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The Functional Morphology of Penile Erection: Tissue Designs for Increasing and Maintaining Stiffness[1]

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SYNOPSIS. **Inflatable penises have evolved independently at least four times in amniotes, specifically in mammals, turtles, squamates, and the archosaurs. Males in these lineages therefore share the functional problem of building a penis out of soft and flexible tissues that can increase its flexural stiffness and resist bending during copulation. Research on penile erectile tissues in mammals and turtles shows that these two taxa have convergently evolved an axial orthogonal array of collagen fibers to reinforce the penis during erection and copulation; in both lineages, the collagen fibers in the array are crimped and folded in the flaccid penis. Collagen fiber straightening during erection increases the stiffness of the tissue and allows changes in penile radius that increase its second moment of area: both of these changes increase the flexural stiffness of the penis as a whole. And once erect, axial orthogonal arrays have the highest flexural stiffness of any fiber arrangement. The high degree of anatomical convergence (to the level of microanatomical features) within mammals and turtles suggests that the stiffness requirements for copulation produce an extremely restrictive selective regime in organisms that evolve inflatable penises.**

INTRODUCTION

The fitness of individual organisms is closely tied to the mechanical behavior of their reproductive structures. This is not to say that fitness is unaffected by other organic systems; in order to even get to the point of breeding an organism must be proficient in a vast array of activities, including prey capture, predator evasion, food processing, and dispersal. But if reproductive structures do not perform their specific mechanical functions correctly, an individual's offspring either do not survive to be born or are not conceived at all. The close relationship between fitness and reproductive structures has inspired an enormous body of research on sexual selection during the past two decades (for reviews see Eberhard, 1985, 1996; Birkhead, 2000), but as yet little work has focused on the functional morphology of these systems.

Intromittent organs are reproductive structures with the primary function of placing gametes in mates. They are a common adaptation in organisms that use internal fertilization, and have arisen multiple times in a number of vertebrate and invertebrate lineages (Romer, 1970; Pennak, 1975; van Tienhoven, 1983). In general, intromittent organs are found in males and are used to inseminate females. There are a few exceptions to this pattern, most famously in seahorses where females have an ovipositor which places unfertilized ova into the male's pouch for insemination (Masonjones and Lewis, 1996).

The basic design requirements for an intromittent organ are simple: it must be stiff enough to enter a mate without bending during copulation, and it must have some mechanism for transferring gametes from one individual to the other. Little is known about the methods intromittent organs use to meet these requirements. A few authors have examined the anatomy of structures within the shafts of intromittent organs and made inferences about their functional roles (Watson, 1964; Long and Frank, 1968; Goldstein *et al.*, 1982; Dixson, 1995; Kelly, 1997*a*, 2000), but this approach alone can neither quantify the behavior of those tissues during erection and copulation, nor explain how changes in tissue mechanical properties and arrangement within the structures contribute to overall intromittent organ function. A full understanding of intromittent organ function therefore requires a broader approach, combining both detailed anatomical studies and mechanical tests of the structure and its component tissues.

INTROMITTENT ORGANS IN AMNIOTES

Shelled eggs are a synapomorphy of amniote vertebrates (Liem *et al.*, 2001); amniote males are obligate internal fertilizers because their sperm cannot penetrate the shell. But although all amniote taxa share internal fertilization, not all amniotes have intromittent organs. They are found in mammals (Williams-Ashman, 1990), turtles (Zug, 1966; McDowell, 1983), squamates (Dowling and Savage, 1960; Conner and Crews, 1980), and crocodilians (King, 1981), as well as a few bird taxa, particularly ratites (King, 1981) and ducks (Leibe, 1914; McCracken, 2000). But most birds (King, 1981) and *Sphenodon* (Romer, 1970; Alexander, 1990) lack intromittent organs and transfer sperm by cloacal apposition.

