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# A Neuroanatomical Comparison of Humans and Spotted Hyena, a Natural Animal Model for Common Urogenital Sinus: Clinical Reflections on Feminizing Genitoplasty

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**Purpose:** Surgical treatment of the common urogenital sinus phallus has been one of the most challenging areas in pediatric urology. To better understand the neuroanatomy of the common urogenital sinus phallus, we evaluated an animal model naturally having this condition, the spotted hyena, *Crocuta crocuta*. We compared the neuroanatomy of male and female humans and spotted hyenas using anatomical, immunohistochemical and 3D reconstruction techniques. We also examined the implications of the pattern of clitoral innervation for the unique challenges faced by female spotted hyenas, the only extant species of mammal that mates and gives birth through the clitoris.

**Materials and Methods:** Three adult male and 3 female spotted hyenas were studied. With the animals under anesthesia gross anatomical examination was performed before and after artificial erection. Histological analysis was performed on one 95-day fetal male and female spotted hyena specimens, and on 18 human male and female fetal external genitalia specimens using antibodies raised against the neuronal marker S-100. Three-dimensional computer reconstruction using serial sections allowed analysis of the neuroanatomy of the penis, clitoris and common urogenital sinus of the fetal spotted hyena and human.

**Results:** Compared to other mammals, the clitoris and penis of spotted hyenas were remarkably similar in size and configuration in the flaccid and erect states. Male and female hyenas had a single opening on the tip of the glans penis/clitoris. The basic anatomical structures of the corporeal bodies in both sexes of humans and spotted hyenas were similar. As in humans, the dorsal nerve distribution was unique in being devoid of nerves at the 12 o'clock position in the penis and clitoris of the spotted hyena. Dorsal nerves of the penis/clitoris in humans and male spotted hyenas tracked along both sides of the corporeal body to the corpus spongiosum at the 5 and 7 o'clock positions. The dorsal nerves penetrated the corporeal body and distally the glans in the hyena. In female hyenas the dorsal nerves fanned out laterally on the clitoral body. Glans morphology was different in appearance in both sexes, being wide and blunt in the female and tapered in the male.

**Conclusions:** The neuroanatomy of the male and female external genitalia in the spotted hyena, *Crocuta crocuta*, although grossly similar, has distinct anatomical and functional characteristics. The clitoris of the spotted hyena is a classic example of a natural animal model of a common urogenital sinus. The neuroanatomical characteristics of the spotted hyena may be a useful model to simulate the anatomy of common urogenital sinus anomaly in humans.

*Key Words: neuroanatomy, urogenital abnormalities, adrenal hyperplasia, congenital, models, animal urogenital surgical procedures*

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The treatment of ambiguous genitalia is one of the most challenging areas in pediatric urology. A precise understanding of the neuroanatomy of male and female external genitalia is crucial for sound surgical correction of ambiguous genitalia.

Previously, we have reported on the anatomy of the human male and female external genitalia using immunohis-

tochemical techniques and 3D computerized reconstruction of serial histological sections.<sup>1</sup> Based on these studies of normal male and female specimens, we have extrapolated the results to patients with intersex abnormalities such as common urogenital sinus.<sup>2</sup> Extrapolation is based on the hypothesis that in patients with severe prenatal androgen exposure the clitoris will masculinize into a structure analogous to the male phallus. In incomplete forms of masculinization, which are clinically more common, the morphology of the female clitoris lies somewhere in between the normal male and female, and is often indistinguishable from the congenital anomaly, hypospadias. Surgical experience, gross anatomical examination and data from incomplete pathological specimens suggest that the enlarged clitoris is analogous to the male phallus.<sup>1</sup> However, confirmation that normal clitoral neuroanatomy is not altered by the exposure to androgens has not been shown, mainly due to the diffi-

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culty in obtaining adequate specimens for analysis. Furthermore, does virilization of the clitoris result in the clitoris becoming neuroanatomically indistinguishable from the penis?

The spotted hyena, *Crocota crocuta*, presents a unique opportunity to study a natural animal model of common urogenital sinus. The female spotted hyena has the most masculinized external genitalia of any female mammal, having a hypertrophied clitoris that closely resembles the penis in size and structure, lacking an external vagina and having a pseudo scrotum presumably due to fusion of the labia majora.<sup>3-6</sup> This configuration is analogous to severely virilized human females with congenital adrenal hyperplasia, who have a penis-like clitoris with fused labia (fig. 1). Traversing the hyena female phallus is a common urogenital sinus through which the female urinates, copulates and gives birth. First births are exceptionally difficult due to the large size of the fetus (approximately 1.1 to 1.5 kg), the tight urogenital meatus, and the length and angulation of the birth canal.<sup>7</sup> Copulation through a peniform clitoris can be awkward for the male, requiring agility and persistence.<sup>8,9</sup>

The female spotted hyena represents a natural common urogenital sinus model with severe masculinization. We performed a neuroanatomical study of the male and female spotted hyena genitalia, and compared findings in the hyena with that of normal male and female human fetal external genitalia. The neuroanatomical findings are discussed in relationship to the human condition of in utero virilization and the treatment of patients with common urogenital sinus malformation. We also examined the implications of the pattern of clitoral innervation for the unique challenges faced by female spotted hyenas, the only extant species of mammal that mates and gives birth through the clitoris. Sensory information, derived from stimulation of the clitoral nerves of the spotted hyena, must contribute crucial information required for appropriate sociosexual behavior and reproduction. The dorsal nerve of the clitoris in all mammals would be stimulated as the result of contact/pressure on the external surface. However, in contrast to other female mammals, in the spotted hyena expansion of the central urogenital sinus (particularly during mating and birth) would also contribute essential sensory information. Description of the patterns of clitoral innervation constitutes a critical step toward understanding the basic biology of this remarkable animal.

