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THE FEMALE EXTERNAL GENITALIA OF THE SPOTTED HYENA

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The female genitalia of the spotted hyena (*Crocuta crocuta* Erxleben) have attracted widespread attention among zoologists since they were first described by Watson in 1877 from an immature individual. Several careful morphological studies (along with a good deal of unbridled speculation) have appeared since Watson's original work. Matthews (1939) has recently made a masterly study of the reproductive system of this animal at various stages of pre- and postpubertal development, and of its sexual cycle. His work, for which he personally collected 63 males and 40 females in Tanganyika, has cleared up most of the morphological questions surrounding this curious structure.

It is strange, however, that despite the attention that has been lavished on the reproductive organs of the spotted hyena during the past 70 years, the external genitalia of the adult female have never been adequately illustrated. The internal reproductive organs of the female are in no way remarkable, and interest therefore centers around the external genitalia. Watson's specimen was immature and had been removed from the body before he received it, and the lithograph accompanying his description is not entirely satisfactory. This is true also of the lithograph in Chapman's (1888) paper. Perhaps the best illustrations are the photographs in Neuville's (1936a, b) studies, but even these leave much to be desired.

Recently Chicago Natural History Museum received the body of an old adult female *Crocuta crocuta* from the Lincoln Park Zoo of Chicago, for which thanks are due Mr. R. Marlin Perkins, the Director of the zoo. This individual had been in captivity for many

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years, and had borne young. The body was excellently embalmed by the General Biological Supply House, of Chicago, which permitted examination of the organs fixed in situ. The genitalia of this individual agree fairly closely with Matthews' description of the parous female.

The perineal region (fig. 68) is a well-defined, ovoid, essentially hairless area situated between the thighs and in front of the anus. This area is 175 mm. in length and 75 mm. in greatest breadth. Anteriorly the preputial part of the perineal integument hangs loosely from the belly wall like the preputial pouch of the male. The preputial opening is a longitudinal aperture, 45 mm. in length, in the antero-ventral surface of this pouch. The clitoris does not protrude from the opening, as it does in younger animals.

The perineal region is sharply divided into three areas. The anterior third (the "prepuce" of Matthews) is sparsely haired, and is prominently pitted with numerous gland openings, situated about 2 mm. apart. These openings become increasingly large posteriorly, the most posterior ones having a diameter of a millimeter or more. This glandular area is sharply delimited posteriorly, and is followed by a central region about 50 mm. wide that is devoid of glands and is entirely hairless. Matthews says that the abdominal hair is carried across at the juncture of these two regions, but no such hair is present in our specimen. The central naked area shows a tendency to be thrown up into transverse folds or wrinkles. There is no indication whatever of a median raphe such as Neuville described. Behind the naked area there is a third sharply delimited region. This is the region of the so-called "scrotal swellings." Anteriorly it is pitted like the preputial region, and everywhere it is well covered with rather short hairs. The "scrotal" swellings, (which contain only fat and connective tissue) are situated on either side of the midline, and each is divided into an anterior and posterior prominence, as described by Neuville and Matthews. Pigmentation stops abruptly at the posterior border of the "scrotal" swellings, and this line is separated by 17 mm. from the anus.

The anus is a puckered vertical opening above the posterior border of the "scrotal" swellings. The anus and the outlet of the anal pouch are in the center of an area covered with short, thinly spaced hairs. Immediately above the anus, so that the two together form a T, is the transverse opening, 20 mm. in width, of the anal pouch. The pouch is a purse-shaped cavity about 30 mm. deep and 55 mm. wide, lying on top of the rectum. It is lined with short hairs except

along its anterior wall. At the bottom of the pouch, directly opposite its mouth, is a regular transverse line of openings representing the outlets of a row of small anal glands. There are thirteen of these openings, regularly spaced about 3 mm. apart, with two or three additional openings above the line at either end. Ventrad of this