There are two ways to interpret the distribution of intromittent organs in amniotes. They could be a synapomorphy of amniotes that is subsequently lost in most of the modern birds and the Lepidosauria, but is regained in the squamates as an autapomorphy of that group (Gauthier *et al.*, 1988) (Fig. 1A). Or intromittent organs could have multiple origins within the amni-

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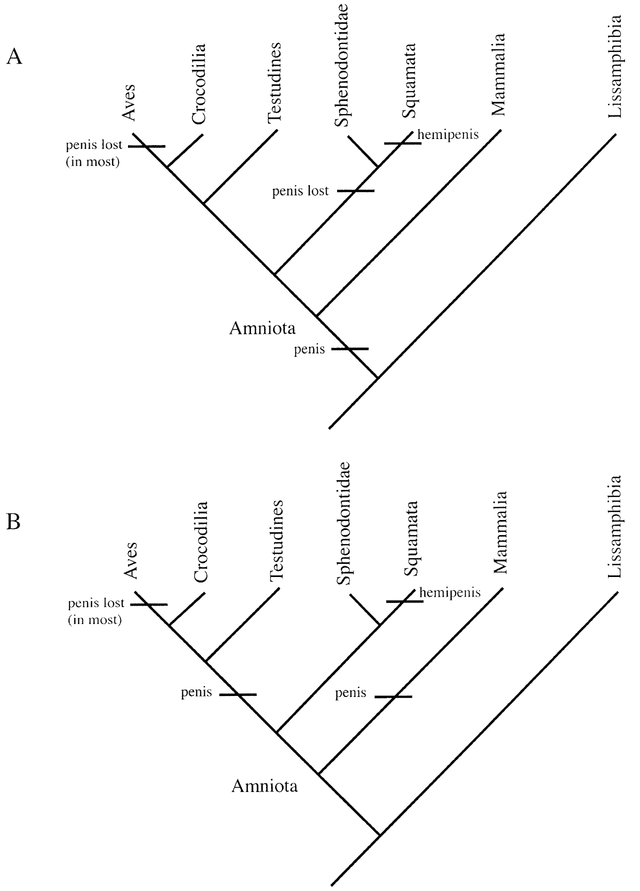

FIG. 1. Phylogeny of extant amniotes after Janke *et al.* (2001) illustrating alternate hypotheses for the distribution of intromittent organs in amniotes. A. The penis is an amniote synapomorphy. B. The penis as a convergent trait. The position of the Testudines is disputed; alternate hypotheses (*i.e.,* Romer, 1966; Rieppel and DeBraga, 1996) increase the possible number of independent penile origins, as does the patchy distribution of the organ within Aves.

otes, evolving independently three times or more depending on the placement of major amniote taxa within the phylogenetic hypothesis (Fig. 1B).

There are significant morphological and developmental differences among amniote intromittent organs that support the independent origin hypothesis. Mammalian penises are single medial organs containing two separate vascular erectile bodies (Andersson and Wagner, 1995) that are derived from noncloacal tissue (Hunter, 1995); turtle and crocodile penises are also single medial organs, but contain only one vascular erectile body which develops on the ventral cloacal wall (King, 1981). Bird penile tissue, where it exists, also develops on the ventral cloacal wall. But waterfowl erect their penile tissue with a lymphatic system instead of a vascular one (King, 1981; McCracken, 2000); it is not known whether ratites use a vascular or lymphatic system for penile inflation. Squamate hemipenes develop from the lateral walls of the cloaca (Gauthier *et al.,* 1988) and are the only paired intromittent organ within amniotes; erection seems to be primarily vascular, although the concurrent use of a lymphatic system has been suggested (Dowling and Savage, 1960).

