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Descriptive and Functional Morphology of the Locomotory Apparatus of the Spotted Hyaena (*Crocuta crocuta*, ERXLEBEN, 1777)

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With 3 Figures and 3 Tables (Accepted September 15, 1987)

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Abstract

The musculature of the limbs, neck and back of *Crocuta crocuta* is described and some functional aspects are discussed. The myology of *C. crocuta* generally corresponds with that of *H. hyaena*. Both species show adaptations to lifting and carrying heavy loads, but the larger size and more robust morphology of *C. crocuta* enables it to master larger prey than *H. hyaena*. A remarkable over-extension of the tarsus in *C. crocuta* is described which was observed both in the cadaver and in vivo, during the gallop.

Introduction

The body proportions and the locomotion of the spotted hyena *(C. crocuta)* were discussed in SPOOR (1985) and SPOOR and BELTERMAN (1986), respectively. This paper describes the myology of the limbs, neck and back and some of their functional aspects. Previous descriptions of the myology of the spotted hyena were given by WATSON and YOUNG (1879), BUCKLAND-WRIGHT (1969) and GOMERCIC (1985).

Material and Methods

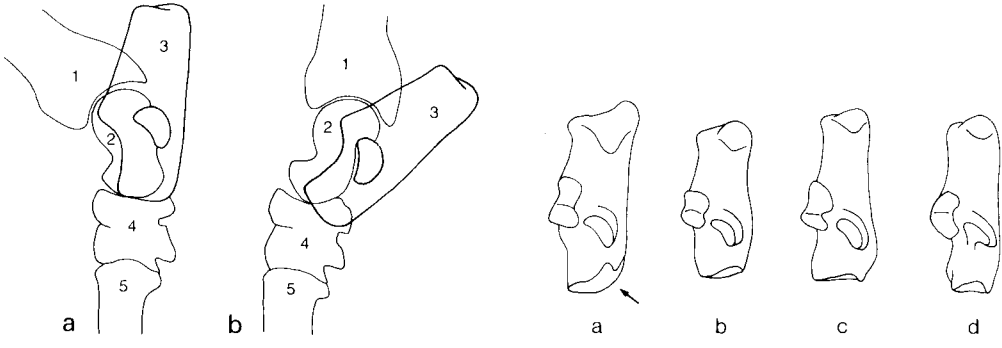
This paper is based on the dissection of an adult female of *C. crocuta* which was obtained from Artis Zoo (Amsterdam). The animal measured 128 cm from the tip of the nose to the anus and weighted 630 N (the visceral organs excluded). Only those muscles are described which are judged to differ significantly from those in *H. hyaena* (SPOOR, BADOUX 1986a, 1988). The relative weight of the wet limb muscles expressed as a percentage of the total weight of the forelimb or hindlimb muscles was calculated. Comparative measurements (DUERST 1926) from the limb bones of Hyaenidae, Canidae and Felidae from the collection of the Rijksmuseum van Natuurlijke Historie, Leiden were taken to the nearest millemetre with Vernier callipers. Motion pictures of *C. crocuta* at Artis Zoo (Amsterdam) and Amersfoort Zoo and of *H. hyaena* at Burgers Zoo (Arnhem) were analysed (technical references see SPOOR and BELTERMAN 1986). Additional dissections of the tarsus in various carnivores were made.

Description

The M. cleidocervicalis, M. sterno-occipitalis, sternomastoideus and cleidomastoideus are cranially fused to a single flat muscle which inserts along the entire nuchal crest and the mastoid part of the temporal bone. The M. biventer cervicis and the M. complexus are completely fused on the

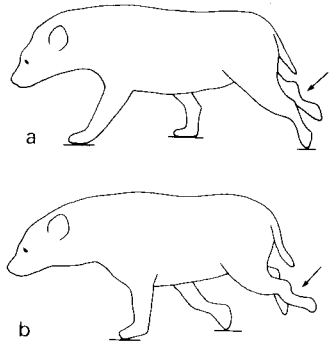
left but are seperate on the right side. As in *H. hyaena* the M. biventer cervicis and the M. longissimus cervicis have a strong origin from the spinous process of the second and third thoracic vertebrae. However, in *C. crocuta* the M. longissimus capitis and the M. longissimus atlantis lack such an origin and the latter is partly fused with the M. complexus.