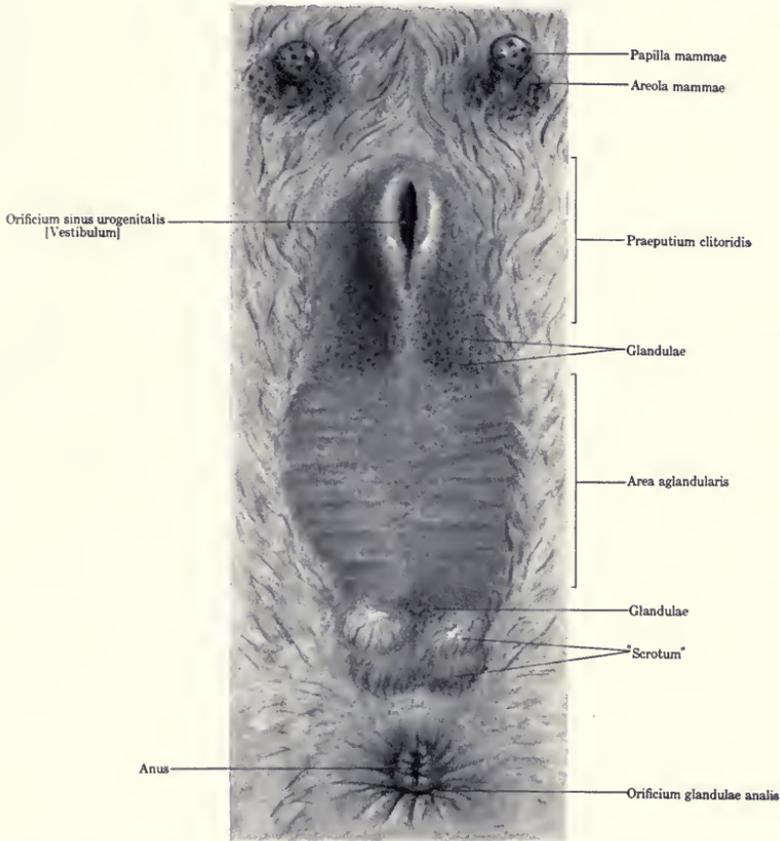


FIG. 68. External genitalia of old parous female *Crocota crocuta*, ventral view. The anus is pulled apart slightly to expose the outlet of the anal pouch. $\times \frac{1}{2}$.

row, at either corner of the pouch, is the much larger opening of the pair of large anal glands.

When the perineal region is opened (fig. 69), an extensive urogenital sinus extending almost the entire length of the perineal region is revealed. The backwardly-directed clitoris is situated prominently at the mouth of the sinus, and posteriorly the sinus arches up around the posterior border of the pubis to enter the body cavity.

The anterior or "preputial" part of the urogenital sinus is lined with pigmented epithelium similar to that on the outer surface; the outer skin is reflected around the lips of the urogenital opening and continued on the inside. The pigmentation stops abruptly at the distal border of the frenum of the clitoris, where it meets the unpigmented mucous membrane covering the ventral surface of the frenum and lining the remainder of the sinus. In the sinus the mucous membrane is thrown up into irregular, more or less longitudinal, folds. The abdominal part of the sinus is 105 mm. in length, and becomes increasingly narrow posteriorly, so that it is a narrow canal only about 8 mm. in diameter where it passes dorsad into the abdomen. The urethra, as noted by Matthews, opens into the urogenital sinus far proximally, only about 13 cm. from the os uteri.

The clitoris is directed backward. It is a prominent finger-like structure, its free part measuring about 50 mm. in length and 20 mm. in transverse diameter. The skin over the clitoris is loose and baggy, and ventrally it extends out on either side into an extraordinarily large wing-like frenum, which is carried anteriorly beyond the tip of the glans. The frenum is truncated anteriorly, where it has a width of 35 mm., and its dorsal surface is pigmented like the lining of the prepuce, its ventral surface (actually the distal part of the dorsal wall of the urogenital sinus) unpigmented like the lining of the sinus. The frenum is not split longitudinally, as Matthews says is characteristic for the parous female. Actually, of course, the wing-like flaps of the frenum represent the labia minora.

Matthews has shown clearly the age changes that take place in the relations of the frenum. In the prepubertal female it is scarcely larger than the frenulum of the male and the clitoris is directed forward. The urogenital meatus, situated at the tip of the glans, is thus "similar in appearance and position to the urethral meatus of the male." It is to be noted, however, that the similarity to the meatus of the male is more apparent than real. Contrary to what has repeatedly been stated, the urogenital canal does *not* perforate the clitoris like the male urethra; it lies *beneath* the clitoris in the normal way, and the masculine-appearing meatus in the young female is the temporarily much restricted outlet of the urogenital sinus; the labia minora have not yet developed. In the nulliparous adult female the frenum hypertrophies and becomes "slack and baggy," with a corresponding increase in the size of the meatus. Finally, in the parous female there is further hypertrophy of the frenum, until in the condition represented by our specimen (where the clitoris is

apparently normally directed backward in the unerected state) the outlet of the urogenital sinus bears no resemblance to the urethral meatus of the male, and a pair of well-developed labia minora are present. Thus the resemblance to the male, which is deceptively