## MATERIALS AND METHODS

**Spotted hyena.** The spotted hyenas, *Crocota crocuta*, were members of a captive colony housed socially at the Field Station for the Study of Behavior, Ecology, and Reproduction, University of California, Berkeley. A total of 3 adult male and 3 adult female spotted hyenas were studied by gross examination with the animals under general anesthesia. Ages of adult hyenas were 3 to 7 years. All adult females were nulliparous.

External genital organ measurements (flaccid and erect length and width of phallus, and width of urethral or common urogenital sinus opening) of the hyenas were taken following immobilization with intramuscular injections of ketamine (4 to 6 mg/kg) and xylazine (1 mg/kg). With the animals under anesthesia gross examination with photographic documentation before and after artificial erection

was performed. Artificial erection was induced by intracorporeal injection via a 23 gauge butterfly needle of sterile saline following tourniquet application to the base of the phallus (fig. 1, C and D). Selected animals (1 male and 1 female at age 7 years) were euthanized, and the entire urogenital tract was preserved in formalin for histological analysis. Fetal male and female (1 each) spotted hyenas at 95 days of gestation (normal gestation 110 days) were also euthanized, and the entire urogenital tract was preserved in formalin for histological analysis. Sex identity was determined by gross and histological analysis of the gonads. Gestational age was calculated from the day of copulation, with pregnancy confirmed early in gestation by ultrasound (using general anesthesia).<sup>5</sup>

**Human fetuses.** A total of 18 male and 18 female normal human fetal external genitalia were studied at 18 to 36 weeks of gestation. Separate anatomical studies with these specimens have previously been reported.<sup>1,2</sup> Sex identity was determined by gross and histological analysis of the gonads. Human specimens were dated on the basis of fetal heel-to-toe length since crown-rump measurements were not possible.<sup>10</sup>

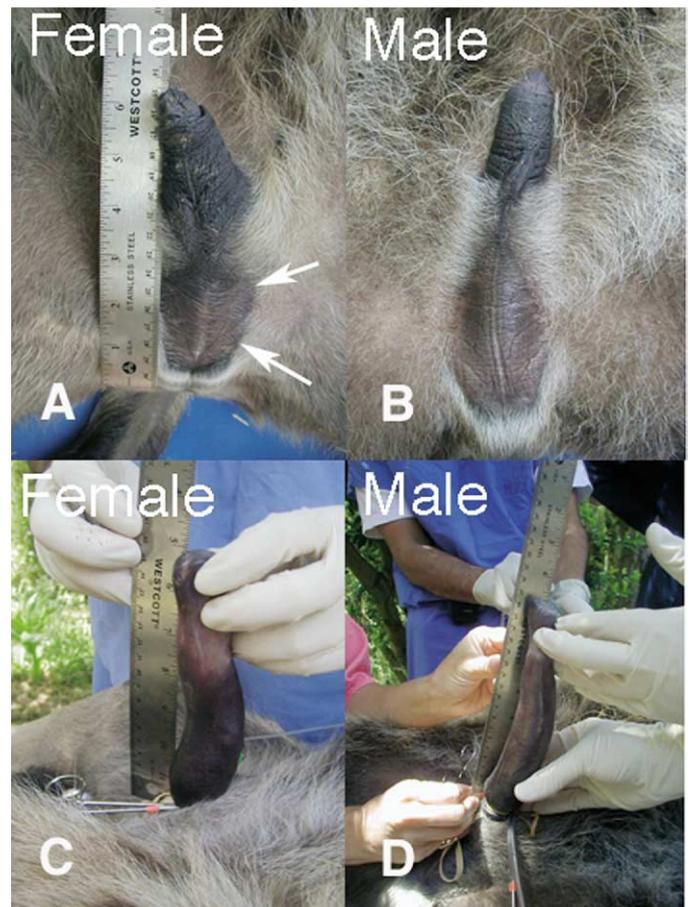


FIG. 1. External genitalia in flaccid and erect states of female and male 3-year-old spotted hyenas, *Crocota crocuta*. Female spotted hyena phallus in flaccid (A) and artificially erect (C) states. Note pseudo scrotum (arrow) of female (A). Male spotted hyena penis in flaccid (B) and artificially erect (D) states. Note differences in glans shape in female (broad) and male (tapered).

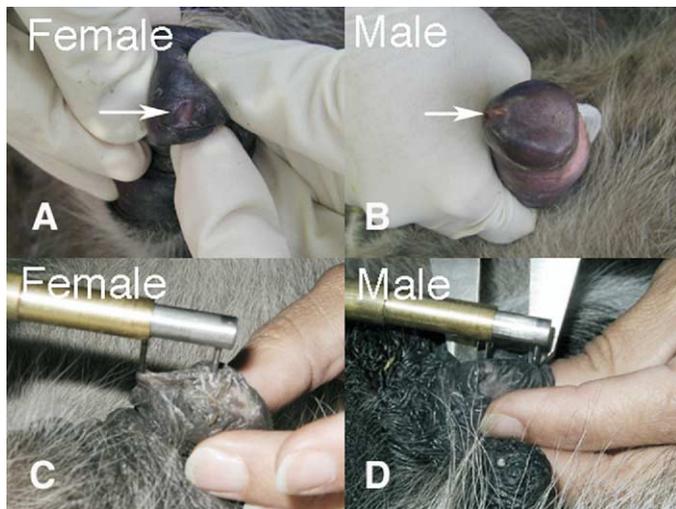


FIG. 2. Location of common urogenital sinus/external urethral meatus on glans of female and male 3-year-old spotted hyenas, *Crocuta crocuta*. A, female spotted hyena phallus, glans and common urogenital sinus opening (arrow). B, male external urethral meatus (arrow). Stretched opening of female (C) is larger than that of male (D).

**Histology, immunohistochemistry and 3D computerized reconstruction.** Histological processing of the human and hyena specimens was performed by paraffin embedding, followed by serial sectioning at 6 microns. Specimens older than 26 weeks were decalcified as described previously.<sup>1</sup> The

entire external genitalia were serially sectioned and mounted on glass slides.