The most caudal fibres of the M. latissimus dorsi originate from the lumbar fascia and not from that from the ilium as in *H. hyaena*. The 2 almost completely separated heads of the M. extensor digitorum lateralis send tendons to the third and fourth and the fifth digit. The M. flexor digiti brevis is not present on the lateral tendon of the M. flexor digit. superficialis. The M. interflexorius is equally developed as in *H. hyaena* and reveals a proximal tendinous origin from the medial epicondyle of the humerus. There are 4 well-developed Mm. lumbricales.



Figs. 1 a, b. Drawing after a radiograph of the left tarsus of *Crocuta crocuta*, a. normal and b. over-extended position. 1 – tibia, 2 – talus, 3 – calcaneus, 4 – tarsal bones (1–4, c) 5 – metatarsal bones.

Figs. 2 a–d. Medial aspect of the calcaneus of a. *Crocuta crocuta*, b. *Hyaena hyaena*, c. *Canis lupus* d. *Panthera pardus*.



Figs. 3 a, b. Silhouettes of a galloping *Crocuta crocuta*. a. beginning of the swing phase of the left hindfoot and b. 1/17 s later.

The M. psoas minor is situated on the ventral side of the last (fifteenth) thoracic and first 2 lumbar vertebrae. The M. psoas major arises from the third lumbar vertebrae to the sacrum and with a seperate head from the fascia from the last rib. The latter head is less-developed than in *H. hyaena*. The M. biceps femoris is entirely fused with the M. gluteofemoralis. The M. gluteus profundus consists of one head. The M. quadratus femoris is developed as in the domestic dog and cat. The M. obturator internus is fused with the Mm. gemelli. There are 3 Mm. interflexorii in the hindlimb, with tendons to digits II, III and IV. A M. flexor digiti V brevis is present, which extends from the proximal end of the fifth metatarsal bone to the lateral side of the head of the proximal phalanx. The M. abductor digiti V is muscular on the dorsal and tendinous on the plantar side.

In the fresh cadaver of the spotted hyena a remarkable extension (plantar flexion) in the hindfoot was noticed. The metatarsus could be extended to an angle of around 70 degrees to the calcaneal tuber. Radiographs of the (embalmed) crus show that this over-extension entirely occurs in the joints between the talus and central tarsal and the calcaneus and the fourth tarsal bone (Fig. 1). The ability of these joints to perform this movement is related to the shape of their articular surface and ligaments. The plantar half of the articulation surfaces of the calcaneus and the fourth tarsal bone are both sagittally convex in *C. crocuta,* while they are approximately flat in other large carnivores, which hardly allows over-extension (Fig. 2). The oval-shaped articulation surface for the central bone of the talus is more transversely oriented in *C. crocuta* than that in other large carnivores. In these aspects *C. crocuta* differs more from species of Canidae, than from some species of Felidae and *H. hyaena.* In *Canis familiaris* (and *Ursus americanus* and *Meles meles*) over-extension of the joints under consideration is prevented by strong ligamentous reinforcements of the tarsal joint capsule. The 2 most important extend from the distal end of the lateral ridge of the talus to the proximal end of the third metatarsal bone (distal part of proximal extensor retinaculum) and from the dorso-distal end of the calcaneus to the fourth tarsal and metatarsal bone. In *Felis catus* and *Acinonyx jubatus* these reinforcements are less developed, especially that between the talus and the third metatarsal bone, and in *C. crocuta* they are absent. Motion pictures of *C. crocuta* show that this over-extension occurs in the first half of the swing phase (protraction) of the hindlimb during the gallop (Fig. 3). The tarsal movement can also be seen in the silhouettes of a galloping *C. crocuta* given by KINGDON (1977). Only a single film fragment of the gallop of *H. hyaena* is available to us in which no over-extension could be observed.