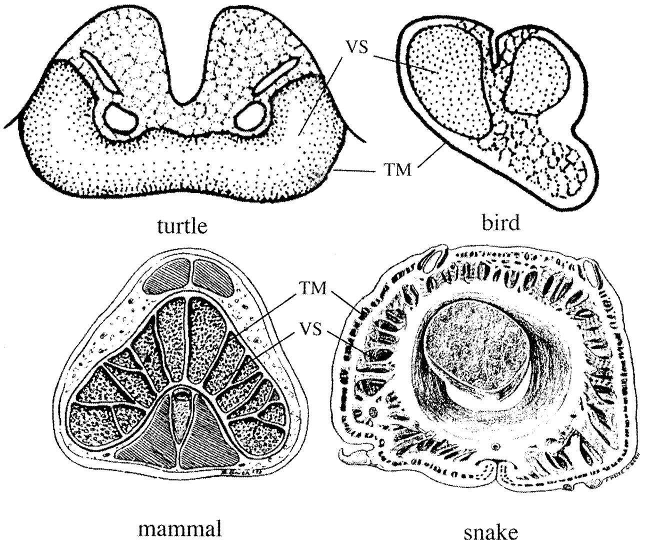

FIG. 2. Diagrams illustrating transverse sections of amniote intromittent organs. A turtle penis is at the upper left, a bird penis is at the upper right, a mammalian penis is at the lower left, and a snake hemipene is at the lower right. All the structures are hydrostatic: each contains a central vascular space (VS) and surrounding tensile membrane (TM) characteristic of hydrostats. (Figure adapted from respectively, Zug, 1966; King, 1981; Kelly, 1997*a*; Dowling and Savage, 1960.)

Despite these anatomical differences, amniote penises and hemipenes share some basic similarities: they are all more or less cylindrical, and they are all hydrostatic. Hydrostats are characterized by a central volume of pressurized incompressible fluid surrounded by a membrane in tension (Wainwright *et al.,* 1976); all amniote intromittent organs include a central space surrounded by a tensile membrane (Fig. 2). Since amniote intromittent organs are hydrostatic, it follows that the wall of their erectile structures must be reinforced with inextensible fibers to prevent aneurysms (Wainwright, 1988). Histological examination of penile wall tissue in mammals (Hanyu, 1988; Kelly, 1997*a*; Pinheiro *et al.,* 2000), turtles (Seshadri, 1956), and birds (Liebe, 1914) has indicated that the walls of the erectile structure in these taxa are reinforced with collagen fibers.

The underlying mechanism of erection is also the same in all of these structures: the erectile space fills with fluid and inflates the membrane to full erection. All of these amniotes therefore face the same functional problem: how to build an intromittent organ out of soft and flexible tissues that can nevertheless become stiff enough to enter the female's reproductive tract without bending.

How do the taxa in each amniote lineage solve this particular problem? Have they each evolved unique methods to produce stiffness, or have they independently evolved similar design features? I have begun to address these questions by examining the solutions

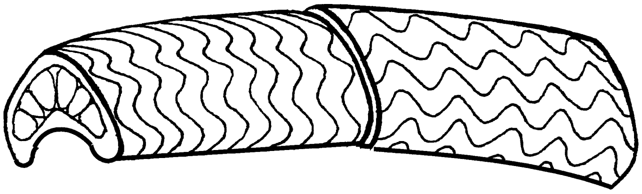

FIG. 3. Diagram of collagen fiber arrangement in the wall tissue of a flaccid mammalian penis. There are two layers forming an axial orthogonal array: an outer layer with fibers at 0° to the long axis of the penis and an inner layer with fibers at 90° to the long axis. Collagen fibers are highly crimped in the flaccid penis, but straighten upon erection. (Figure adapted from Kelly, 1997*a*.)

used by amniote taxa for two major mechanical problems:

(1) How do erect intromittent organs resist bending? Which arrangements of soft tissues are sufficiently stiff to permit successful copulation?

(2) How do intromittent organs increase their stiffness during erection? Do changes in the material properties of the tissues increase stiffness, or is it solely the result of tissue rearrangement during inflation?

