

Turtle and mammal penis designs are anatomically convergent

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Males in many modern amniote taxa have a hydraulic penis that inflates for copulation. Hydraulic skeletons are typically reinforced with inextensible fibres; the specific arrangement of the fibres within the skeleton determines whether it is flexible or resists bending. I show that the hydraulic skeleton in the turtle penis is reinforced by an axial orthogonal array of collagen fibres. This microanatomy is evolutionarily convergent with that of mammalian penises, and implies that there is a limited number of mechanical designs for an inflatable structure with high bending stiffness.

Keywords: penis; convergence; mammal; turtle

1. INTRODUCTION

Penises are found in four amniote lineages: mammals (Williams-Ashman 1990), turtles (Zug 1966; McDowell 1983), squamates (Dowling & Savage 1960; Conner & Crews 1980) and archosaurs (Liebe 1914; King 1981; McCracken 2000). It has been proposed that a penis is an amniote synapomorphy (Jones 1915; Gauthier *et al.* 1988). However, anatomical and developmental differences among penises in these groups (Kelly 2002) mapped on independent phylogenetic hypotheses of their relationships (Rieppel & deBraga 1996; Hedges & Poling 1999; Janke *et al.* 2001) strongly suggest that each penis-bearing group arose independently from ancestors that had internal fertilization without intromission (such as the cloacal apposition seen in *Sphenodon* (Romer 1970) and passerine birds (Birkhead *et al.* 1993)).

Nonetheless, penises in these taxa share several gross similarities: they are all fleshy cylinders that are normally flexible and inconspicuous, and they contain a hydraulic skeleton that fills with fluid before copulation, enlarging the penis and increasing its resistance to bending, or *flexural stiffness*. Like other biological hydraulic systems, their walls are reinforced with relatively inextensible fibres to prevent aneurysms (Wainwright *et al.* 1976); all of these taxa use collagen fibres for this purpose (Owen 1841; Liebe 1914; Seshadri 1956; Conner & Crews 1980; Pinheiro *et al.* 2000).

The arrangement of the collagen fibres in the wall of the hydraulic skeleton has a strong effect on the mechanical behaviour of the structure. When reinforced with fibres arranged in left- and right-handed helices (a 'crossed helical' array), an inflated skeleton can extend, contract

and bend in smooth curves (Wainwright 1988); when reinforced with fibres arranged parallel to and perpendicular to the long axis of the skeleton (an 'axial orthogonal' array), it resists extension, contraction and bending (Wainwright 1988; Kelly 1997). Work with physical models of fibre-reinforced hydraulic skeletons suggests that skeletons reinforced with axial orthogonal arrays of fibres have higher flexural stiffness than skeletons reinforced with fibres arranged in crossed helices (Koehl *et al.* 1995). In skeletons reinforced by cross-helical fibres, flexural stiffness depends upon the specific angle of the fibres to the skeletal long axis; skeletons containing fibres arranged at angles smaller than 45° have higher flexural stiffness than skeletons containing fibres arranged at angles greater than 45° (Koehl *et al.* 2000).

In this study, I used polarized light to examine collagen fibres in the penile wall of two species of cryptodiran turtle, and measured the fibre angles relative to the long axis of the penis. This procedure allowed me to identify the type of fibre reinforcement used by turtle penises. Nearly all hydraulic skeletons are reinforced with crossed helical fibre arrays (Wainwright 1988; Niklas 1992); one known exception is the hydraulic skeleton found in the mammalian penis, which is reinforced with an axial orthogonal fibre array (Kelly 1997). The fibre arrangements in other amniote penises are not known, and although axial orthogonal arrays produce the stiffest hydraulic skeletons there is no *a priori* reason to assume that each lineage will converge on that morphology.

2. MATERIAL AND METHODS

Flaccid penile tissue was collected from preserved specimens of two turtle species, the loggerhead (*Caretta caretta*; $n = 1$) and the redeared slider (*Trachemys scripta*; $n = 3$). They are not closely related: *Caretta* is a member of the clade Chelonioidae, whereas *Trachemys* is in the Emydidae (Gaffney & Meylan 1988). Turtle penises contain a single vascular erectile body divided into a dense corpus fibrosum and a more expandable corpus spongiosum (Zug 1966); fibre angles were measured on unstained sections from both parts of the penis to determine the orientation of collagen fibres relative to the penile long axis. The tissue was cut parallel to the outer surface of the wall, photographed digitally under polarized light (magnification $\times 400$) and analysed with IMAGE 1.57f (National Institutes of Health) using the method described by Kelly (1997). Three repeated angle measurements were within 0.6° of each other.

