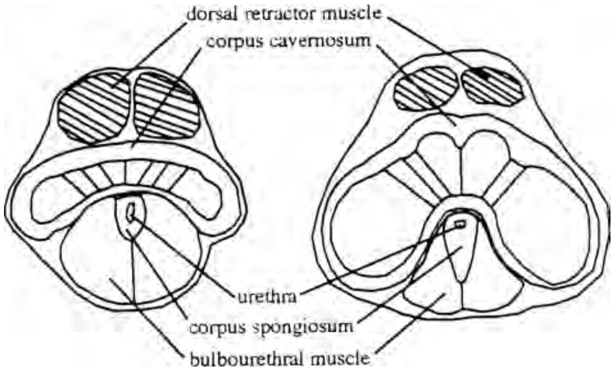

FIGURE 2. Transverse sections of flaccid (left) and erect (right) *Dasypus novemcinctus* corpora cavernosa showing the changes in internal morphology that occur during erection. Both sections were samples from the proximal end of the free part of the penis. Scale bar = 1 cm. (Reprinted from Kelly,[48] with permission from Company of Biologists.)

Changes in Young's Modulus (E)

Folding of the tunica albuginea also contributes to its nonlinear increase in Young's modulus during erection (FIG. 3). The tunica albuginia is initially compliant during erection.[48] As intracavernosal volume increases, low stresses produce large extensions of the wall tissue as collagen fibers unfold. When the fibers reach full extension their high elastic modulus makes the wall tissue much stiffer. In nine-banded armadillos, tunica albuginea stiffness increases by 3–4 orders of magnitude during the last 2–3% of tissue strain.[48]

Behavior of the Penile Hydroskeleton during Copulation

Mammalian copulation often involves repetitive intravaginal thrusting,[52] producing forces that place compressive and bending stresses on the end of the erect corpus cavernosum. In some species, copulation also involves vaginal ties or locks which squeeze the corpus cavernosum.[52,53] An erect axial orthogonal fiber array helps the corpus cavernosum resist these external forces and retain its shape. An erect corpus cavernosum has a constant volume because its venous outflow is restricted.[54,55] Forces on the end of the erect penis that would tend to telescope its length and increase its girth are directly opposed by the high tensile modulus of the circumferential collagen fibers. Similarly, compressive forces that would tend to extend the erect penis are directly opposed by the longitudinal collagen fibers.[14] The axial orthogonal array also maximizes the penis's resistance to bending. Hydroskeletons supported by axial orthogonal arrays have a higher flexural stiffness than any supported by a crossed-helical fiber array.[18] If they contain fibers that are not in a normal axial orthogonal

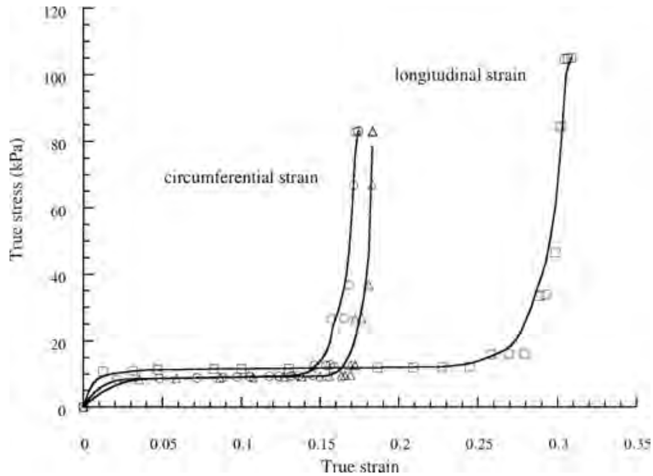

FIGURE 3. Mean smooth stress–strain curves illustrating the extension of mammalian tunica albuginea from *Dasypus novemcinctus* along three axes during artificial inflation. Tissue stiffness is represented by the instantaneous slope of the line, and increases by 3–4 orders of magnitude once the tissue is strained 25% longitudinally and 15% circumferentially. The symbols denote the direction of tissue strain: squares are longitudinal strain, circles are circumferential strain viewed laterally, triangles are circumferential strain viewed dorsally. (Reprinted from Kelly,[58] with permission from Allen Press. Inc.)

array because of either abnormal development[56] or injury[57] the penis does not develop a normal erect shape.

Reinforcement by an axial orthogonal collagen array also explains some unusual behavior of the corpus cavernosum. The penile kinking that has been observed in copulating dogs[53] and that may in extreme cases lead to human penile fracture occurs because collagen is stiff in tension but folds under compression.[12] Bending one end of an erect corpus cavernosum puts the longitudinal collagen fibers on one side of the structure into tension and the fibers on the opposite side into compression.[50] Large bending forces eventually lead to failure on the side that is under compression, kinking the penis at a sharp angle.

CONCLUDING REMARKS

The behavior of the mammalian corpus cavernosum during erection and copulation is consistent with the behavior predicted of an inflatable hydroskeleton with folded wall tissue reinforced by an axial orthogonal fiber array. The axial orthogonal array gives the erect mammalian penis a fixed size and shape and prevents shape changes during copulation. The fiber organization of the wall tissue in the corpus spongiosum and most of the inflatable penises found in other amniotes is still unknown. Future research on these structures should be informed by the biomechanics of biological hydrostats.

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