STIFFNESS IN INTROMITTENT ORGANS

If intromittent organs are to be stiff during copulation, it follows that the material properties and mechanical behavior of their tissues must resist bending. If the tissues cannot stiffen the structure, the intromittent organ will be unable to function correctly. The obvious way to produce a stiff intromittent organ is to build it out of materials that have relatively high flexural stiffness. Indeed, intromittent organs in many organisms are reinforced with skeletal elements made of materials that resist bending: the claspers of elasmobranchs and the gonopodia of some groups of teleost fish are modified fins supported by cartilage or bone (Wourms, 1981; van Tienhoven, 1983; Dodd and Dodd, 1985), the eversible cloaca in some caecilians contains cartilaginous elements (Wake, 1998), insect aedeagi are supported by chitin and scleroprotein (Eberhard, 1985), and nematode spicula are supported by sclerotized cuticle (Hyman, 1951). But there is another, less obvious way to build a flexurally stiff intromittent organ—by using a hydrostatic system like those found in amniotes.

The elements that make up a hydrostatic system are not themselves stiff in bending: fluids are sensitive to the rate of deformation rather than amount of deformation (Denny, 1993; Vogel, 1994), and the thin fibers that reinforce the tensile membrane are stiff in tension but bend easily (Wainwright *et al.*, 1976). Support in hydrostats comes instead from the interaction of the tensile membrane and the pressurized fluid it surrounds, and the specific arrangement of fibers within the tensile membrane determines how well a hydrostat resists bending. A hydrostat reinforced with fibers wrapped in left- and right-handed helices around its long axis (in ‘‘crossed-helices’’) can extend, contract, and bend in smooth curves (Wainwright, 1988), although its flexural stiffness depends upon the specific angle of its fibers (Koehl *et al.*, 2000). A hydrostat reinforced with fibers arranged exactly parallel and perpendicular to its long axis (in an ‘‘axial orthogonal array’’) resists extension, contraction, and bending (Wainwright, 1988; Kelly, 1997*a*).

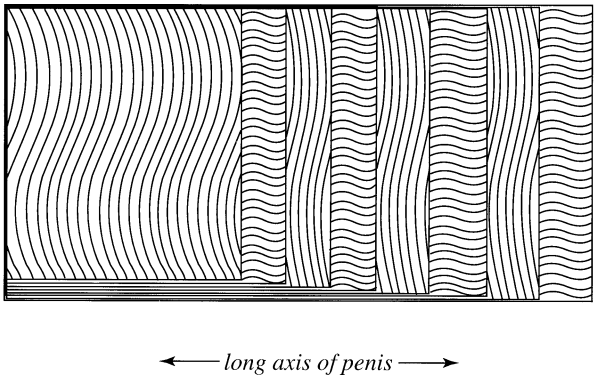

FIG. 4. Diagram of collagen fiber arrangement in the wall tissue of a flaccid turtle penis. There are multiple layers that alternate between fibers at 0° to the long axis of the penis and fibers at 90° to the long axis. Collagen fibers are highly crimped in the flaccid penis, but straighten upon erection.

Resisting bending during copulation

In both mammals (Kelly, 1997*a*) and turtles (D.A.K., unpublished data), the collagen fibers in the wall of the erectile structure are arranged in an axial orthogonal array. In mammals, the fibers are arranged in two layers in the wall of the corpus cavernosum (Fig. 3); the outer layer contains fibers arranged at 0° to the long axis of the penis and the inner layer contains fibers arranged at 90° to the long axis of the penis (Kelly, 1997*a*). In turtles, fibers are laid down in multiple layers (Fig. 4) that alternate between orientation at 0° and at 90° to the penile long axis, producing an axial orthogonal plywood (D.A.K., unpublished data). Nothing is known about the specific fiber orientation in the erectile tissue of squamates, crocodilians, or birds.

I have inferred from this specific microanatomy that penises in both mammals and turtles will be able to resist bending forces when erect. Any bending of the erect penis would put a tensile load on one side of the structure (Smith and Sidebottom, 1969), where it is resisted by longitudinally-oriented collagen fibers. Experiments with fiber wound models by Koehl *et al.* (1995) show that a hydrostat reinforced by an axial orthogonal array has higher flexural stiffness than similar structures reinforced by crossed-helical fiber arrays.

