Urogenital System of the Spotted Hyena (*Crocuta crocuta Erxleben*): A Functional Histological Study

Gerald R. Cunha,[1]* Yuzhuo Wang,[1] Ned J. Place,[2] Wenhui Liu,[3] Larry Baskin,[3] and Stephen E. Glickman[2]

[1]*Department of Anatomy, University of California, San Francisco, California 94143*
[2]*Department of Psychology, University of California, Berkeley, California 94720*
[3]*Department of Urology, University of California, San Francisco, California 94143*

ABSTRACT The unique urogenital anatomy and histology of female spotted hyenas (*Crocuta crocuta Erxleben*) was reexamined to identify adaptations of "structure" that enable/facilitate urination, mating, and parturition through the clitoris. Unusual features of penile anatomy required for meeting ceremonies and successful mating through a clitoral point of insertion were also examined. As reported previously, the upper urogenital tract of the female spotted hyena is typical of other carnivores and consists of the oviducts, uterine horns, uterine body, and vagina. An anatomically defined cervix is absent, even though a histologically defined transition zone between the uterine body and vagina was demonstrated. Adaptive features of the upper genital tract were a helical-shaped uterine cavity, extensive smooth muscle in the uterus and vagina, and a newly discovered submucosal mucous urogenital gland (SMUG) located immediately caudal to the vagina. The extensive smooth muscle facilitates the expulsion of the large pups at parturition through the recurved birth canal. Secretions of the SMUG provide lubrication and protection for the urogenital mucosa during mating and parturition. Two types of "erections" are suggested by behavioral observations: the common hemodynamic erection required for insertion and thrusting by the male, and phallic "flipping" that commonly occurs earlier in the mating sequence and is sometimes seen during meeting ceremonies. Phallic "flipping" appears to be accomplished by the coordinated contractions of the large ischiocavernosus and retractor muscles acting on the semirigid organ. The extremely thick tunica albuginea and interstitial collagen of the common corporal body of the penis and clitoris gives the flaccid phallus some degree of rigidity even in the resting state in males and nulliparous females. Phallic "flipping" implies a hinge region in which flexibility is the key feature. Such a proximal hinge region of the male and female phallus was defined and was notable for its diminished collagen content. The urogenital sinus traversing the clitoris was specialized for distensibility, thus facilitating receipt of the penis during mating and for passage of the infant to the tip of the glans clitoris, where it emerges at parturition. The morphology of the glans penis is notable for the tapered common corporal body that extends to the distal tip of the glans. This adaptation is suggested to be required for a clitoral (as opposed to a vaginal) point of insertion during mating. Finally, additional segments of erectile tissue devoid of a thick collagenous capsule were demonstrated in the glans penis and glans clitoris, which appear to account for the "partially-locking" of the male into the female during the late stages of a mating sequence. Taken together, it is evident that the unusual sexual behaviors of the male and female spotted hyenas are facilitated by unique structural modifications of the relevant organs. J. Morphol. 256:205–218, 2003.

KEY WORDS: spotted hyena; female urogenital tract; male urogenital tract; clitoris; penis

The unique urogenital anatomy of the female spotted hyena has drawn human attention for several thousand years to ideas about hermaphroditism and/or the ability of these animals to change sex from year to year, commonly expressed in Western writings well into the last century (Glickman, 1995). Female spotted hyenas (*Crocuta crocuta*) have no external vagina, as the labia have fused during fetal life to form a pseudo-scrotum (Fig. 1). The clitoris has developed until it is the approximate size and shape of the male penis and is traversed by a central urogenital canal, which serves as a common passageway for urinary and reproductive functions. The clitoris also has erectile capabilities roughly equivalent to those of the male (Fig. 2). In considering the functional aspects of the urogenital anatomy of the female spotted hyena, three unique aspects of the system must be kept in mind: 1) the female spotted hyena receives the male during mating through the clitoral meatus and the clitoral portion of the urogenital canal (Fig. 3); 2) the female spotted

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*Correspondence to: G.R. Cunha, Department of Anatomy, University of California, 3rd and Parnassus, San Francisco, CA 94143. E-mail: grcunha@itsa.ucsf.edu

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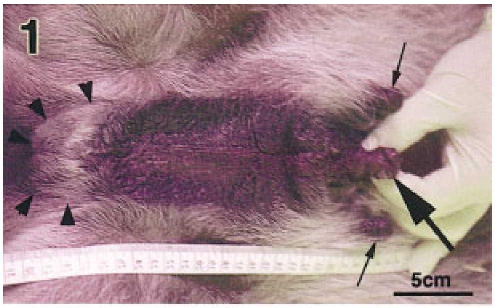
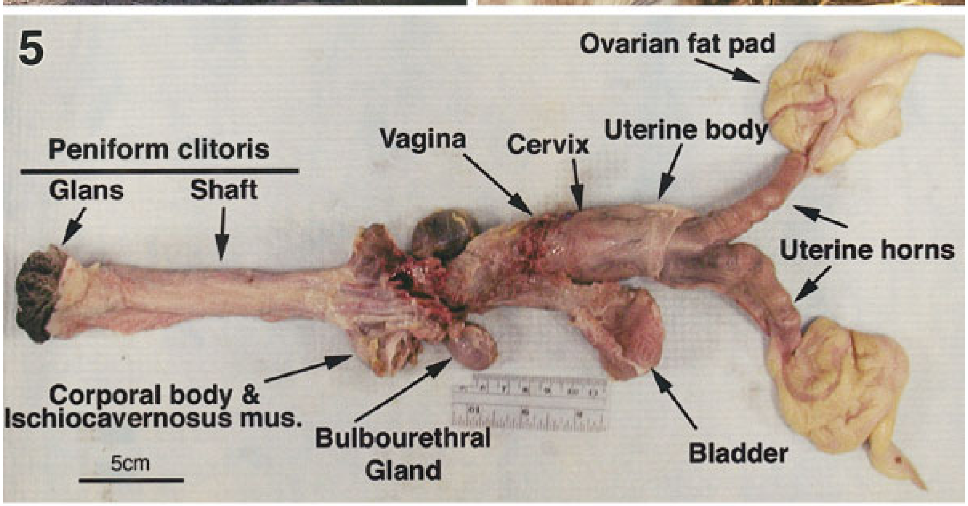




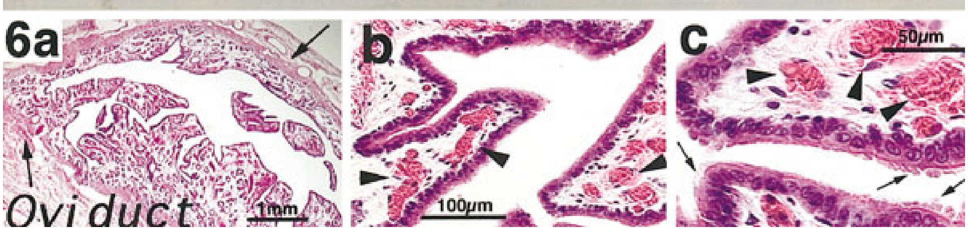


Fig. 1. Abdominal region of an adult female spotted hyena (*Crocuta crocuta*). Note the presence of a pseudo-scrotum (arrowheads) and the absence of an external vagina. The clitoris is in its nonerect retracted state. The glans (large arrow) has been extracted by the investigator from its normal internal retracted position (compare with the erect clitoris in Fig. 2). Note the nipples (small arrows).

Fig. 2. Prepubertal female spotted hyena (*Crocuta crocuta*) with an erect clitoris (arrow).

Fig. 3. Mating pair of the spotted hyena (*Crocuta crocuta*). The male has achieved insertion into the anteriorly located clitoral meatus. The anterior position of the clitoral meatus requires an acute angle of approach for the erect penis. The white arrow points to the area of the pseudo-scrotum (not shown, see Fig. 1) and indicates the angle of approach if the female of this species had an external vaginal opening.

Fig. 4. Toward the end of an extended period of labor, a fetal hyena fills and stretches the clitoris (outlined by white dots) of a primiparous female. The clitoral meatus (large arrow) will eventually tear and permit birth to occur. Subsequent deliveries, through the stretched and torn clitoral meatus, are much more rapid. Note nipples (small arrows).

Fig. 5. Entire reproductive tract of the female spotted hyena (*Crocuta crocuta*). Ovaries and oviducts are encased in the ovarian fat pad.