3. RESULTS AND DISCUSSION

In both species, the wall of the erectile body contains folded collagen fibres arranged in alternating layers (figure 1*a*). In each layer, fibres are either parallel to the long axis of the penis or perpendicular to it (figure 1*b*); there is no difference in fibre arrangement among samples from the corpus spongiosum and corpus fibrosum. In *C. caretta*, the average fibre angle in layers with fibres that run parallel to the penile long axis is $0.3^\circ \pm 1.0$ ($n = 17$ measurements); the average fibre angle in layers with fibres perpendicular to the penile long axis is $89.7^\circ \pm 0.2$ ($n = 19$ measurements). In *T. scripta*, the average fibre angle in layers with parallel fibres is $-0.8^\circ \pm 0.6^\circ$ ($n = 34$ measurements), the average fibre angle in layers with perpendicular fibres is $89.6^\circ \pm 0.3^\circ$ ($n = 34$ measurements). Pooled values of fibre angles from layers with parallel fibres are not significantly different from 0° (Student's *t*-tests for *C. caretta*, $t = -0.0258$, $p = 0.80$; for *T. scripta*, $t = -1.293$, $p = 0.21$); pooled values from layers with perpendicular fibres are not significantly different from 90° (Student's *t*-tests for *C. caretta*, $t = 1.223$, $p = 0.24$; for *T. scripta*,

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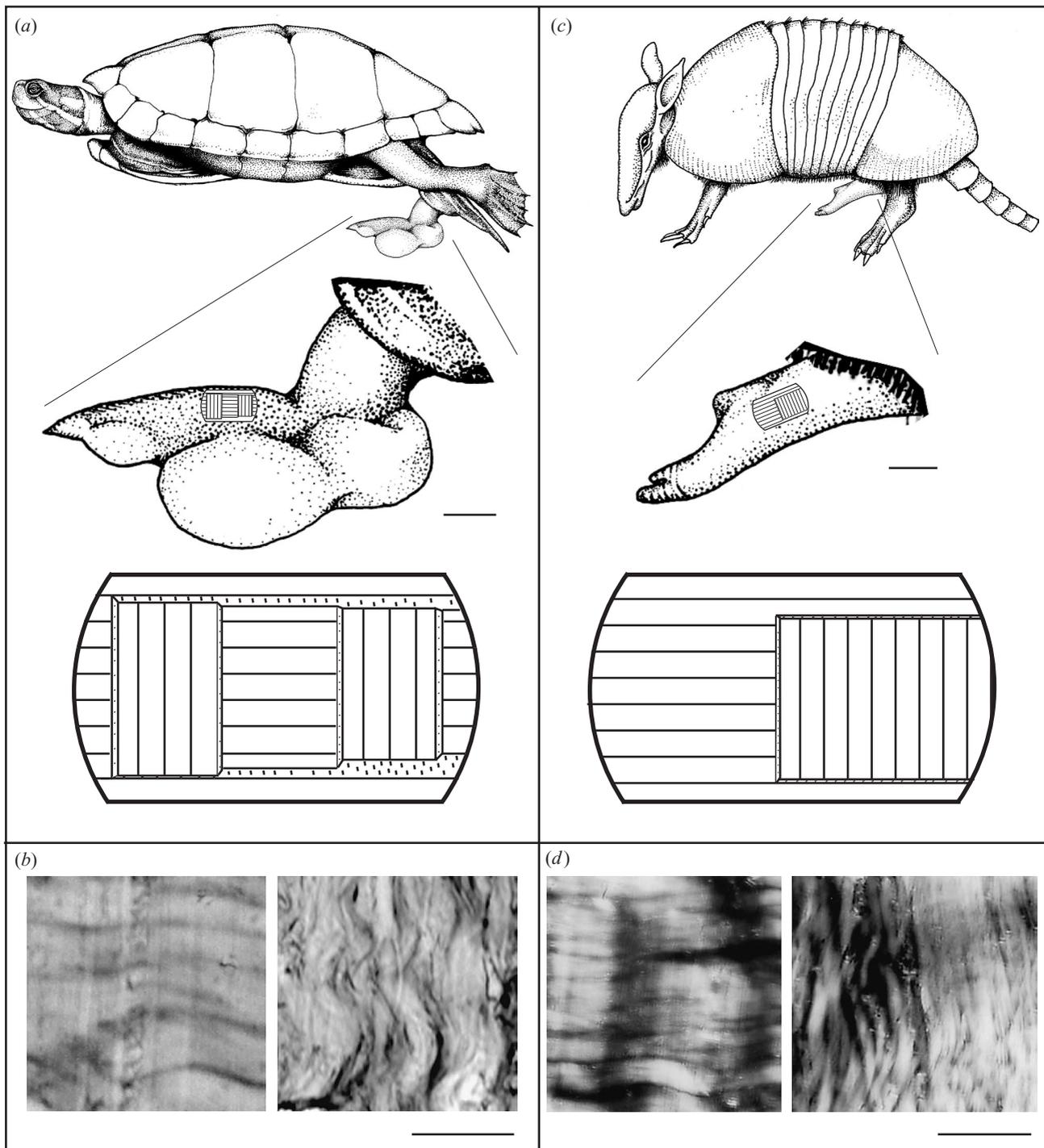