Every 10th section was stained with hematoxylin and eosin, and Masson's trichrome. Immunohistochemical studies were performed on select sections with the nonspecific neuronal marker S-100. Briefly, the avidin-biotin-peroxidase procedure was performed using a Vectastain® ABC kit with cobalt intensification.<sup>2</sup> All immunohistochemical analysis was controlled with nonimmune or preimmune serum or IgG at equivalent dilutions.

Computer reconstruction of serial sections was created using digital images, SURFdriver 3.5 software and a Power Macintosh® G4 computer. Every fifth to 10th section was digitized. The corporeal body, glans, urethra or common urogenital sinus, and muscular and neuronal structures were manually outlined and checked against the original histological sections. Three-dimensional analysis of the course of dorsal nerves in relation to crural bodies and other surrounding structures was performed in the x and y axes as an animated motion picture, and views of interest were captured as static images.<sup>1,11</sup>

## RESULTS

The size and gross appearance of the adult spotted hyena penis and clitoris were similar in the erect and flaccid states (fig. 1). Although the penis and clitoris are strikingly similar (compared to other mammals), the male phallus is longer and thinner than the clitoris.<sup>12,13</sup> The external meatus was

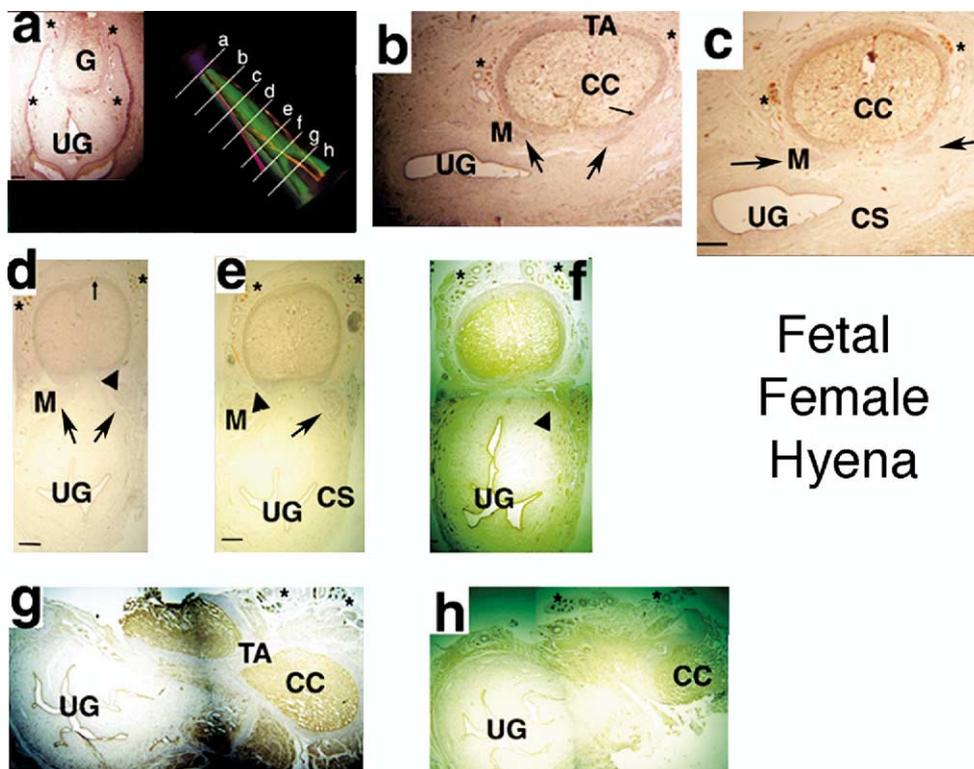


FIG. 3. Representative serial sections of female fetal spotted hyena clitoris at 96 days of gestation immunostained with neuronal marker S-100. Three-dimensional reconstruction in center demonstrates relative location of sections a to h. Note that clitoris has only 1 lumen, ie urogenital (UG) sinus, for copulation, urination and delivery of fetus that is surrounded by thick elastic connective tissue layer (CS) corresponding to corpus spongiosum in males. Two retractor muscles (M, arrows) are located immediately ventral and lateral to corporeal body of clitoris (CC) and dorsal to urogenital sinus. Note lateral course of dorsal nerves of clitoris (asterisks) along clitoral body (b to f). Dense neural network is noted precisely at junction of urogenital sinus and clitoral body (d and e, arrowheads). Also note penetration of thick tunica albuginea (TA) of clitoral body by dorsal nerve of clitoris (b and d, arrows). Bar represents 250 microns.

Fetal  
Female  
Hyena

located on the glans of the male and female spotted hyenas (fig. 2, A and B). Comparison of parts C and D of figure 2 reveals a remarkable tolerance for expansion of the female urogenital sinus meatus compared to the male external meatus. Glans morphology was also different in appearance in both sexes, with the female having a broader glans compared to the tapered male glans as reported previously (fig. 1, C and D, and fig. 2, A and B).<sup>5</sup>

Proximally, a single fused corporeal body splits into 2 crural bodies. The histological structure of the corporeal/clitoral body in the fetal male and female spotted hyena was similar, with the 2 crural bodies attached proximally to the inferior ischiopubic rami (figs. 3 and 4). The microstructure of the erectile corporeal/clitoral body consisted of sinusoids lined with endothelium surrounded by smooth muscle. A notable difference was the thickness of the tunica albuginea, which was markedly thicker in the male spotted hyena in comparison to the female. In the male the thick collagenous tunica albuginea surrounds the corporeal body and the urethra (fig. 4). In contrast, in the female the tunica surrounds the erectile body only (fig. 3).

The retractor muscles in both sexes were prominent in hyena. In the clitoris the retractor muscles were located adjacent to the corporeal body dorsal to the common urogenital sinus (fig. 3). In contrast, in the penis the retractor muscles were located ventral to the urethra (fig. 4). Three-dimensional reconstruction of the female and male phalluses illustrates similarities and differences in the arrangement of penile and clitoral anatomy, and emphasizes sex differences in the location of the retractor muscles (figs. 5 and 6).