Fig. 6. Oviduct of the spotted hyena (*Crocuta crocuta*). Note complex mucosal folds, musculature (**a**, arrows), blood vessels (**b,c,** arrowheads), ciliated (**c**, arrows), and nonciliated epithelial cells.

hyena gives birth to relatively large (1.1–1.6 kg) precocial infants via a tortuous "recurved" passageway, with the fetus emerging through the urogenital meatus at the tip of the glans clitoris (Fig. 4); and 3) as described below, both female and male hyenas frequently engage in ritualized nonsexual "meeting ceremonies," involving olfactory and gustatory inspection of the erect clitoris or penis.

Watson (1877) provided the first modern anatomical description of the spotted hyena urogenital system, supplemented with a set of fine half-tone illustrations. This work should have put to rest all discussions of hermaphroditism, as Watson's dissection clearly demonstrated that the gross "masculinization" of the female hyena was limited to the external genitalia, with the internal urogenital system displaying the essential morphological features of a typical female mammal. More than 60 years later, Matthews (1939) published a classic monograph on the unusual urogenital anatomy of this unique species. For the first time, histological material was presented. Matthews reported the existence of a true vagina, interposed between the uterus and the clitoris, and supplied novel information regarding the arrangement of the corpora cavernosum, the corpus spongiosum, and positioning of various glands and muscles with regard to the central urogenital canal. Neaves et al. (1980) added significant additional information regarding penile/clitoral sexual dimorphism and expanded upon Matthew's discussion of the unusual functional problems presented by hyena urogenital morphology.

However, over the past several decades a much more detailed picture has emerged with regard to the functional demands placed on both female and male hyenas by the unique anatomical features of female spotted hyenas. A major goal of the present article is a reexamination of urogenital anatomy of the spotted hyena in functional terms. Specifically, we focus on the adaptive nature of "structure," which enables/facilitates urination, mating, and parturition through the clitoris. We also note some unusual features of penile anatomy that are required for successful mating through a clitoral, as contrasted with the more typical vaginal, point of insertion.

Functional Considerations: Urination, Mating, Parturition, and Meeting Ceremonies

Urination through the tip of the clitoris poses no special difficulties and is found in other mammalian species, e.g., European moles (Matthews, 1935) and some prosimians (Drea et al., 1999), although there are some interesting mechanistic questions posed by linkage of the urinary and reproductive systems in a common canal in female hyenas. A detailed morphological account is the base from which any physiological analysis must proceed. Accordingly, we have made a special effort to provide a detailed description of the confluence between the urethra and reproductive tract as they join to form the urogenital sinus that traverses the shaft of the clitoris.

Anatomical obstacles do appear with regard to mating, as the male has to achieve entry through a small target, placed in a position that is considerably anterior to the normal location of an external vagina. A description of hyena mating behavior by Schneider (1952) is in general accord with our own observations. The female hyena completely retracts the clitoris during mating and stands in near-immobile fashion, while the male assumes an upright posture and clasps the sides of the female with his forepaws just in front of her hindlegs. He then "flips" the semierect penis towards the abdomen of the female, until the glans penis penetrates the urogenital meatus of the female. Thrusting begins after intromission of the erect penis into the retracted clitoris. As Neaves et al. (1980) suggest, this sequence could not proceed unless the opening of the urogenital meatus, and the clitoral portion of the urogenital canal, had sufficient size and elasticity to accommodate the male. It is apparent that postnatal ovarian secretions (estrogens in particular) play a critical role in the development of a large clitoral canal with a highly elastic urogenital meatus (Glickman et al., 1992, 1998; Drea et al., 1998; Licht et al., 1998). In addition, the tissues of the retracted clitoris would have to be firmly "stabilized." Neaves et al. (1980) hypothesized that this stabilization is dependent on the substantial retractor muscles that course through the clitoris. Finally, Schneider (1952) noted, and we have confirmed, that during the late stages of a mating sequence the male is "partially locked" to the female. This "partial-lock" can be broken, in contrast with that of a dog; and it is apparently the swelling of the distal glans penis and clitoris, rather than the proximal bulb at the base of the shaft, that is responsible for retention of the male in the female.

In this study we have paid particular attention to the manner in which tissue arrangements in the female facilitate retraction and stabilization of the clitoris, as well as permitting expansion of the glans to accommodate the male. We have also considered the structural features of the male that permit "flipping" of the semierect phallus during the early stages of mating, followed by extreme rigidity during thrusting, and expansion of the eitoral glans, which is associated with the "semi-lock" that occurs during the later stages of the mating sequence.

Parturition requires that large (i.e., 1.1–1.6 kg) precocial fetuses descend from a uterine horn and, after filling the clitoris, emerge from the urogenital meatus of the glans clitoris (Frank et al., 1995). Neaves et al. (1980) noted a number of sexually dimorphic features of clitoral/penile morphology that would serve to facilitate mating and delivery of young. In particular, they suggested that the ventral placement of the urogenital canal within the clitoris, and the absence of a surrounding corpus spongiosum, would permit the expansion of the urogenital canal to accommodate the male during mating and the fetus during parturition. However, this specialization is perhaps not sufficient to solve the problem. The fetus moves along an exceptionally tortuous route, first following a caudal-ventral path from the uterus through the bony pelvic outlet, and then making a sharp turn in an anterior direction to traverse the clitoral canal to emerge through the meatus of the glans clitoris (Frank et al., 1995).

As noted above, estrogens enhance the size and elasticity of the urogenital meatus. Plasma relaxin concentrations also increase markedly during the final stages of gestation; and this hormone could well synergize with estrogens to facilitate delivery (Steinetz et al., 1997). However, we now understand that, despite the size and elasticity of the meatus at term, the urogenital meatus has to tear in order to permit delivery in a primiparous female. In our captive colony, approximately 60% of first-births resulted in stillborn cubs, presumably because the placenta detached and the cubs became anoxic during the hours of labor that commonly follow detachment of the placenta, but precede delivery in a nulliparous female (Frank et al., 1995). Once again, particular attention has been directed toward the

TABLE 1. Sex, age, and reproductive status of the seven spotted hyenas used for histological study

Hyena number	Sex	Age	Reproductive state
1	F	10 year	nulliparous/mated
2	F	10 year	virgin
3	F	13 year	multiparous
4	M	16 year	mature
5	M	17 year	mature
6	F	fetus 96 day	—
7	M	fetus 96 day	—

arrangement of tissues in the female that permit the unusual birth process to proceed. For example, we were interested in reexamining the distribution of urogenital musculature, with a view to understanding the exceptional peristaltic actions required to move, and ultimately expel, the fetus from the uterus through the tip of the clitoris. A special effort was also made to identify the distribution of local glandular structures that would be expected to secrete lubricating agents, facilitating the passage of the fetus, and to examine the structure of the clitoral shaft and glans, with regard to playing the dual roles of expansion during parturition and erection during "meeting ceremonies."

Female and male spotted hyenas routinely display erections in nonsexual contexts when participating in "meeting ceremonies." Such ceremonies, which are displayed by male and female hyenas, involve two hyenas standing side-by-side, head to tail, and inspecting one another's external genitalia. These "meeting ceremonies" are common events for hyenas in nature, occurring when meeting after a period of separation and during periods of excitement or tension. Hyena etiquette requires that the subordinate hyena initiate the ceremony by presenting its erect genitalia for inspection by the dominant animal (Kruuk, 1972; East et al., 1993). In our colony, meeting ceremony erections often occur in less than 5 sec (Krusko et al., 1988), with the organ capable of reverting to a flaccid state and retracting into the abdomen within a similar time interval. Kruuk (1972) speculated that the social benefits accruing from participation in meeting ceremonies were the driving force in selection of the masculinized clitoral morphology of the spotted hyena. Our focus was on the possible existence of structural mechanism(s) in spotted hyenas that would permit rapid erection and equally rapid detumescence/retraction of the clitoris or penis.

MATERIALS AND METHODS

Animals and Tissue Specimens

Spotted hyenas, *Crocuta crocuta Erxleben,* examined in this study were maintained at the Field Station for Behavioral Research of the University of California, Berkeley, CA. The internal and external reproductive tracts of seven animals were examined. Table 1 gives the ages and reproductive history of the animals used in this study. Table 2 is a cross-list of specific animals used in specific figures. Reproductive tracts of two adult female hyenas were removed after the animals were euthanized as part of a larger study. The animals were 10 years old; both were nulliparous. Each animal was immobilized with ketamine and xylazine administered by blow-dart. Animals were then intubated and transferred to the Department of Anatomy at the University of California, Davis, under general anesthesia. The external jugular vein was incised for exsanguination and infusion of 10% formalin. After adequate fixation, the reproductive tracts were removed as an intact unit from the oviducts to the prepuce of the clitoris and placed in 10% formalin. A multiparous female, age 13 years, had a ovohysterectomy while under general anesthesia. This female was similarly immobilized and transferred to a surgical suite on the UC, Berkeley, campus. The oviducts, uterine horns, and upper uterine corpus were removed and placed in 4% paraformaldehyde.