Increasing stiffness during erection

Erectile tissues expand in response to increases in the hydrostat's internal fluid volume. As the tissues expand, the normally flexible intromittent organ becomes larger and more resistant to bending. Three-point bending experiments of progressively inflated

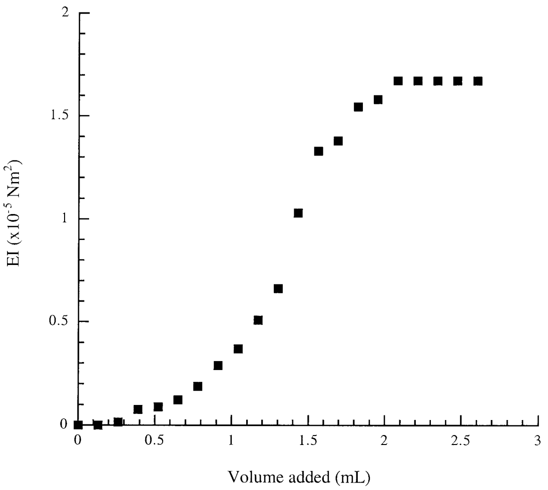

FIG. 5. Change in the average flexural stiffness of mammalian penile erectile tissue (corpus cavernosum) during inflation, as measured by three-point bending tests in the nine-banded armadillo (*Dasypus novemcinctus*). Flexural stiffness increases as internal volume increases, and is highest when the corpus cavernosum reaches maximum volume. There is not a statistically significant difference in the flexural stiffness of the corpus cavernosum when the structure is bent laterally or dorsoventrally ($n = 4$; F-ratio $= 2.70$; $0.05 < P < 0.1$). (Figure adapted from Kelly, 1997*b*.)

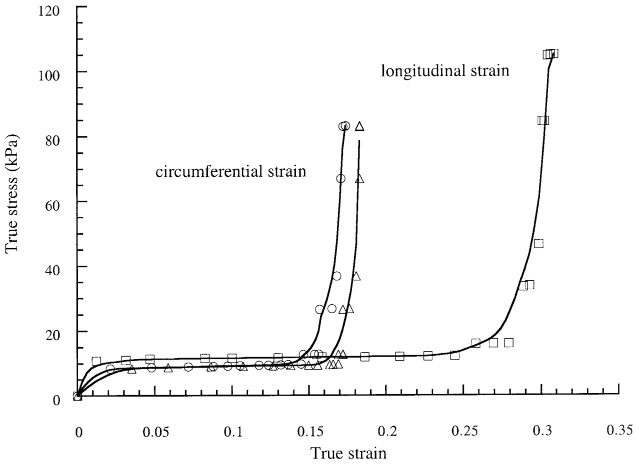

FIG. 6. Mean smooth stress-strain curves illustrating the extension of mammalian tunica albuginea (from the nine-banded armadillo) along three axes during artificial inflation. Tunica albuginea stiffness, represented by the instantaneous slope of each line in the graph, increases by 3–4 orders of magnitude once the tissue strain is 0.25 longitudinally and 0.15 circumferentially—from approximately 3 kPa to 17×10^3 kPa along the longitudinal axis and from approximately 10 kPa to 10×10^3 kPa along either circumferential axis. Symbols denote the direction of tissue strain: square represent longitudinal strain, circles represent circumferential strain viewed laterally and triangles represent circumferential strain viewed dorsally. (Figure adapted from Kelly, 1999.)

corpora cavernosa from the nine-banded armadillo (*Dasypus novemcinctus*) (Fig. 5) confirm that mammalian penile flexural stiffness increases as internal volume increases (Kelly, 1997*b*).

In both mammals (Kelly, 1997*a*) and turtles (D.A.K., unpublished data), erectile tissue can expand both longitudinally and circumferentially because the collagen fibers reinforcing it are crimped and the tissue is folded when the penis is flaccid. As with fiber orientations, it is not yet known whether the flaccid erectile tissues of squamates, crocodilians, or birds show similar collagen crimping and tissue folding. The folded tissue and crimped collagen fibers allow the erectile tissue to expand during erection; penile extensibility seems to be a direct result of this morphology (Tejada *et al.*, 1991; Goes *et al.*, 1992).