In the hyena the dorsal nerves were absent at the 12 o'clock position along the corporeal body (figs. 3, 4 and 7). In the male spotted hyena the pathway of the dorsal nerves was along both sides of the corporeal body from approximately the 11 and 1 o'clock positions to the junction of the corpora spongiosum at the 5 and 7 o'clock positions, as seen in 3D reconstructed images (figs. 6 and 7). The dorsal nerves penetrated the corporeal body through the tunica albuginea (fig. 3, B and fig. 4, C).

The female spotted hyena phallus was unique in the distribution of the dorsal nerves compared to the male, with the nerves coursing in a lateral position along the clitoral body. The extensive network of the dorsal nerve surrounding the erectile body was particularly notable in the clitoris (figs. 4 and 5). The ventral midline of the clitoris and penis was lacking nerves in the spotted hyena.

The anatomy of the hyena external genitalia was compared to that of the human (figs. 8 and 9). The cavernospongiosal junctional area in the human penis was distinctive in having a dense neural network (fig. 8, D to F and fig. 9, D to F). In the human clitoral specimens due to the shorter urethra, there was no cavernospongiosal junction (fig. 8, A to C and fig. 9, A to C). In the penis of the spotted hyena a similar neural configuration at the cavernospongiosal junctional area was observed. In contrast, in the spotted hyena clitoris there was a much more diffuse nerve structure at the junction of the clitoral body and common urogenital sinus.

## DISCUSSION

The neuroanatomy of the normal human clitoris has been described in detail.<sup>1</sup> Extrapolation of normal anatomy has been applied to the reconstruction of cases of severe clitoral

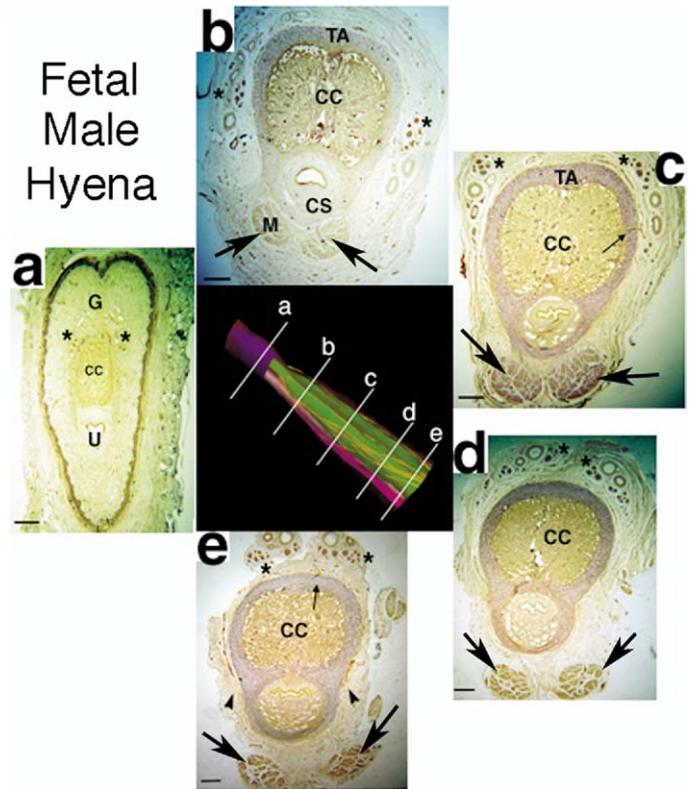


FIG. 4. Representative serial sections of male fetal spotted hyena penis at 96 days of gestation immunostained with neuronal marker S-100. 3D reconstruction in center shows relative location of sections a to e. Urethra (U) traverses through penis and is surrounded by vascular layer and corpus spongiosum (CS), similar to that in man. Glans (G) is innervated by dorsal nerve of penis (asterisks). Two retractor muscles (M, arrows) are located ventral to urethra (CS, (b to e) in contrast to dorsal location in female (fig. 3). Dorsal nerve of penis courses laterally along corporeal body (CC), terminating at 5 and 7 o'clock positions (e, arrowheads). Also note penetration of thick tunica albuginea (TA), which surrounds corporeal body and urethra by dorsal nerve of penis (c and e, small arrows). Bar represents 250 microns.

enlargement secondary to congenital adrenal hyperplasia due to exogenous or endogenous androgen exposure.<sup>2</sup> The goal of reconstructive surgery has been to preserve the sensory and erectile capability of the clitoris by avoiding irreversible disruption of the neurovascular structures.<sup>2</sup> Although this approach appears rational, the question remains as to whether the topography of the neuroanatomical structures of the clitoris changes after masculinization due to excess androgen exposure. In this study we sought to examine whether the neuroanatomy of a virilized clitoris is similar to that of the penis by investigating a natural model of virilization of the external genitalia with a common urogenital sinus, the spotted hyena, *Crocota crocuta*.

The spotted hyena is a naturally occurring model of clitoral hypertrophy with a common urogenital sinus (figs. 1 and 2).<sup>5</sup> As in humans, there is a paucity of nerves in the spotted hyena at the 12 o'clock position (figs. 4 to 6, 8 and 9).<sup>14</sup> In this study we have also demonstrated that the dorsal nerves of the penis send small branches into the corpora cavernosa by piercing the thick tunica albuginea in the hyena. Although this observation seems unique to the spotted hyena, penetrating dorsal nerve branches have been shown to be present in humans.<sup>14</sup> This observation is par-