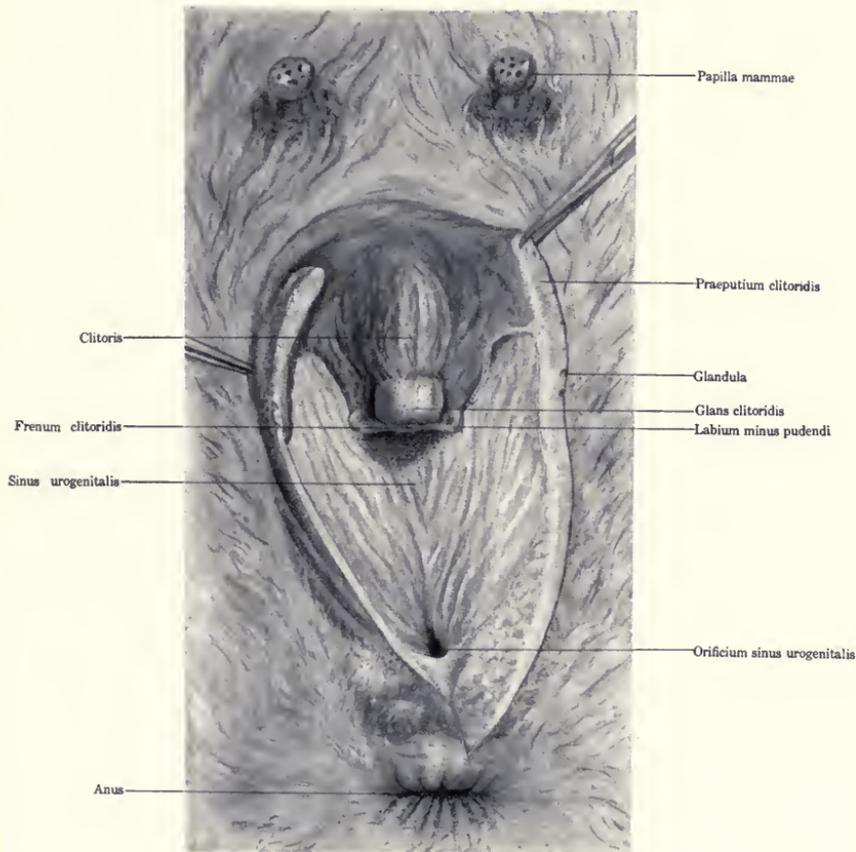


FIG. 69. The same individual shown in figure 68, the urogenital sinus exposed by an incision to the right of the midline.

close in young animals, becomes increasingly less with further sexual development.

The glans of the clitoris is well defined. It is cylindrical, truncated distally, and exhibits a prominent dimple in the center of its free end. The surface, except anteriorly, and ventrally where the frenum attaches, is covered with short, backwardly-directed, unpigmented spines.

The two nipples are situated 65 mm. apart and 40 mm. in front of the urogenital opening. Each is a more or less globular structure set on a short, heavy peduncle, with seven or eight conspicuous openings scattered irregularly over its distal surface. The nipple and a hairless areola about 35 mm. in diameter surrounding it are pigmented like the perineal skin. The areola is pitted with numerous gland openings, similar to those on the prepuce, situated about 3 mm. apart.

Nearly every investigator who has studied the female genitalia of the spotted hyena has made a more or less careful comparison and homologization of its parts with the external genitalia of the male. Impressed by the astonishingly close correspondence he was able to demonstrate, each has then proceeded to "explain" it. The interpretations follow fairly closely the changing vogues of research in experimental biology, and the final result is more than a little reminiscent of the fable of the blind men and the elephant. Thus, Chapman (1888) attributes it all to "arrested development." Grimpe (1917) concludes that it is clearly "a striking secondary approximation of sexual characters," such as is found, for example, in the antlers of female reindeer! Neuville (1936a) is satisfied with labeling it an atypical state of development leading to partial hermaphroditism, but later (1936b), after recounting a case of pseudohermaphroditism in man, he concludes that the "mimetic" convergence of the female spotted hyena toward the male is a "freak of nature." Matthews (1939) suggested more recently that "the peculiar male facies of the female may be produced by an excess of androgenic substance, accompanied probably by a deficiency of oestrogenic ones, derived from the ovary," and pointed out the resemblance between the conditions in the normal female *Crocuta* and those found elsewhere in cases of "adrenal virilism." Watson (1877), and Schmotzer and Zimmermann (1922), merely described their findings.