Discussion

The myology of the spotted hyena generally corresponds with that of the striped hyena as described by SPOOR and BADOUX (1986a). The comparison between the relative weights of the muscles of the forelimb and hindlimb of *C. crocuta* and those of *H. hyaena* (after SPOOR and BADOUX, 1986a, 1988) and various Canidae and Felidae (after GAMBARYAN 1974; DAVIS 1949) is given in Tables 1 and 2. The M. brachiocephalicus of *C. crocuta* is relatively thin, covering the extraordinary well-developed extensors of the neck, which render the hyenas their massive neck. However, no comparative data of the relative weights of these muscles in the Canidae and Felidae are available. The M. biventer cervicis and the M. longissimus cervicis of both *C. crocuta* and *H. hyaena* have the characteristic origin from the spinal process of the second and third thoracic vertebra, which renders these extensors of the neck an optimal lever arm. The M. trapezius, M. rhomboideus and M. serratus ventralis, which attach the scapula to the trunk are better developed in *C. crocuta* than in *H. hyaena* (Table 1). The M. interflexorius and M. flexor digit. profundus have a strong tendinous sheet, however, the tendinous intersections are not as well developed as observed by GOMERCIC (1985). This author correctly describes the former muscle as the M. flexor digit. superficialis and the M. flexor digit. superficialis (according to the N.A.V.) as the M. palmaris longus (SPOOR, BADOUX 1986b). However, he erroneously homologizes the M. palmaris longus in *C. crocuta* with the M. interflexorius in the domestic dog. In the hindlimb the gluteal muscles and the M. biceps femoris/M. gluteofemoralis which are better developed in *H. hyaena* than in Canidae and Felidae, are even larger in *C. crocuta.* These muscles, in combination with the relatively long os femoris, are powerful stabilizers and retractors of the hindlimb. The M. psoas minor and the M. quadratus femoris which were poorly developed in *H. hyaena,* have the same relative weight in *C. crocuta* and species of Canidae and Felidae. Since the *H. hyaena* has 4 and *C. crocuta* 5 lumbar vertebrae, the difference in development of the M. psoas minor (a flexor of the lumbar spine) might be related to the different relative length of the lumbar region in the 2 species.

The limbs of *H. hyaena* are relatively longer than those of *C. crocuta,* a difference which is largely related to the difference in body size (SPOOR 1985). The limb bones of *C. crocuta* are notably more massive than those of *H. hyaena* and Canidae and Felidae of comparable size (Table 3). Various articulation surfaces of the limb bones have a characteristic shape in the Hyaenidae, which

Table 1. Relative weight of the muscles of the forelimb of *Crocuta crocuta* and their relation to those of *Hyaena hyaena* (SPOOR, BADOUX 1986a) and various species of Canidae and Felidae (GAMBARYAN 1974; DAVIS 1949). < smaller, > larger and = equal.

	C. crocuta	in relation to *H. hyaena*	Canidae	Felidae
M. brachiocephalicus	7.5	<	>	=
M. cleidocervicalis (3.7)				
M. cleidomastoideus (1.5)				
M. cleidobrachialis (2.3)				
M. trapezius	3.5	>	>	=
M. rhomboideus	2.9	>	=	=
M. latissimus dorsi	12.0	=	>	>
M. sternomast./occ.	5.0	=	≫	≫
Mm. pectorales superf.	3.5	=	≦	<
M. pectoralis profundus	7.8	=	<	<
M. serratus ventralis	11.0	>	>	>
M. omotransversarius	1.7	<	=	>
M. deltoideus	1.6	<	<	≦
M. supraspinatus	5.1	=	<	=
M. infraspinatus	5.7	=	>	≧
M. subscapularis	3.2	=	<	<
M. teres major	2.1	>	=	<
M. teres minor	0.1	<	=	<
M. coracobrachialis	0.1	=	≦	=
M. triceps brachii				
Caput longum	10.0	>	=	≧
Caput lat./acc. (4.5)				
Caput mediale (0.7)				
M. tens. fasc. antebr. (0.3)				
M. anconeus (0.3)	5.8	<	<	=
M. biceps brachii	1.4	=	<	<
M. brachialis	1.7	=	>	≧
M. pronator teres	0.2	=	=	<
M. supinator	0.1	=	=	<
M. extensor carpi radialis	1.4	=	=	=
M. extensor digit. com. (0.6)				
M. extensor digit. lat. (0.3)				
M. extensor digit. I (0.03)	0.9	=	=	≦
M. abductor digit. I long.	0.3	=	=	<
M. extensor carpi ulnaris	0.7	=	=	=
M. flexor carpi ulnaris	1.2	=	>	=
M. flexor carpi radialis	0.4	=	=	=
M. flexor digit. superf.	0.3	=	<	<
M. flexor digit. prof./M. interflexorius	2.8	<	=	<