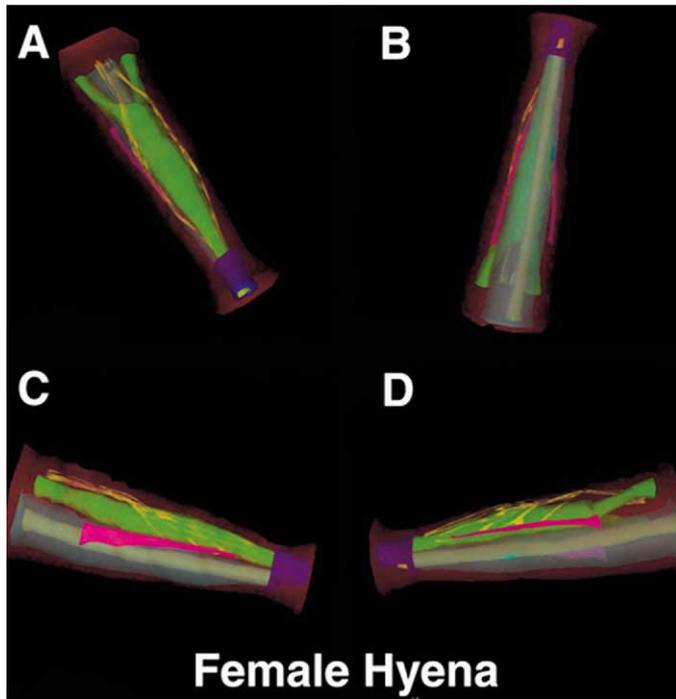


FIG. 5. 3D computerized reconstruction of female fetal spotted hyena clitoris derived from serial histological sections immunostained for neuronal marker S-100. *A*, dorsal. *B*, ventral. *C* and *D*, lateral views. Two crural bodies (green) fuse proximally into clitoral body and extend distally to glans (purple). Common urogenital sinus (gray) and lumen (light gray) lie ventral to clitoral body. Between common urogenital sinus and clitoral body note location of retractor muscles (magenta). Dorsal nerves of clitoris (yellow) arise as 2 separate bundles medial to 2 crura and course along lateral aspects of clitoral body, forming dense neural network that extends to glans. Skin is represented by transparent red shading.

ticularly important in cases where the neurovascular bundle is mobilized during reconstructive surgery. We believe that it is impossible to protect surgically the neurovascular bundle in humans as previously described without damaging nerve branches that wrap around the corporeal bodies and terminate at the 5 and 7 o'clock positions in the male and female.<sup>1,14</sup> In this regard the spotted hyena is an informative and unique animal model because the pattern of penile/clitoral nerves is similar to that seen in humans.

In the spotted hyena and human we confirmed the absence of nerves at the 12 o'clock position.<sup>1</sup> The highly masculinized spotted hyena clitoris also displayed a similar nerve distribution to the hyena penis, with a lack of nerves at the 12 o'clock position. The only difference in the dorsal nerve pattern between the hyena penis and clitoris was the early fanning out of nerves to the lateral sides of corporeal body in the hyena clitoris. This difference was not seen in the human clitoral specimens, but this may be due to the relatively small size of the clitoris in the normal human female, in comparison to the female spotted hyena. We speculate that in patients with virilization of the clitoris the nerve distribution fans out more proximally on the corporeal body, implying that the lateral walls of clitoral/corporeal body should be avoided during surgical reconstruction.

In the spotted hyena the penis and clitoris were also similar with respect to the position of the dorsal nerves as they coursed along the corporeal/clitoral body to the junction

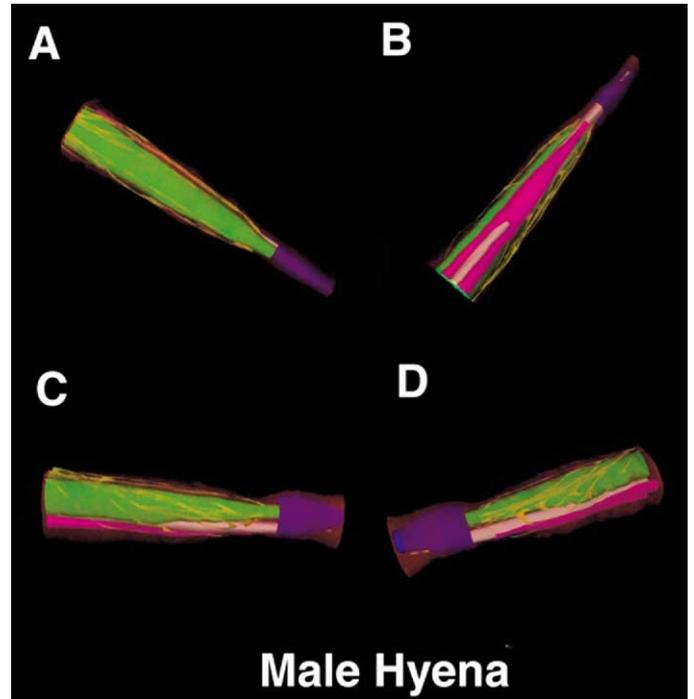


FIG. 6. 3D computerized reconstruction of male fetal spotted hyena penis derived from serial histological sections immunostained for neuronal marker S-100. *A*, dorsal. *B*, ventral. *C* and *D*, lateral views. Two crural bodies (green) fused together at proximal phallus extend distally to glans (purple). Urethra (pink) is located ventral to corporeal body (green). Retractor muscles (magenta) are located ventral to urethra. Dorsal nerves of penis (yellow) arise as 2 separate bundles and extend distally, coursing laterally to 5 and 7 o'clock positions relative to corporeal body to form dense neural network along penile shaft and glans. Skin is represented by transparent red shading.