How is tissue expansion related to an increase in overall penile stiffness? I have hypothesized that erectile tissue expansion can change both the distribution of tissue within the erectile structure and the material properties of the tissue itself. Increases in either or both of these variables will produce an increase in flexural stiffness—a composite variable derived from the product of the second moment of area, I, which describes the distribution of tissue around a central plane of bending, and the Young's modulus of elasticity, E, which is a measure of the stiffness of the material (Smith and Sidebottom, 1969).

Thus far, morphological measurements and materials testing of inflating erectile tissue supports the hypothesis. In mammals, corpus cavernosum diameters increase during erection, changing the tissue distribution around the central bending axes of the penis and significantly increasing its second moment of area (Kelly, 1999). It is still unknown whether changes in second moment of area play a role in increasing penile flexural stiffness in other amniotes, but increases in penile diameters and thinning of the erectile tissue during erection have been observed in snakes (Dowling and Savage, 1960) and turtles (D.A.K., unpublished data). The similarity of these gross morphological changes to mammals suggests that increases in second moment of area also play a role in increasing penile stiffness in these taxa.

Artificial inflation of mammalian erectile wall tissue indicates that its material properties change during erection. Wall tissue is extensible when collagen fibers are folded, but nearly inextensible when collagen fibers near full extension. The reduction of tissue extensibility (Fig. 6) reflects an increase in tissue stiffness of three to four orders of magnitude (Kelly, 1999). Preliminary inflation tests of *Trachemys scripta* penile tissue suggests that turtles have a similar increase in wall stiffness due to collagen straightening during erection (D.A.K., unpublished data).

THE EVOLUTION OF INFLATABLE PENISES

If, as hypothesized, mammals and turtles independently evolved inflatable penises from ancestors who lacked intromittent organs, the similarity of the anatomical designs used by these taxa to produce penile stiffness is astonishing. Mammals and turtles have converged upon a hydrostatic penis with axial orthogonal reinforcement, and they also share a fiber array that can unfold during erection. This particular anatomical design can, as described above, increase the flexural stiffness of the penis during erection and resist bending forces during copulation.

Convergent anatomies are a response to selection by the same environmental or mechanical factors in distantly related taxa (Losos and Miles, 1994). Where they occur, they are clearly adaptive responses and thus give us a way to identify the specific anatomical features that have important functional significance in a given selective regime (Vogel, 1998). But examining convergence is complicated by the fact that there is not always a one-to-one relationship between a particular selective regime and the anatomical traits that evolve in response to it (Losos and Miles, 1994). It is possible to have more than one anatomical ''solution'' for a given mechanical, physiological, or ecological problem; for example, moles and mole-rats have independently become fossorial, but moles have modified their forelimbs for digging while mole rats dig with their teeth. It is also possible for organisms to converge upon the same mechanical effect using very different materials and arrangements of materials, for example, birds and bats share a cambered wing but clearly build their wings of different materials. And to further confuse the issue, structures that are clearly convergent at an anatomical level can nevertheless share homologous patterning genes (Raff, 1996). In short, convergence on one level of biological organization is no guarantee that structures and functions are also convergent on other levels.

What, then, can we conclude if we observe convergence at more than one anatomical or functional level? Multiple levels of convergence could imply that there are more constraints on the system—that there are fewer possible anatomical designs that successfully meet the selective regime (Wake, 1991). Therefore, if there is only one way to solve the problem imposed by the selective regime, we will see convergence at more levels than if many equally successful anatomies can evolve.

If this hypothesis is true, the evidence from mammals and turtles suggests that the amniotes that have evolved inflatable penises have been subjected to an extremely restrictive selective regime. Penile convergence in mammals and turtles does not stop at gross functional similarity; they have converged on a single anatomical design down to the level of specific collagen fiber arrangements. The differences in penile collagen fiber layering that exist between mammals and turtles do not, as of yet, seem to have any functional effect on penile stiffness. It may be that the way the axial orthogonal array is put together is less critical to the problem of increasing penile flexural stiffness than the presence of the array itself.

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