contributes to the stabilization of the joints and enables the transmission of large forces (SPOOR, BADOUX 1986a, 1988).

The over-extension of the hindfoot in *C. crocuta* seems to contradict the stability in the joints; however, the extensor effect of the propulsive forces in the tarsal joints is sufficiently counteracted by te tension of the plantar ligaments of the tarsus. Analysis of the motion pictures suggests that the over-extension occurs as a completely passive result of inertia on the hindfoot during the protraction of the hindlimb. The functional aspects of over-extension during the swing phase of the gallop is not yet understood. It may be related to the difference in forelimb and hindlimb length and

Table 2. Relative weight of the muscles of the hindlimb of *Crocuta crocuta* and their relation to those of *Hyaena hyaena* (SPOOR and BADOUX, in press) and various species of Canidae and Felidae (GAMBARYAN, 1974). > larger, < smaller, = equal.

	C. crocuta	in relation to *H. hyaena*	Canidae	Felidae
M. iliopsoas	3.9	<	=	=
M. psoas minor	1.2	>	=	=
M. gluteus superficialis	3.5	=	⩾	⩾
M. gluteus medius	9.8	>	⩾	⩾
M. gluteus profundus (1.0) M. piriformis (0.9)	1.9	=	>	≥
Mm. obturatorius int./ext./Mm. gemelli	2.3	=	=	=
M. quadratus femoris	0.4	>	=	=
M. sartorius	5.3	=	>	=
M. rectus femoris	3.1	<	<	<
Mm. vastus lat./int./med.	10.6	<	<	<
M. pectineus	0.9	=	≥	≥
M. gracilis	2.6	<	<	≤
Mm. adductores	9.1	<	≤	<
M. biceps femoris/M. gluteofemoralis	18.6	>	⩾	⩾
M. semitendinosus	5.2	>	≥	≥
M. semimembranosus	6.6	>	<	<
M. tibialis cranialis	2.5	>	>	=
M. extensor digit. longus	1.0	=	<	<
M. peroneus long./brev./ M. extensor digit. lat.	1.1	=	=	=
M. gastrocnemius	3.3	=	=	≤
M. flexor digit. superf.	1.5	<	<	<
M. flexor digit. prof./M. tibialis caudalis	2.2	=	=	=

Table 3. Index of robustness (sagittal midshaft diameter given as a percentage of the length between the proximal and distal articulation surfaces).

	humerus	radius	ulna	os femoris	tibia
Crocuta crocuta	14.9	7.4	10.7	8.4	13.4
Hyaena hyaena	12.7	5.6	6.6	7.0	10.7
Canis lupus	9.2	5.2	5.1	7.3	6.4
Panthera pardus	11.1	5.0	8.1	6.9	9.1

to the relatively minor importance of the sagittal back movements during the gallop. However, the morphology and the analysis of the filmfragment indicate that tarsal over-extension is absent in *H. hyaena,* which differs from *C. crocuta* by a smaller body weight and slightly longer limbs.

In general, the morphological adaptations to lifting and carrying large and heavy loads observed in *H. hyaena* (SPOOR, BADOUX 1986a, 1988), also occur in *C. crocuta.* As far as this study is concerned the more predatory and less scavenging way of life of *C. crocuta* when compared to *H. hyaena,* may only be related to the difference in length of the lumbar region and the development of the psoas minor, suggesting a more important role of the back during

fast locomotion in the former. The larger size and more robust morphology of *C. crocuta* enables it to hunt and master large prey, including the large ungulates.

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