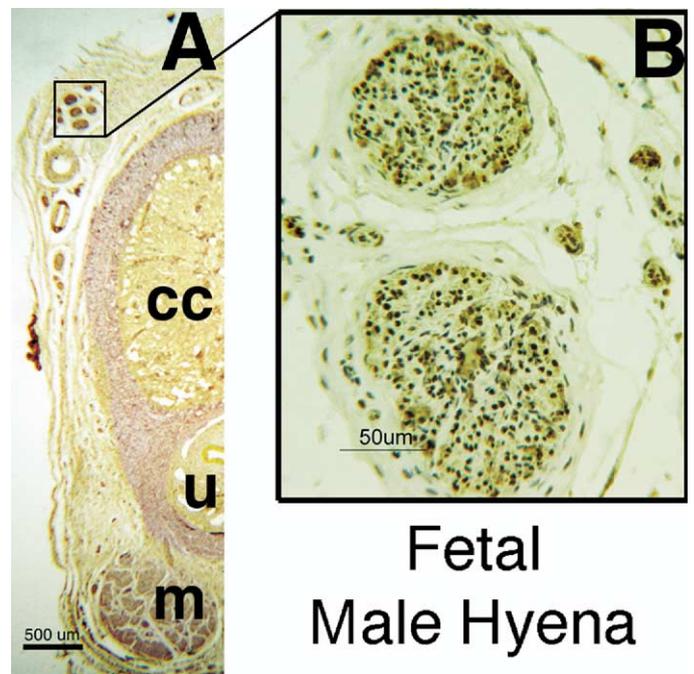


FIG. 7. S-100 immunostaining of male fetal spotted hyena penis. *A*, note location of dorsal nerve of penis (small rectangle), corpus cavernosum (cc), urethra (u) and retractor muscle (m). *B*, higher magnification reveals cytoplasmic staining of nerves by S-100 antibody.

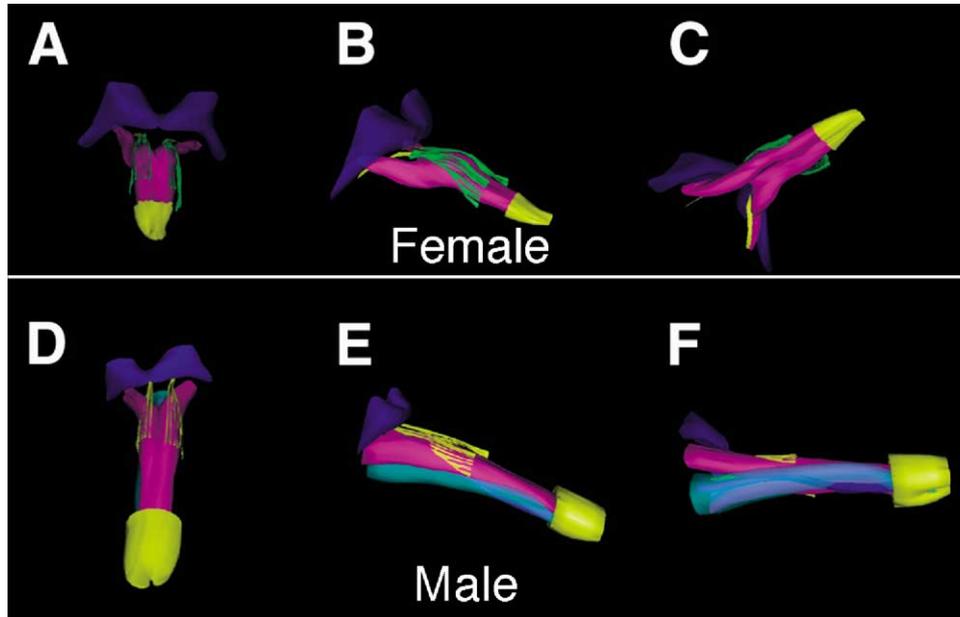


FIG. 8. 3D computerized reconstruction of 32-week human fetal clitoris and penis, derived from serial sections immunostained with neuronal marker S-100. *A to C*, female. *D to F*, male. Note pubic arch (purple), clitoral/corporeal body (magenta), glans (yellow), corpus spongiosum and urethra in male (turquoise), dorsal nerve of clitoris (green) and dorsal nerve of penis (yellow). Note midline 12 o'clock position is nerve-free in clitoris and penis.

between the corporeal/clitoral body and urethra/common urogenital sinus. Based on these observations, care should be taken when dissecting the ventral aspect of the tunica of the corporeal/clitoral body to avoid damaging the lateral branches of the dorsal nerve (figs. 3 and 5).

Historically, the enlarged clitoris or phallic structure in humans was treated with amputation.<sup>15</sup> Subsequently, more refined techniques such as recession clitoroplasty were developed. To achieve this goal, Spence and Allen proposed subtotal resection of the clitoral shaft.<sup>16</sup> Our neuroanatomical studies have demonstrated that clitoral reduction (when indicated) should be done by incising the corpora cavernosa on the ventral surface or at the 6 o'clock position to remove erectile tissue preserving the clitoral nerves over the tunica (fig. 5, *A to C* and fig. 9, *A to C*).<sup>1,2</sup> The enlarged clitoris of the female spotted hyena showed a similar pattern of dorsal nerve distribution to that of the normal human clitoris (fig. 6). The main difference between the course of the dorsal nerves in the normal human clitoris and the enlarged hyena clitoris was the extensive lateral deviation of the neurovascular bundle in the hyena as the dorsal nerve coursed from the junction of the crural bodies onto the corporeal body (figs. 6 and 9, *A to C*).

Glandular reduction is another controversial area in feminizing genitoplasty surgery. In the normal human clitoris the glans is a separate structure covering the distal ends of the clitoral body. The innervation of the glans comes from an extension of the dorsal nerves that pierce the glans (fig. 5, *A to C*).<sup>1,2</sup> In the spotted hyena the glans size in the clitoris was comparable to that of the penis, consistent with the more severe forms of clitoromegaly.

In the spotted hyena clitoris the innervation of glans was mainly from the dorsal nerve coursing on the lateral aspect of the clitoral body (fig. 3, *A to D*). It is unclear whether this is the case in the hypertrophied human clitoris. Investigation of glandular reconstructive surgery

has revealed that nerves are clearly present in the resected clitoral glans.<sup>2</sup> To avoid injury to the clitoral glans, consideration should be given to avoid any reduction surgery. However, if clitoral reduction surgery is deemed necessary, the incision should be at the 6 o'clock position to avoid the lateral aspect of the glans where the nerves course distally.