The urogenital systems of two adult male hyenas, ages 16 and 17 years, were also removed and examined. Animals were immobilized and transferred to a necropsy suite on the UC, Berkeley, campus. Shortly after a lethal injection of sodium pentobarbital, the internal and external reproductive tracts were rapidly dissected and placed in 4% paraformaldehyde. One of these male hyenas was euthanized because of disseminated lymphoma. The lymphoma did not appear to grossly infiltrate the urogenital system.

Lastly, the urogenital systems from a male and a female fetus, estimated gestational age 96 days of a 110-day gestation, were collected after a fetectomy was performed via a cesarean section under general anesthesia. The pregnant female had been immobilized as above and transferred to a surgical suite on the UC, Berkeley, campus. The fetuses were euthanized by decapitation as part of a larger study. The urogenital tracts were rapidly dissected and placed in 4% paraformaldehyde. All tissues were transported to UC, San Francisco, for anatomical and histological analysis.

Anatomical Methods

After fixation as described above, the entire genital tract was dissected en block and photographed. The adult genital tracts were sectioned transversely into 1–2 cm segments representing all of the organs (Fig. 5). Individual segments were stored in 70% ethanol and either photographed or scanned on an Epson G810A flat-bed scanner. The actual confluence of the urethra and the genital tract was identified by dissection. After photography of the cranial or caudal surfaces of each transverse block, 2–3-mm thick sections were excised from each segment and subsequently embedded in paraffin. Alternatively, a segment was bisected in the midsagittal or a coronal plane and then a 2–3-mm thick section was excised and embedded in paraffin. Six μm-thick sections were prepared from the thick sections and stained with hematoxylin and eosin. Masson's trichrome stain was used to localize collagen in the

TABLE 2. Animals used in specific figures

Figure numbers	Hyena number
1–4	Animals other than those listed in Table 1
5–7	#1
8a	#3
8b	#2
9–16	#1
17a–b	#1
17c	#6
18a	#1
18c–d	#4
19	#5
20	#7
21	#2
22	#5

corporal body as described previously (Lillie, 1965). Briefly, sections were dewaxed, rehydrated, and postfixed in Bouin's solution overnight at room temperature. After rinsing in tap water, sections were stained with Weigert's hematoxylin for 10 min and Biebrich scarlet and acid fuchsin for 1 min, respectively. After a tap-water rinse, the sections were treated with 1% phosphotungstic acid for 15 min, stained with 2% light green for 1 min, rinsed in water, fixed with 1% acetic acid for 3 min, and then dehydrated for mounting.

Uterine luminal casts were prepared using Batson's No. 17 plastic replica and corrosion kit (Polysciences, Warrington, PA). Briefly, the liquid plastic was catalyzed and perfused into the lumen of fixed or unfixed uterine horns using a catheter and a 10 ml syringe. After polymerization of the plastic, the uterine tissue was digested with 1N potassium hydroxide. The resultant uterine luminal cast was photographed in several orientations.

RESULTS

Gross Anatomy: An Overview. Figure 5, a photograph of the female urogenital tract of the spotted hyena, confirms most aspects of the line drawing in Matthews (1939) (Fig. 12, page 19). The ovary and oviduct are embedded within the extensive ovarian fat pad and thus are not visible without further dissection. Emerging from the ovarian fat pad are the uterine horns that fuse caudally to form the uterine body. The uterine body, cervix and the vagina extend caudally from the junction of the uterine horns to the confluence with the urethra. These female genital organs are not discernable by gross anatomical features. About midway along the urogenital tract the two corpora cavernosa attach laterally to the pubic rami. At their bony attachments relatively large ischiocavernosus muscles cover the corpora. The large bulbourethral glands lie within the pelvic cavity immediately cranial to the attachment of the corporal bodies to the pubic rami. At its approximate midpoint the urogenital tract undergoes an almost 180 degree turn so that the tip of the clitoris points ventral-cranial (compare with the male genital tract, Fig. 18). The urinary bladder and urethra lie ventral to the uterine body, cervix and vagina. The urethra runs caudally on the ventral aspect of the genital tract as a grossly defined structure before merging with it to form the urogenital sinus. Thus, the angle of the intersection of the urethra with the urogenital tract is low, a fact verified by histological analysis.

Histology of the Internal Female Urogenital System

The ovary is surrounded by an extensive ovarian fat pad containing the ovarian bursa and the oviduct. The histology of the ovary will be the subject of a separate article. The oviducts are coiled and contain a highly folded mucosa lined by a typical oviductal epithelium composed of both ciliated and nonciliated epithelial cells (Fig. 6). Individual epithelial folds projecting into the lumen of the oviduct have a core of loose connective tissue and are highly vascular. Deep to the mucosa is a muscular layer containing slender bundles of smooth muscle embedded in loose connective tissue. The oviducts merge with the uterine horns at the utero–tubule junction.

The uterine horns are about 7–8 cm in length in the nonpregnant female. The wall of each uterine horn contains outer longitudinal and inner circular myometrial layers with an intervening vascular layer (Fig. 7a). The circular myometrial layer surrounds the endometrial stroma (Fig. 7a,b). The inner circular and outer longitudinal myometrial layers are composed of a complex weave of smooth muscle bundles with little intercellular space or connective tissue between muscle bundles (Fig. 7a,b). At the endometrial stroma/myometrial interface individual smooth muscle bundles sometimes project into the endometrial stroma (Fig. 7b). The inner circular myometrial layer is separated from the outer longitudinal myometrial layer by a thick, well-defined vascular layer that contains large blood vessels, loose connective tissue, and slender bundles of smooth muscle (Fig. 7a).

Transverse sections of the uterine horns revealed 3–5 large epithelial-lined luminal spaces (Fig. 7b). The diameters of individual uterine lumina are variable, but in many cases sufficiently similar in size that it was impossible to identify the actual main uterine channel. Each lumen is lined with a typical simple columnar uterine epithelium and has its own constellation of associated uterine glands (Fig. 7b). Uterine glands lined with a simple columnar nonciliated epithelium projected radially from the uterine lumen into the endometrial stroma (Fig. 7b,c). The uterine glands are generally straight and unbranched, although a subset of the glands is branched. The uterine glands are embedded in an endometrial stroma containing fibroblasts and many small-diameter blood vessels.

Plastic corrosion casts were prepared to reveal the complexity of the uterine lumen. Plastic luminal casts of fresh specimens demonstrated that the uterine lumen is not a single straight tube, but instead is coiled into a helix (Fig. 8a). For this reason the length of the uterine lumen is much longer (cranial to caudal) than the external length of the uterine horn. The coiled nature of the uterine lumen explains in part the fact that multiple uterine lumina can be seen in a transverse section. However, given the geometry of the helical uterine lumen, transverse sections could potentially contain only 2–3 separate lumina. Corrosion casting of fixed uterine horns revealed luminal diverticula extending peripherally from the main uterine lumen (Fig. 8b). This complex organization of the luminal cavity of the uterine horn was also corroborated by examination of thick (1 mm) serial sections of the uterine horn (not illustrated).

The two uterine horns merge to form the uterine body. Initially, the right and left endometrial stromas and associated uterine lumina are separated by a central myometrial septum within the uterine body (Fig. 9a). This midline myometrial septum maintains a constant thickness down to its blunt termination within the uterine body (Fig. 10). Cau-

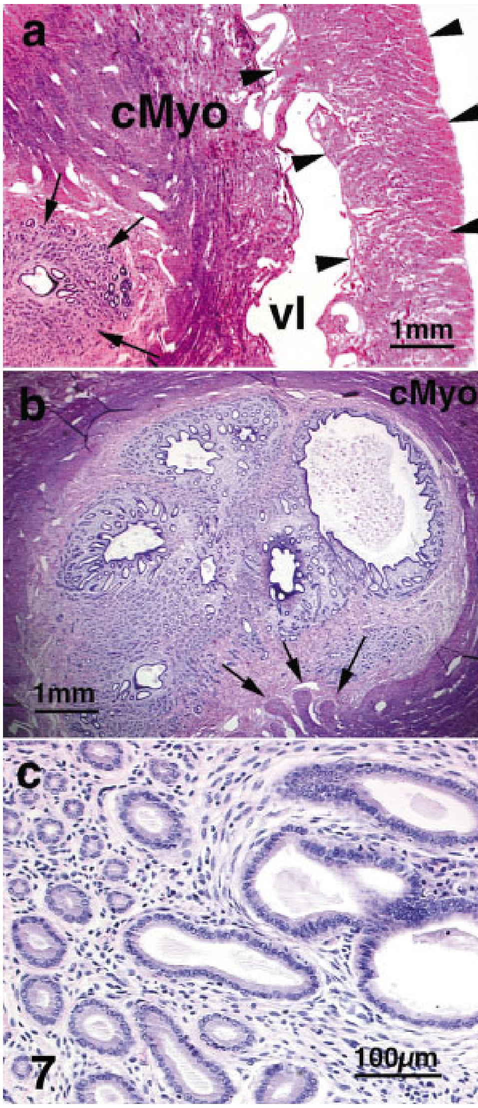


Fig. 7. Transverse sections through the uterine horn of a spotted hyena (*Crocuta crocuta)*. **a:** Low-magnification view survey showing the endometrium containing glands (arrows), the circular myometrium (cMyo), the vascular layer (VL), and the longitudinal myometrium (arrowheads). **b:** Endometrium and circular myometrium (cMyo). Note multiple uterine lumina and associated uterine glands embedded in the lightly stained endometrial stroma. Individual strands of myometrial bundles (arrows) are seen at the endometrial stroma/myometrial interface. **c:** High magnification of uterine glands.