Figure 1. Morphology of penile wall tissue in turtles and mammals. (a) Left lateral view of a turtle penis; insert shows the pattern of fibre layers in parasagittal section (not to scale). (b) Parasagittal sections of unstained flaccid tissue from the red-eared slider (*Trachemys scripta*) viewed under polarized light. The crimping of collagen fibres can be seen as alternating bright and dark bands in the direction of the collagen fibres; most of this crimp is lost in erect tissue. Left is a layer of fibres orientated at 0° to the penile long axis, right is a layer of fibres orientated at 90° to the penile long axis. (c) Left lateral view of a mammalian penis; insert shows pattern of fibre layers in parasagittal section (not to scale). The nine-banded armadillo (*Dasypus novemcinctus*, pictured) has a penis design typical of mammals (Kelly 1997). (d) Parasagittal sections of unstained erect tissue from the nine-banded armadillo (Kelly 1997). Left is the outer layer of fibres orientated at 0° to the penile long axis, right is the inner layer orientated at 90° to the penile long axis. Scale bars: (a) 0.5 cm; (b) 0.1 mm; (c) 1.0 cm; (d) 0.02 mm. In (b) and (d), scale bars also denote the direction of the penile long axis.

$t = 1.098$, $p = 0.28$). These data cannot detect any difference in the observed fibre arrangement from an axial orthogonal array, in which fibres are arranged parallel and perpendicular to the long axis of the hydrostatic skeleton (Kelly 1997).

This basic fibre arrangement is identical to that of the mammalian penis (figure 1c,d), except that turtle penile wall tissue contains many layers of alternating parallel and perpendicular fibres where mammals have only one layer of fibres in each orientation (Kelly 1997; figure 1a,c).

Current phylogenies suggest that turtles and mammals are very distantly related (Rieppel & deBraga 1996; Hedges & Poling 1999; Janke *et al.* 2001) and although penile development is controlled by the genes *Hoxa13* and *Hoxd13* in both groups (Dolle *et al.* 1993; Loredo *et al.* 2001) their penises appear to originate from nonhomologous tissues (King 1981; Hunter 1995; Perritin *et al.* 2002). This difference suggests that while the developmental signal to build a penis is homologous in turtles and mammals, the resulting anatomical structures are not (Raff 1996).

Axial orthogonal fibre arrangement in turtles and mammals is consistent with convergence, and can be explained by the specific functional requirements of an inflatable penis, which must be able to expand during erection and resist shape changes during copulation. A penis reinforced by an axial orthogonal array will expand to a size predetermined by the length of the collagen fibres, and once erect will resist forces during intromission and copulation that would tend to elongate, shorten or bend it (Koehl *et al.* 1995; Kelly 1997). Hydrolic skeletons reinforced with fibres arranged in crossed-helices also resist bending forces if the fibres are at very low angles, but these structures are not as stiff as hydrolic skeletons reinforced by axial orthogonal arrays (Koehl *et al.* 2000) and could elongate and shorten during copulation (Wainwright 1988). Thus, the presence of axial orthogonal reinforcement optimizes these penises for high flexural stiffness.

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