Presumably, the dorsal nerve of the hyena clitoris is stimulated by erection, or distention of the urogenital sinus during mating or delivery, as well as by physical contact with the external surface of the clitoral shaft and glans. Erection of the clitoris (or penis) is a routine event in non-sexual social interactions among spotted hyenas, constituting a critical element in the hyena "meeting ceremony."<sup>17</sup> According to traditional hyena etiquette, the subordinate hyena (male or female) lifts its leg and offers its erect phallus for inspection by the dominant animal.<sup>18</sup> The dominant animal may or may not reciprocate. Although olfactory investigation predominates, there is often contact with the nose or tongue of the partner. It would seem essential that sensory information regarding its own erection, as well as investigatory contact by a partner, be available to the subordinate animal.

Mild distention of the urogenital sinus occurs during urination. Male and female spotted hyenas squat and expel a stream of urine toward the ground. However, substantially greater distention occurs during mating.

When receiving the male the female spotted hyena assumes an immobile upright stance, with deviated tail.<sup>8,9</sup> The clitoris is not visible, having been withdrawn into the abdomen through the action of the retractor muscles.<sup>14</sup> Then, the male "flips" the semierect penis toward the abdomen of the female, until he locates the preputial point of entry and begins thrusting.<sup>8,9</sup> At least in nulliparous females the male inserts the erect penis into the urogenital meatus, at the tip of the glans clitoris. We can infer such entry from permanent

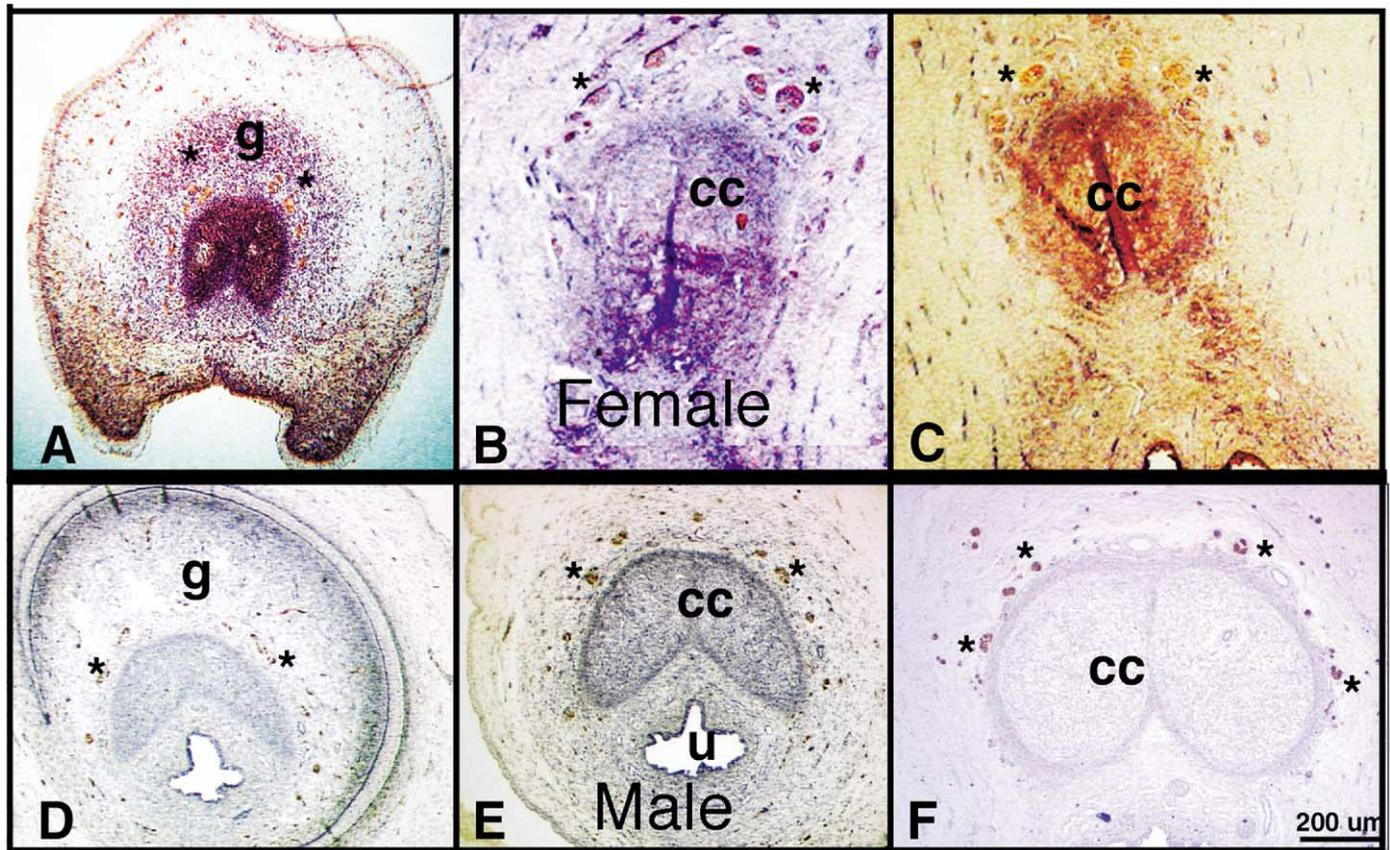


FIG. 9. Representative serial sections of 32-week female and male human fetal clitoris and penis immunostained with neuronal marker S-100. A to C (top row) and D to F (bottom row) are clitoris and penis, respectively, oriented distal (left) to proximal. *g*, glans. *cc*, corpus cavernosum. Asterisks indicate dorsal nerve of clitoris and penis. Note absence of nerves at 12 o'clock position in female and male. Bar represents 200 microns.

stretching of the urogenital meatus, observed after the first copulatory experience of a virgin female.<sup>19</sup> After the cessation of thrusting (associated with ejaculation) the male remains inserted, and rests his head and forequarters on the back of the female.