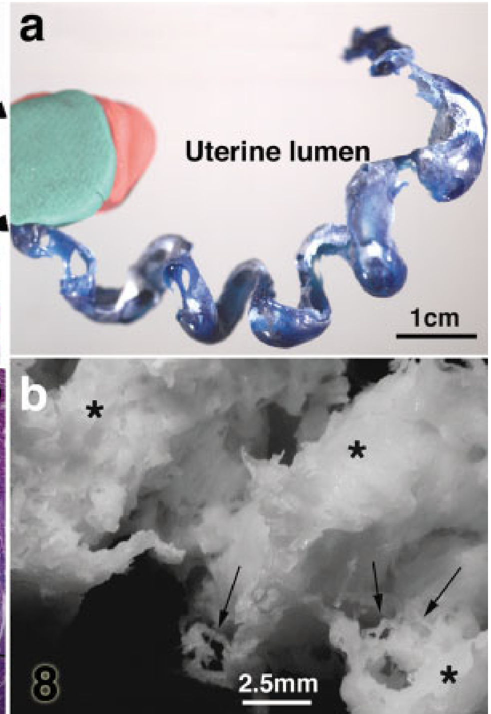


Fig. 8. Plastic casts of the lumen of the uterine horn of the spotted hyena (*Crocuta crocuta)*. **a:** Liquid plastic was injected into a fresh unfixed adult uterine horn as described in Materials and Methods. Under these conditions the uterine glands are not filled and the high pressure at injection obliterates the luminal evaginations. Note the helical organization of the uterine lumen. The red and green material (left) is modeling clay used to mount the plastic cast. **b:** Liquid plastic was injected into the lumen of a fixed uterine horn. Adjacent turns of the helix can be seen (*). Note the complicated luminal projections and uterine glands (arrows). Most of the uterine glands were removed to reveal the larger features.

dal to the central myometrial septum the two uterine lumina fused into a single midline uterine cavity surrounded by a constellation of uterine glands (Fig. 9b). It is important to note that the smooth muscle of the uterine horns and uterine body (myometrium) constitute the bulk of the uterus. This continuous muscle mass extends caudally into the fibromuscular wall of the cervix and vagina and provides the force required to expel the pups during delivery.

In agreement with Matthews (1939), the spotted hyena has a histologically recognizable vagina. The state of vaginal epithelial differentiation surely varies throughout the estrous cycle. In the females examined in this study a thickened cornified epithelium was observed having the classical histodifferentiation of vaginal epithelium in estrus (Fig. 11). The basal aspect of the vaginal epithelium has an undulating surface with numerous stubby papillae projecting into the underlying stroma. The stroma contains many blood vessels of variable size. In the vicinity of the vaginal epithelium the stroma is primarily fibroblastic. At a deeper plane smooth muscle bundles are separated by connective tissue septa.

Between the vagina and the uterine body is the cervical zone, which is not demarcated in any way by gross external features. Thus, the uterine body, cervix, and vagina cannot be distinguished grossly, even though histological features clearly distinguish these organs. The cervix is a transition zone, an area in which the stratified squamous cornified epithelium of the vagina coexists with large multiple cystic lumina lined with simple columnar epithelial cells (Fig. 12). These cystic lumina clearly define this region as distinct from the uterus above and the vagina below. True uterine glands were not observed in the cervical zone. The size of the cervical zone was difficult to discern, but is rather small, perhaps only a few millimeters from cranial to caudal.

Caudal to the vagina the stratified squamous vaginal epithelium changes abruptly to a urethral-like epithelium about 1–2 cm above the confluence of the

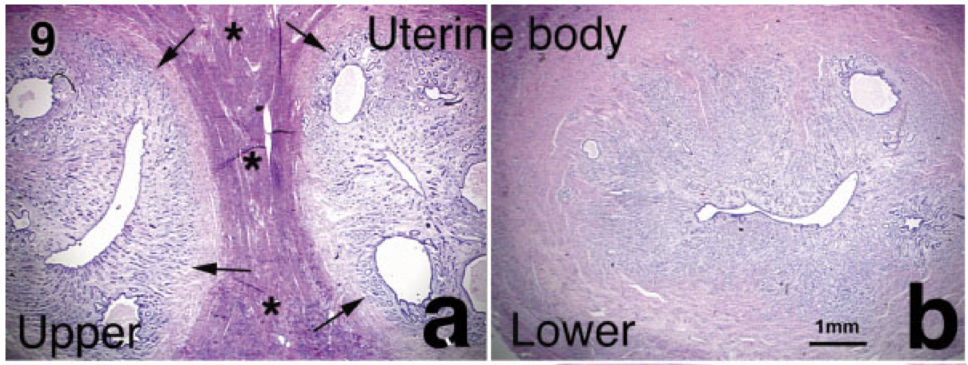


Fig. 9. Transverse sections of the uterine body of the spotted hyena (*Crocuta crocuta*). **a:** The upper cranial segment of the uterine body shows the central myometrial septum (*) separating the right and left endometria (arrows), each containing the multiple uterine lumina. **b:** This transverse section is more caudal (lower) where the two endometria and associated uterine lumina have fused.

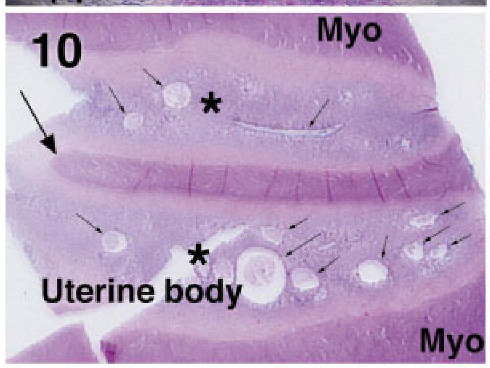


Fig. 10. Coronal section through the uterine body of the spotted hyena (*Crocuta crocuta*). Note that the central fused myometrial septum terminates caudally (large arrow) as a blunt projection of muscle tissue separating the right and left endometrial stromas (*) containing multiple lumina (small arrows). Both endometrial stromas are in turn surrounded by myometrium (Myo).

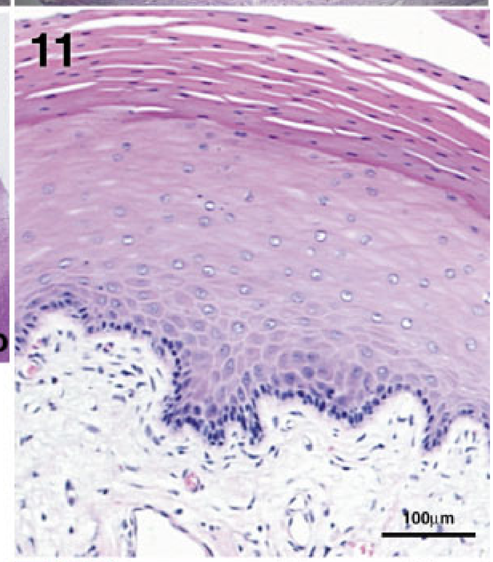


Fig. 11. Section of the vagina of an adult spotted hyena (*Crocuta crocuta*). Note that the epithelium is very thick, indicative of the proestrous/estrous state.

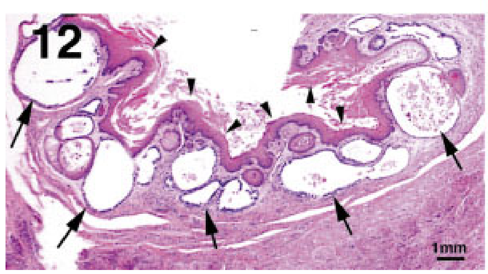


Fig. 12. The cervix of the spotted hyena (*Crocuta crocuta*) is a zone containing two types of epithelium: stratified squamous vaginal epithelium (arrowheads) and simple columnar epithelium (arrows) organized into cystic structures.