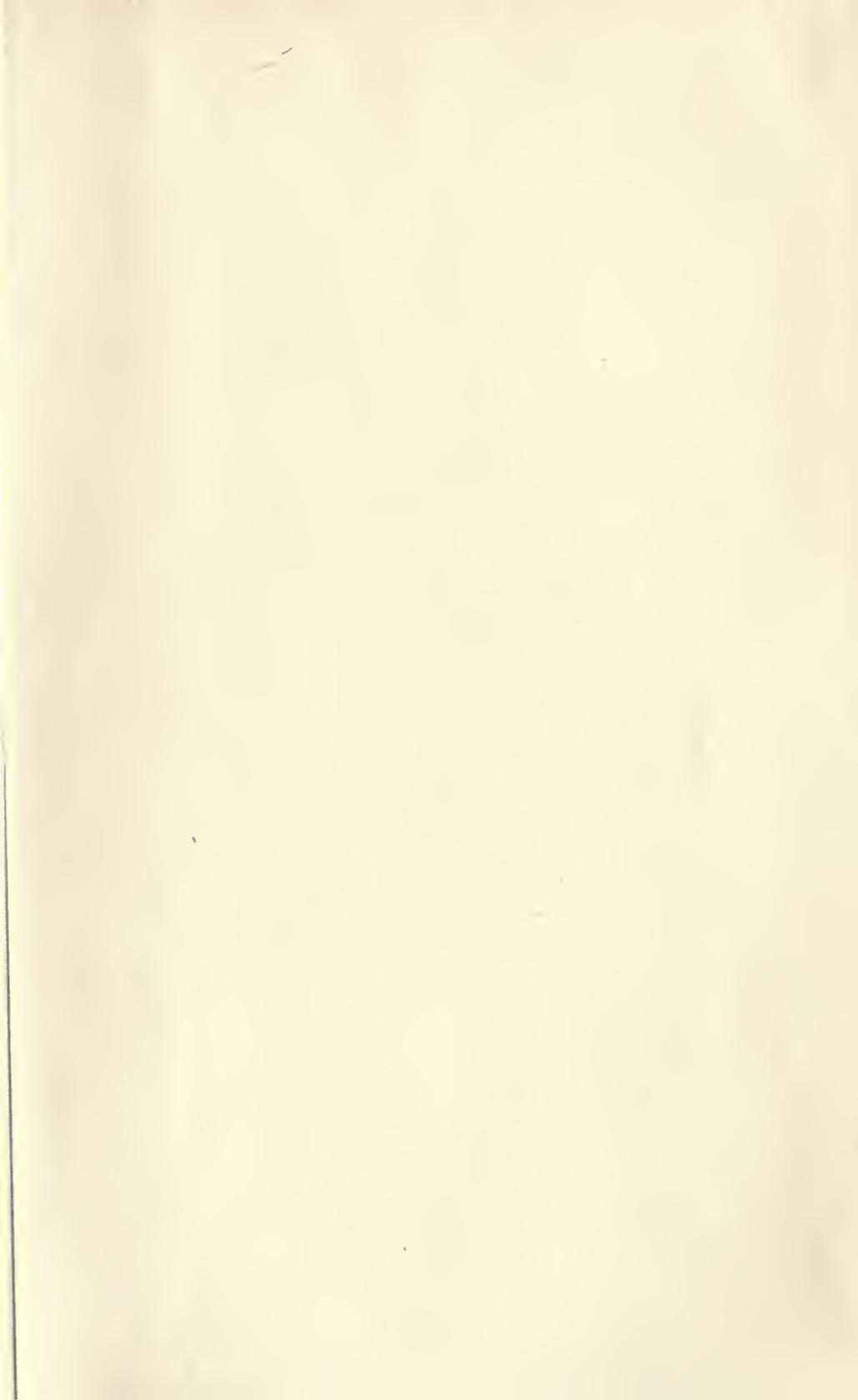
It is generally agreed that the closest living relatives of the Hyaenidae are the Viverridae. Unfortunately the anatomy of the civets is very inadequately known. If, however, the female genitalia of *Crocuta* are compared with those viverrids in which they are known in detail, most of the mystery and *all* the uniqueness are dispelled. Lönnberg, describing the female genital organs of *Cryptoprocta*, long ago pointed out their striking similarity to the corresponding organs of *Crocuta*. Indeed, now that the often repeated misstatement that in *Crocuta* the clitoris is perforated by the urogenital canal has been corrected, the resemblance is known to be even closer than Lönnberg suspected. *Cryptoprocta* even has the

"scrotal swellings" that have so astonished anatomists, and is even more "masculine" than *Crocota* in having a "very well developed ossicle which extends from the extreme tip to the base of the clitoris." Even in *Arctictis binturong* (Story, 1945), where the form of the genitalia is somewhat modified by the presence of large scent glands, the structure of the female genitals is fundamentally similar to that of *Crocota*.

This resemblance between *Crocota* and certain viverrids does not, of course, account for the difference between the female genitalia of *Crocota* and the more "normal" genitalia of *Hyaena*. The Viverridae are the most primitive of living carnivores. Either *Crocota* has retained a more primitive form of the genitalia than *Hyaena*, or *Hyaena* and *Crocota* have arisen independently from separate viverrid stocks. The latter alternative does not appear probable.

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