From the time of initial insertion until the male dismounts the female remains immobile for a period of approximately 5 minutes. We might assume that stimulation of the dorsal clitoral nerve would accompany thrusting, and continue during the prolonged period of postejaculatory insertion (when the glans penis swells and "locks" the male to the female). Information transmitted by the dorsal nerve of the clitoris could serve to maintain the immobile standing posture of the female spotted hyena, much as stimulation of the flanks and pudenda of the female rodent serves to maintain lordosis.<sup>20</sup>

Finally, extraordinary distention of the urogenital sinus occurs during the birth process.<sup>21</sup> Passage of a 1.3 kg fetus through the shaft of the clitoris, and expulsion through the clitoral meatus (which tears at the time of initial parturition<sup>22</sup>), requires precise sensory feedback to trigger appropriate contractions of urogenital musculature (fig. 1). It seems likely that such feedback involves the dorsal nerve of the clitoris.

## CONCLUSIONS

We have defined the neuroanatomy of the external genital of the spotted hyena, *Crocuta crocuta*, a naturally occurring an-

imal model of masculinization of the external genitalia with a common urogenital sinus. The dorsal nerves are distributed on the virilized clitoris of the spotted hyena in a similar fashion to the normal human clitoris. The anomalous enlargement of the clitoris does not seem to change the pattern of dorsal nerve distribution other than early and exaggerated lateral coursing of the nerves around the corporeal body.

## Abbreviations and Acronyms

3D = 3-dimensional

## REFERENCES

1. Baskin, L. S., Erol, A., Li, Y. W., Liu, W. H., Kurzrock, E. and Cunha, G. R.: Anatomical studies of the human clitoris. *J Urol*, **162**: 1015, 1999
2. Baskin, L. S.: Anatomical studies of the female genitalia: surgical reconstructive implications. *J Pediatr Endocrinol Metab*, **17**: 581, 2004
3. Matthews, L. H.: Reproduction in the spotted hyaena, *Crocuta crocuta* (Erxleben). *Philos Trans R Soc Lond B Biol Sci*, **230**: 1, 1939
4. Neaves, W. B., Griffin, J. E. and Wilson, J. D.: Sexual dimorphism of the phallus in spotted hyaena (*Crocuta crocuta*). *J Reprod Fertil*, **59**: 509, 1980

5. Cunha, G. R., Wang, Y., Place, N. J., Liu, W., Baskin, L. and Glickman, S. E.: Urogenital system of the spotted hyena (*Crocuta crocuta* Erxleben): a functional histological study. *J Morphol*, **256**: 205, 2003
6. Drenth, J. J.: The story of the spotted hyena and the hermaphrodite: biological order and enigma. *J Psychosom Obstet Gynaecol*, **21**: 121, 2000
7. Frank, L. G., Weldele, M. L. and Glickman, S. E.: Masculinization costs in hyaenas. *Nature*, **377**: 584, 1995
8. Schneider, K. M.: Enige bilder zur paarung der fleckenhyaene, *Crocotta crocuta* Erxl. *D Zool Garten*, **19**: 135, 1952
9. Drea, C. M., Coscia, E. M. and Glickman, S. E.: Hyenas. In: *Encyclopedia of Reproduction*. Edited by E. Knobil, J. Neill and P. Licht. San Diego: Academic Press, vol. 2, pp. 718–724, 1999
10. Hern, W. M.: Correlation of fetal age and measurements between 10 and 26 weeks of gestation. *Obstet Gynecol*, **63**: 26, 1984
11. Yucl, S., Cavalcanti, A. G., Wang, Z. and Baskin, L. S.: The impact of prenatal androgens on vaginal and urogenital sinus development in the female mouse. *J Urol*, **170**: 1432, 2003
12. Frank, L. G., Glickman, S. E. and Powch, I.: Sexual dimorphism in the spotted hyaena (*Crocuta crocuta*). *J Zool (Lond)*, **221**: 308, 1990
13. Glickman, S. E., Coscia, E. M., Frank, L. G., Licht, P., Weldele, M. L. and Drea, C. M.: Androgens and masculinization of genitalia in the spotted hyaena (*Crocuta crocuta*). 3. Effects of juvenile gonadectomy. *J Reprod Fertil*, **113**: 129, 1998
14. Baskin, L. S., Erol, A., Li, Y. W. and Cunha, G. R.: Anatomical studies of hypospadias. *J Urol*, **160**: 1108, 1998
15. Gross, R. E., Randolph, J. and Crigler, J. F., Jr.: Clitorectomy for sexual abnormalities: indications and technique. *Surgery*, **59**: 300, 1966
16. Spence, H. and Allen, T.: Genital reconstruction in the female with adrenogenital syndrome. *Br J Urol*, **45**: 126, 1973
17. Kruuk, H.: *The Spotted Hyena: A Study of Predation and Social Behavior*. Chicago: University of Chicago Press, 1972
18. East, M. L., Hofer, H. and Wickler, W.: The erect 'penis' is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. *Behav Ecol Sociobiol*, **33**: 355, 1993
19. Coscia, E. M.: Unpublished data
20. Pfaff, D. W., Montgomery, M. and Lewis, C.: Somatosensory determinants of lordosis in female rats: behavioral definition of the estrogen effect. *J Comp Physiol Psychol*, **91**: 134, 1977
21. Frank, L. G. and Glickman, S. E.: Giving birth through a female clitoris—parturition and dystocia in the spotted hyaena (*Crocuta crocuta*). *J Zool (Lond)*, **234**: 659, 1994
22. Drea, C. M., Place, N. J., Weldele, M. L., Coscia, E. M., Licht, P. and Glickman, S. E.: Exposure to naturally circulating androgens during foetal life incurs direct reproductive costs in female spotted hyaenas, but is prerequisite for male mating. *Proc Biol Sci*, **269**: 1981, 2002