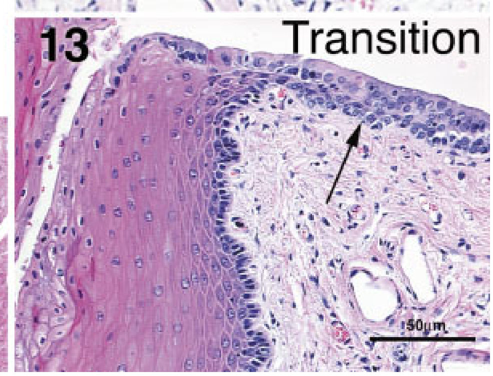


Fig. 13. Transition zone between the thick cornified vaginal epithelium (left) and the thin urethral-like epithelium (arrow) of the spotted hyena (*Crocuta crocuta*).

genital tract and the urethra (Fig. 13). This urethral-like epithelium is about 4–5 cell layers in thickness. Apical cells are cuboidal to low columnar. The most characteristic feature of this last segment of the genital tract before the confluence with the urethra is a submucosal mucous urogenital gland (SMUG) not previously reported (Fig. 14). The cranial aspect of the SMUG is located in the lower segment of the genital tract near the junction between the vaginal and the urethral-like epithelium. The SMUG extends caudally over a linear distance of about 2–3 cm to slightly below the confluence of the urethra with the genital tract. The SMUG has multiple ducts that empty into the urogenital tract. The SMUG is confined to the submucosal tissue and is not recognizable externally. In contrast, Bartholin's glands (bulbourethral glands, BUG) are recognizable as large glands projecting laterally from the urogenital tract just cranial to the ischiocavernosus muscles (Fig. 5). Both the SMUG and the BUG are mucus-secreting glands.

In the female hyena the body of the bladder tapers gradually to become the urethra, and thus a distinct bladder neck is not present (Fig. 5). The urethra is lined by a typical urethral epithelium and extends caudally, first separated from the genital tract, but eventually fusing externally with the genital tract in the region of the vagina. The angle of intersection of the urethra and the vagina is low (~20°). For this reason the internal confluence of the lumina of the

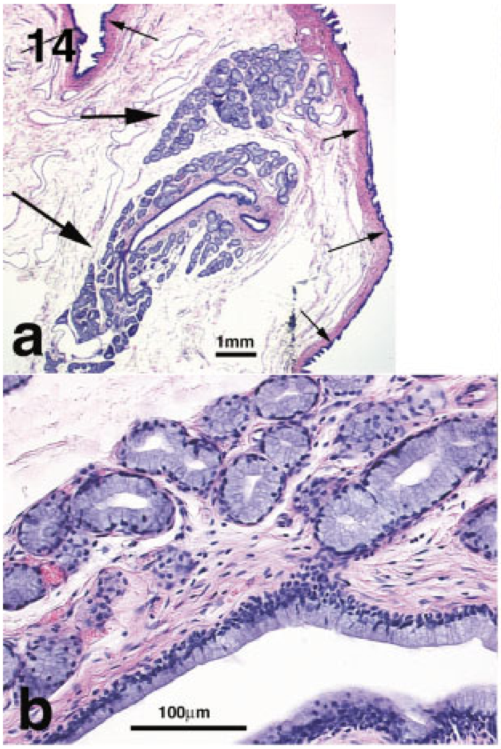


Fig. 14. Submucosal mucous urogenital gland (SMUG) of the spotted hyena (*Crocuta crocuta)*. **a:** Low magnification showing the SMUG (large arrows) and the mucosa (small arrows) **b:** High magnification showing mucous cells.

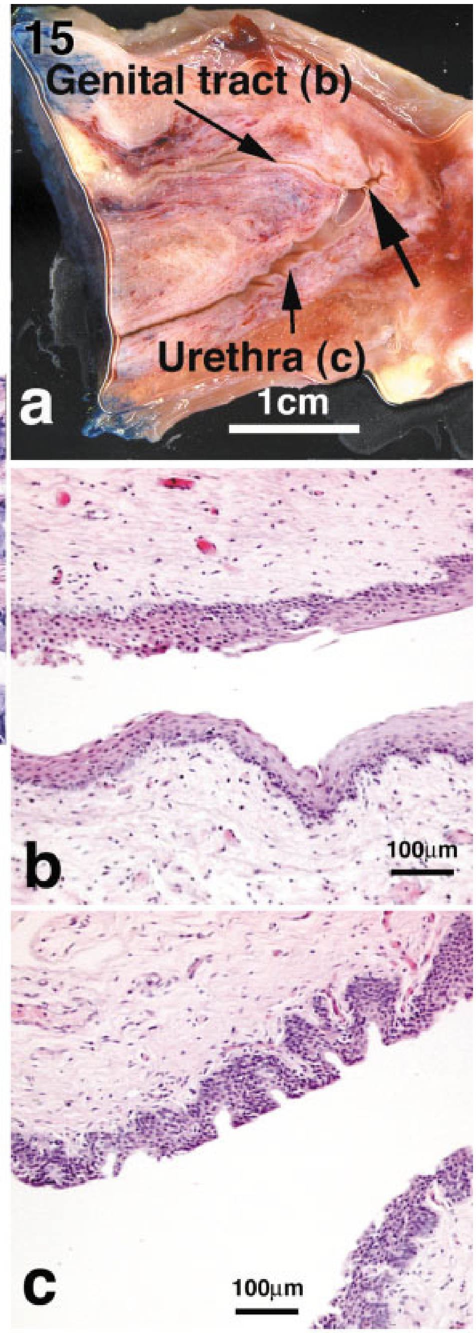


Fig. 15. **a:** Confluence of the urethra with the urogenital tract to form the urogenital sinus (large arrow) of an adult female spotted hyena (*Crocuta crocuta)*. **b:** The genital tract at the level of arrow. **c:** The urethra at the level of the arrow. Both of these epithelia are similar.

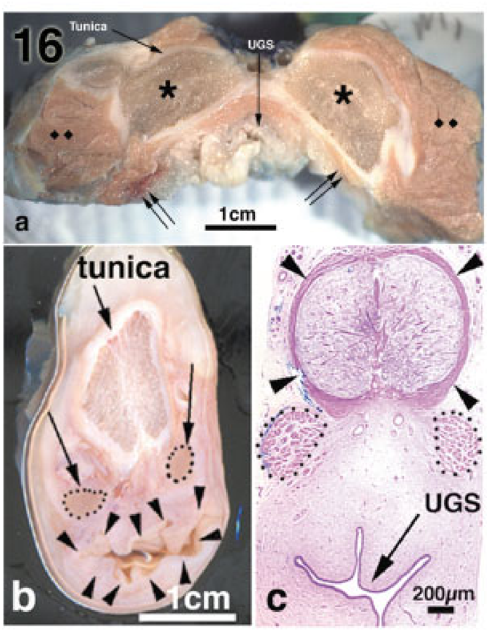


Fig. 16. Transverse sections of the clitoris of the adult (**a,b**) and a near-term spotted hyena (*Crocuta crocuta)* fetus (**c**). **a:** Thick section of the root of the clitoris near the attachment of the corporal bodies (*) to the pubic rami. The two corporal bodies approach each other in the midline and are covered by the large ischiocavernosus muscles (diamonds) and the retractor muscles (double arrows). Note the thick tunica albuginea surrounding erectile tissue of the corporal bodies. Ventral to the corporal bodies is the urogenital sinus (UGS). **b:** Thick section through the midshaft of the adult clitoris. The corporal body is surrounded by the tunica albuginea. Immediately ventral-lateral to the corporal body (**b**) are the retractor muscles (arrows). The most ventral structure is the urogenital sinus (**b**), which has a large collapsed folded wall (arrowheads). **c:** Histological section of the midshaft of the clitoris of a near-term fetus. The corporal body is surrounded by a thick tunica albuginea demarcated by arrowheads. The retractor muscles (outlined by dots) are ventral-lateral to the corporal body. The urogenital sinus (UGS) is the most ventral structure, having a highly folded contour.

urethra and the genital tract occurs about 2 cm caudal to the external confluence of these gross structures.

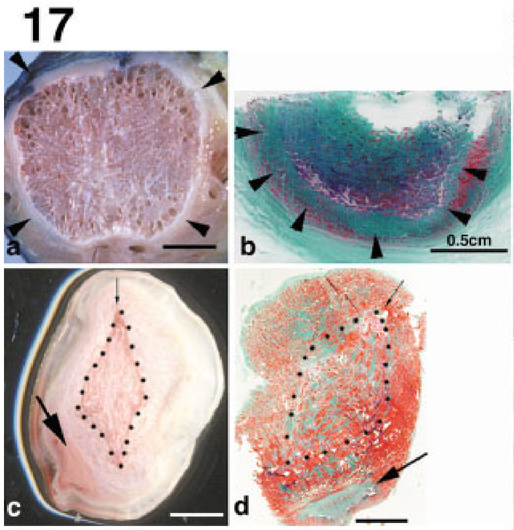
A true urogenital sinus forms at the confluence of the reproductive tract and the urethra (Fig. 15a). The epithelium of the urethra and the lower genital tract are similar at and above the confluence of the reproductive tract and urethra. Both epithelia exhibit features of urethral epithelium (Fig. 15b,c). Once the urogenital sinus is formed at the confluence, it extends caudally within the shaft of the clitoris, which passes dorsal to the symphysis pubis and then curves ventrally and cranially. In this way the direction of the urogenital sinus changes about 180° as it traverses the peniform clitoris. As the urogenital sinus curves ventrally through the pelvic outlet, the right and left corpora cavernosa and associated ischiocavernosus muscles merge with the tubular urogenital sinus to give bulk to the clitoris.

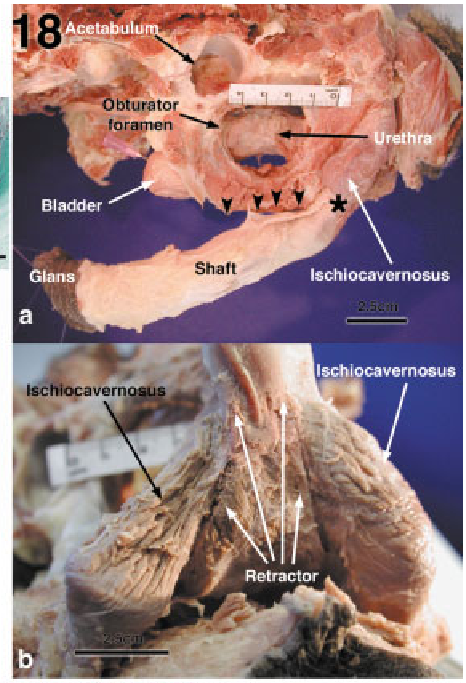
External Genitalia of Female and Male Hyenas: Similarities and Differences

The shaft of the clitoris is formed by a single large corporal body formed by the fusion of the right and left corpora cavernosa near their proximal attachment to the ischiopubic rami where the corporal bodies are covered by exceedingly well-developed ischiocavernosus muscles (Fig. 16a). These two corporal bodies, each surrounded by thick tunica albuginea, meet and fuse in the midline near the pubic symphysis (Fig. 16b,c). The initial fusion of the two corpora cavernosa is represented as a partial or complete midline connective tissue septum within the common corporal body (Fig. 16b,c). However, proceeding distally, this midline septum gradually disappears, and thus a single common corporal body is defined externally by the tunica albuginea (Fig. 17a). The tunica albuginea is a particularly thick sleeve of collagen fibers (Figs. 16a–c, 17a). From the inner aspect of the tunica albuginea, thick collagen bundles extend and intersect throughout the substance of the corporal body (Fig. 17a,b). The abundance of collagen within the corporal body gives the shaft of the clitoris (and penis) a certain degree of rigidity even in the resting state. Immediately ventral-lateral to the corporal body of the clitoris are the paired retractor muscles (Fig. 16b,c). These muscles are attached proximally to the pubic rami, run longitudinally ventral to the corporal body, and attach distally along the tunica albuginea. In the clitoris the urogenital sinus is located ventral to both the corporal body and the paired retractor muscles. The thin wall of the female urogenital sinus has a collapsed and highly infolded contour (Fig. 16). For these reasons the lumen of the female urogenital sinus is highly distensible to accommodate the penis during mating and for delivery of the cubs at parturition.

Certain aspects of the anatomy of the phallus in males and females are distinctly different, reflecting the different functional demands of the penis vs. the peniform clitoris even though certain features are shared in common. Euthanasia of an adult male spotted hyena provided the opportunity to dissect the intact pelvis and examine the spatial arrangement of urogenital tract, its bony attachments, and associated muscles, which are similar in both the male and female. Figure 18a shows the bladder and urethra extending caudally within the pelvis and passing through the pelvic outlet. Not seen are the bilobar prostate and BUGs, which also lie within the pelvic cavity. As the urethra passes caudally through the pelvic outlet, the two corporal bodies attached to the pubic rami approach each other in the midline and fuse to form the common corporal body. The urogenital tract then turns almost 180° so that the tip of the penis (also true for the clitoris) points ventral-cranially. In both sexes extremely large ischiocavernosus muscles (Fig. 18a,b) cover the corporal bodies at their bony attachments. These muscles arise from the pubic rami and insert on the proximal aspects of the corpora cavernosa as they are fusing to form the common corporal body. Lying between the ischiocavernosus muscles and also arising from the pubic rami are the retractor muscles that extend distally along the ventral aspect of the common corporal to insert along the tunica albuginea (Figs. 18b, 19). Given the bulk of the ischiocavernosus and retractor muscles and the geometry of their attachments, it is likely that coordinated contraction of these muscles elicits the "phallic flipping" that occurs during mating and during "erection" in meeting ceremonies in both male and female hyenas. The dramatic movements of the penis (and clitoris) in the nonerect state means that a flexible "hinge" region must exist. This is located proximally just distal to the bony attachment of the corpora and ischiocavernosus muscles (asterisk in Fig. 18a). In the hinge region the diameter of the common corporal body is considerably less than that distally. More importantly, while the distal aspect of the corporal body is stiff and noncompressible, even in the flaccid state, the hinge region is flexible and easily compressible. This difference in rigidity of the hinge vs. the midshaft regions is associated with dramatic differences in cellularity and collagen content in these two regions. Surface scans of the midshaft suggest an abundance of collagen in the tunica and throughout the corporal body (Figs. 17a, 19d). This abundance of collagen in the phallic midshaft was confirmed by Masson's trichrome staining (Fig. 17b). In contrast, the hinge region is more cellular and contains considerably less collagen, as judged in surface scans and in sections stained with Masson's trichrome (Fig. 17c,d). Also, the directionality of the cellular and collagenous elements is distinctly different in the midshaft and hinge regions (Figs. 17, 19d).

In both sexes the midline corporal body of the penis (and clitoris) is surrounded by an exceedingly thick tunica albuginea (Figs. 17a, 19d). From the inner aspect of the tunica albuginea, thick collagen bundles extend and intersect throughout the substance of the corporal body in both sexes (Fig. 17a). This gives the phallic shaft some degree of rigidity even in the flaccid state in both sexes. In the midshaft the shape and diameter of the corporal body is similar in males and females, even though other features at midshaft distinguish the male and female phallus. One difference is the position of the retractor muscles. In females the retractor muscles lie immediately ventral-lateral to the corporal body and dorsal to the urogenital sinus (Fig. 16b,c). In males the retractor muscles lie immediately ventral to the urethra (Fig. 19). In females the cavity of the urogenital sinus is voluminous, having a collapsed, highly infolded thin wall. Erectile tissue and associated tunica albuginea do not surround the urogenital sinus in females (Fig. 16b,c). In contrast, in males the cavity of the urogenital sinus (urethra) is small, oval-shaped, and is surrounded by blood-filled spaces that constitute the corpus spongiosum (Fig. 19). The corpus spongiosum is in turn demarcated peripherally by a connective capsule (Fig. 19a–c). It should be noted that this sexual dimorphism devel-





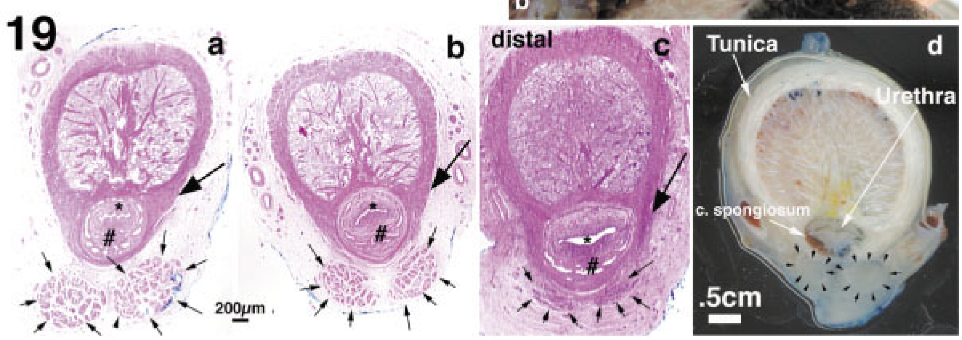


Fig. 17. Transverse sections through the adult peniform clitoris at midshaft (**a,b**) and the hinge region (**c,d**) of the spotted hyena (*Crocuta crocuta)*. **a:** Scan of the female phallus at midshaft; note the thick tunica albuginea (arrowheads) and the intersecting network of coarse collagen fibers emerging from the inner aspect of the tunica albuginea and intersecting throughout the substance of the common corporal body. Not shown in (**a,b**) is the urogenital sinus, which is ventral to the tunica albuginea. The male corporal body at midshaft gave an identical pattern (see Fig. 19d). **b:** Thin section of the female phallus at midshaft stained with Masson's trichrome; note that the tunica albuginea (arrowheads) and most of the common erectile body consist of green-stained collagen fibers. **c:** Scan of the hinge region of the clitoris; note the higher degree of cellularity and corresponding reduction of collagen fibers within the tunica and the common erectile body. The male hinge region gave an identical pattern. **d:** Thin section of the hinge region of the clitoris stained with Masson's trichrome; note that the tunica albuginea is not defined by collagen fibers. Instead, the hinge region is notable for its general paucity of green-stained collagen fibers in the common erectile body. Finally, in (**c,d**) note the dorsal-ventral directionality of cellular and collagenous elements (small arrows). The common corporal body in (**c,d**) is demarcated by black dots. The large arrows in (**c,d**) denote the urethra. Scale bars = 0.5 cm.

Fig. 18. Dissection of the pelvis and genital tract of the male spotted hyena (*Crocuta crocuta)*. **a:** The bladder is partially covered by the pelvic bones. The urethra can be seen through the obturator foramen, which in life is covered by muscle. Attached to the inferior pubic rami are the ishiocavernosus muscles, which arise from the inferior pubic rami and insert into the corporal bodies. Note that the urogenital tract makes an almost 180° turn as it passes caudally out of the pelvis. Most of the shaft of the penis is thick, but the proximal portion of the shaft (*), called the hinge region, just distal to the attachment of the ishiocavernosus muscles is thinner (and more flexible) than the distal shaft of the penis. Arrowheads indicate the pubic symphysis. **b:** View of the root of the penis showing the ishiocavernosus muscles, which cover the corpora cavernosa at their bony attachments. Note the retractor muscle medial to the ishiocavernosus muscles extending distally along the ventral aspect of the shaft of the penis.

Fig. 19. Transverse sections through the penis of the spotted hyena (*Crocuta crocuta)*. **a–c:** Transverse sections of the penis of a near-term male fetus beginning proximally (**a**) and progressing distally (**b-c**). Note in (**a–c**) the common corporal body, the urethra (*), the corpus spongiosum (#) surrounded by the thick connective tissue layer, and the tunica albuginea (large arrows in **a–c**). The retractor muscles in (small arrows **a–c**) are ventral to the corpus spongiosum and in (**c**) insert into the tunica albuginea. **d:** Thick transverse section through the adult penis at midshaft. Note the thick tunica albuginea and the intersecting network of coarse collagen fibers emerging from the inner aspect of the tunica albuginea and extending throughout the substance of the common corporal body. Ventral to the common corporal body is the urethra, surrounded by the corpus spongiosum. Note the position of the retractor muscles (arrowheads) ventral to the urethra.

ops prenatally and is certainly evident in near-term male and female fetuses (compare Figs. 16c, 19a–c).

The epithelium lining the urogenital sinus traverses the clitoris and penis to emerge at the glans. This epithelium is a typical urethral epithelium in both sexes and does not change along the shaft of the phallus until the external meatus, where the urethral epithelium undergoes a transition to an epidermis that extends onto the surface of the glans. Distally the phallus in both sexes terminates at the glans where the common corporal body ends in both sexes. The shape and diameter of the distal aspect of the common corporal body in the glans is profoundly different in males and females. In females the common corporal body decreases only slightly in diameter and ends bluntly in the glans (Fig. 20). In the clitoris a separate erectile body (hyena urogenital glanular extension, HUGE) forms most of the substance of the glans and is located distal to the common corporal body. The HUGE is not encapsulated by a tunica albuginea (Fig. 20). This means that engorgement with blood should result in expansion of the clitoral glans. In males the common corporal body tapers substantially within the glans, where its diameter is only a fraction of that seen at midshaft (Fig. 21a). In the male the tapered common corporal body extends to the most distal aspect of the glans, terminating immediately subjacent to the mucosa of the tip of the glans penis (Fig. 21a). The tip of the penis is not adorned with a separate distal erectile body, as is the case for the female. However, the proximal region of the penile glans does contain erectile tissue, located ventral and lateral to the urethra and the corpus spongiosum (Fig. 21b,c). These latter erectile tissues are not encapsulated and thus may expand during erection.

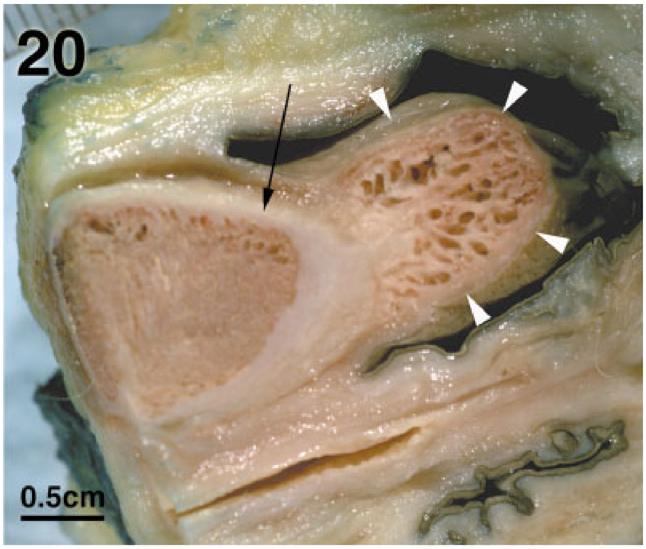


Fig. 20. Midsagittal section of the glans of the peniform clitoris of an adult female spotted hyena (*Crocuta crocuta)*. Note the common corporal body surrounded by the thick tunica albuginea (arrow) terminates bluntly. The tip of the glans is adorned by a separate erectile body (HUGE) not surrounded by a dense connective capsule (white arrowheads).

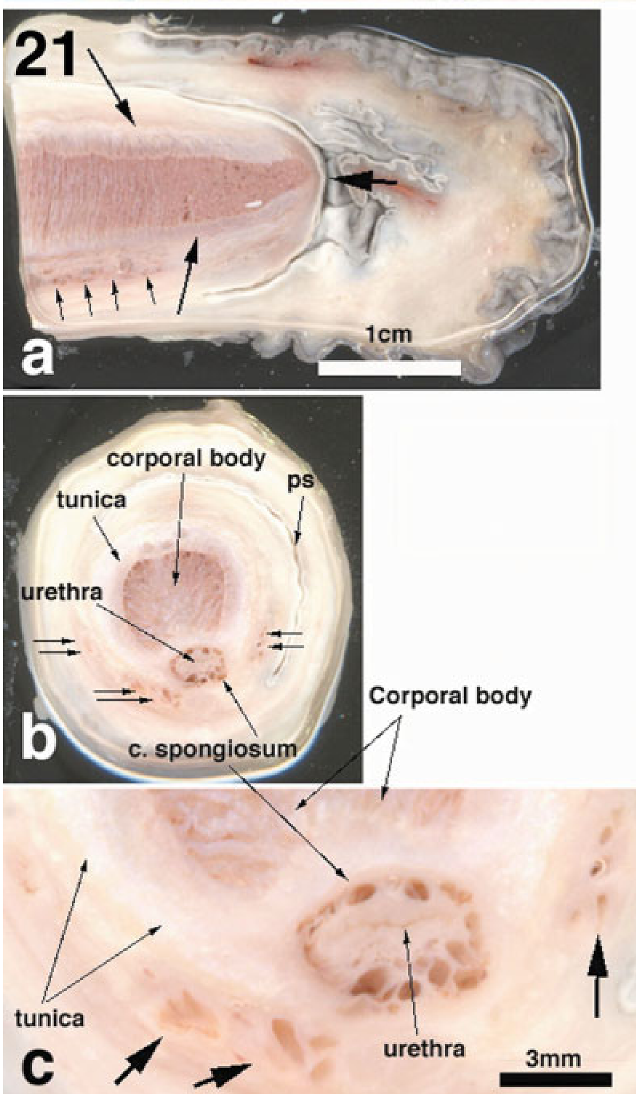


Fig. 21. **a:** Midsagittal thick section through the adult glans penis of the spotted hyena (*Crocuta crocuta)*. Note that the common corporal body tapers to a narrow termination and is surrounded by the thick tunica albuginea (large arrows). Separate erectile tissue is ventral to the common corporal body and is not surrounded by the tunica albuginea (small arrows). **b:** Transverse section immediately proximal to the cut surface in (**a**); note the common corporal body surrounded by the thick tunica albuginea. The urethra is surrounded by the corpus spongiosum. Additional erectile tissue is located ventral and lateral to the corpus spongiosum (small double arrows). **c:** Higher magnification of (**b**); note the corpus spongiosum and additional erectile tissue (large arrows), which are ventral and lateral to the corpus spongiosum. This additional erectile tissue is not surrounded by a definite connective tissue capsule.

DISCUSSION

The detailed histological findings of the present study complement and clarify previous anatomical descriptions (Watson, 1877; Matthews, 1939; Davis and Story, 1949; Wells, 1968; Neaves et al., 1980) regarding the urogenital system of the spotted hyena. Not since Matthew's treatise in 1939 has a study followed the intricacies of the spotted hyena's reproductive tract from the oviduct to the glans clitoris. As such, we have described the histological transitions from an upper reproductive tract that is fairly typical of female carnivores, to the highly masculinized lower genital tract that is unique to the female spotted hyena.

From an external view, the upper reproductive tract appears to be essentially unremarkable. However, the detailed histology in the present study has revealed some interesting findings not reported by other investigators (Matthews, 1939). The helical configuration of the uterine lumen, as demonstrated by the corrosion casts, adds greater length and surface area compared to a straight endometrial cavity. Sokolowski et al. (1973) noted a "corkscrew" appearance to the uterus during metestrus (early luteal phase) in beagle bitches. This "corkscrewing" only occurs shortly after ovulation, perhaps under the influence of high progesterone levels, and is apparent when the uterus is inspected as an intact gross specimen (Sokolowski et al., 1973). The helical configuration of the hyena uterus was not evident on gross inspection; rather, the presence of multiple endometrial lumina on histological cross-section led us to perform the corrosion casts. The diverticula that protrude from the main endometrial canal also contribute to the appearance of multiple uterine lumina. We considered the possibility that this finding might be an artifact of prolonged nulliparity and pathology associated with persistent estrus. The presence of these histological findings in the uterus from a multiparous female argues against this hypothesis. The functional significance of the hyena's uterine morphology is unknown. The placenta of the spotted hyena is unique among carnivores in that the hyena placenta is hemochorial and villous, while the placentae of all other carnivores studied are endotheliochorial and labyrinthine (Amoroso, 1959; Wynn and Amoroso, 1964). Whether the idiosyncrasies of the spotted hyena endometrium and placenta are related awaits further study.

The transition from the uterine corpus to the lower urogenital tract had not been described in detail before the present study. Matthews (1939) improved on the description by Watson (1877) by identifying a vagina, but an intervening cervix was not described until Wells (1968), and then only briefly. Additionally, submucosal mucous urogenital glands (SMUG), never before described, are present in the genital tract as the transition from a vaginal to urethral-like epithelium occurs. The products of the cervical and submucosal glands may prove to be important for lubricating and protecting the urethral epithelium not only during parturition, but during copulation as well. Intromission appears to be traumatic to the urethral epithelium of the female, as postcoital bleeding has frequently been observed, even in multiparous females (Coscia, Weldele, Frank, and Glickman, unpublished observations). The vagina may also prove important for sperm capacitation; this process may be delayed in hyenas as sperm initially travel through a canal lined with a urethral epithelium. The secretory products and histology of cervical glands, SMUG and BUG may vary with the estrous cycle as Matthews (1939) described with regards to the vaginal epithelium. Changes in pH and viscosity of these secretions may prove important as the sperm begin the journey through the tortuous reproductive tract of the female spotted hyena.

The embryological origin of the upper vagina in spotted hyenas is unknown, but is presumed to have differentiated from the Müllerian ducts (Cunha, 1975). Vaginal tissue derived from either the Müllerian ducts or the urogenital sinus is indistinguishable in adult mammals (Kurita et al., 2001); thus, future research on the development of the vagina in spotted hyenas awaits embryological studies. Research to determine the temporal and spatial expression of the estrogen and androgen receptors in the genital tract of the hyena fetus is planned. This type of study should provide insights into the development of a female genital tract whose upper zones are feminized and whose lower zones are masculinized (Shapiro et al., 2000).

A set of functional issues, concerning mating, parturition, and meeting ceremonies, was raised in the Introduction to this paper. A corresponding cluster of morphological features was subsequently identified that relate to each of these events. With regard to parturition, the various muscles identified in the uterine and vaginal passageways would be required for moving a large fetal hyena through the complex passageway that results in birth. Multiple glands, identified in the female uterine and vaginal canals (SMUG and BUG), would also facilitate movement of the fetus during parturition by providing lubrication. Both mating and parturition require that the clitoris expand, either to accommodate the male, or to permit passage of the fetus; albeit the expansion required during parturition is much greater than that during mating. Neaves et al. (1980) observed that the urethra and the urogenital canal are differentially embedded within the penis and the clitoris, respectively, and that these differences permit the expansion of the clitoris when the female gives birth. In particular, they noted that the urethra of the male is surrounded by a corpus spongiosum limiting expansion, while the urogenital canal of the female spotted hyena is encased in loose connective tissue, facilitating such expansion. We agree with these observations, as well as with their conclusions regarding the potential role of the retractor muscles in retaining and stabilizing the clitoris for receipt of the male during mating. In addition, we note that the extensive infolding of the urogenital sinus in the female would also serve to facilitate such expansion, while the broad distribution of collagen within the corporal body of the clitoris could provide an appropriate target for the actions of relaxin. This peptide hormone potentially contributes to the elasticity of clitoral tissues and peaks during the period immediately preceding birth in the female spotted hyena (Steinetz et al., 1997).

In males and females, the existence of a “hinge region” near the proximal attachment of the phallus to the pubic bones, and the mode of attachment of the ishiocavernosus and retractor muscles, facilitate the “flipping” phase of the mating sequence. The presence of a thick collagenous tunica completely enclosing the shaft of the penis would result in the rigidity required for thrusting, while the absence of such a restrictive outer layer in the glans permits expansion of that tissue and serves to retain the penis in the female during the semi-locked terminal portion of the mating sequence. The tapered shape of the glans penis and its corporal body (which contrasts with the rounded contour of the glans clitoris) would also facilitate entry of the male during mating.

Meeting ceremonies require that erection and retraction of both the female and the male phallus be accomplished in a timely manner. By limiting the constraining tunica (surrounding the corporal body) in the female to a dorsal position, she can achieve erections required for participation in meeting ceremonies, without compromising the ability of the clitoral shaft to expand during mating and parturition. In addition, the ubiquitous presence of cross-linked collagen fibers in the shaft of the clitoris and the penis provides more than usual structural rigidity even in the flaccid state, which could speed the appearance of a semierect phallus during meeting ceremonies, prior to full engorgement of penile/clitoral vasculature. In the female, such a collagen-cross-linked organ would also provide a firmer base for receipt of the male during mating.

Close examination of the urogenital system of the female spotted hyena reveals a remarkable array of anatomical adaptations, allowing effective reproductive behavior in the only extant female mammal that mates and gives birth though her clitoris. Substantial requirements are also placed on the male, as he is required to achieve entry during mating through a small opening, located in an unusually anterior position on the surface of the abdomen. As noted above, penile morphology is also adapted to the unique demands of mating for male spotted hyenas.

Experiments have been conducted in which anti-androgens (flutamide or cyproterone) and a 5-alpha reductase inhibitor (finasteride) were supplied to female and male fetuses in utero (Forger et al., 1996; Drea et al., 1998). The results are compatible with the hypothesis that sex differences in the external genitalia of spotted hyenas at birth are due to greater androgenic activity in males. That is, the external morphology of the penis, and associated external musculature, as well as Onuf's nucleus in the spinal cord, assumes the feminine phenotype following anti-androgen treatment (Forger et al., 1996; Drea et al., 1998). It remains to be determined whether the internal structure of the penis is also anatomically feminized by such treatment (i.e., position of the retractor muscles and morphology of the glans). Although we can analyze the mechanisms that produce the uniquely synchronized urogenital adaptations of this species, it remains difficult to visualize the sequence of evolutionary events that produced this unusual co-adapted system.

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