

## Descriptive and Functional Myology of the Back and Hindlimb of the Striped Hyena (*Hyaena hyaena*, L. 1758)

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With 5 Figures and 2 Tables

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### Abstract

The musculature of the back and hindlimb of *Hyaena hyaena* is described and the functional implications of some morphological aspects of muscles and skeleton are discussed. The trunk is characterized by its robustness. The thoracic cage is wide and long, the lumbar spine is short and the sublumbar musculature is less developed than in Canidae and Felidae. The well-developed gluteal muscles, M. biceps femoris and Mm. adductores are, in combination with the long os femoris, powerful stabilizers and retractors of the hindlimb. The relatively wide and flat articulation surfaces enables the transmission of large forces between the joints of the hindlimb. This morphology is considered as an adaptation to stabilizing the body while the hyena carries large and heavy load.

### Introduction

The descriptive and functional myology of the neck and forelimb of the striped hyena was discussed in SPOOR and BADOUX (1986). This paper describes the muscles of the hindlimb and back and discusses their functional aspects. Previous descriptions of the myology of the striped hyena were given by MECKEL (1828), CUVIER and LAURILLARD (1850), YOUNG and ROBINSON (1889) and BUCKLAND-WRIGHT (1969), but those dealing with the limb myology do not give sufficient information for functional interpretation.

### Material and Methods

This paper is based on the dissection of the adult female of *Hyaena hyaena* which was already described in SPOOR and BADOUX (1968). The animal was obtained from "Burgers Dierenpark", Arnhem, the Netherlands, weighed 330 N and measured 106 cm from the tip of the nose to the anus. Dissection of various specimens of domestic dog and cat as well as descriptions of their musculature (EVANS, CHRISTENSEN 1979; NICKEL, SCHUMMER, SEIFERLE 1984; REIGHARD, JENNINGS 1930) served as reference for comparative myology. CUVIER and LAURILLARD (1850), WINDLE, and PARSONS (1898), BARONE (1967) and dissection of a cheetah (*Acinonyx jubatus*) provided information about the myology of Canidae and Felidae. Comparison is restricted to these families since they include species of about the same size as the Hyaenidae which also have cursorial locomotion. Only those muscles are described which are judged to be significantly different from those in the dog and cat. After removing the tendons the wet muscles were weighed 3 times to the nearest tenth of a gram in a period of a month. The mean values were used to calculate the relative weight of each muscle expressed as a percentage of the total weight of all muscles involved. Comparative measurements (DUERST 1926) were taken from bones of the spine and hindlimb of various species of Hyaenidae, Canidae and Felidae in the collection of the Rijksmuseum van Natuurlijke Historie, Leiden (Table 1). The measurements were taken to the nearest millimeter with Vernier callipers.

Table 1. Skeletal material of the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH)

Hyaenidae:	<i>Hyaena hyaena</i> : 575, cat. ost b, 35105 <i>Crocuta crocuta</i> : 35113
Felidae:	<i>Panthera pardus</i> : 449, 3445 <i>P. onca</i> : cat. ost. b, 2470 <i>Felis concolor</i> : 1145, 1944 <i>Uncia uncia</i> : 12898 <i>Acinonyx jubatus</i> : cat. ost. b
Canidae:	<i>Canis familiaris</i> : 1694, 2385 <i>C. latrans</i> : 3298, 3400 <i>C. lupus</i> : cat. ost. a, cat. ost. b <i>Cuon alpinus</i> : 945, 1727 <i>Lycyaon pictus</i> : cat. ost. a

## Description

### 1. Muscles of the trunk

Our specimen of *H. hyaena* has sixteen thoracic and 4 lumbar vertebrae. The *M. iliocostalis* and the *M. longissimus thoracis et lumborum* extend from the wings of the ilium to the first rib and the transverse process of the seventh cervical vertebra, respectively. The *M. spinalis et semispinalis thoracis* arises from the tendinous leaf covering the *M. longissimus thoracis* at the level of the fifteenth thoracic vertebra. Its cranial tendons insert on the spinous processes of the ninth thoracic to the sixth cervical vertebrae.

The *M. obliquus internus abdominis* is characterized by a strong muscular origin from the tuber coxae. The *M. quadratus lumborum* arises from the fourteenth thoracic vertebra and inserts on medial surface of the ilium (Fig. 1).

### 2. The muscles of the hindlimb

The areas of muscle attachment on the lateral aspect of the os coxae are shown in Fig. 2. Fig. 3 shows the lateral aspect of the superficial muscles of the thigh. The small muscular belly of the *M. psoas minor* is situated on the ventral side of the last thoracic and first two lumbar vertebrae (Fig. 1). Its weakly developed tendon inserts on the iliopubic eminence as in the dog and cat. The *M. iliopsoas* has 3 heads (Fig. 1). The *M. iliacus* originates on the ilium but not on the tendon of the *M. psoas minor*. The *M. psoas major* arises with a clearly isolated head from the last ribs and with a second head from all lumbar vertebrae and the sacrum.

The *M. tensor fascia latae* consists of a single head which corresponds with the cranial part of this muscle in domestic dog and cat. The well-developed *M. gluteus superficialis* lies between the *M. tensor fascia latae* and the *M. gluteofemoralis* (s. caudofemoralis). The thick caudal part has its origin from the sacrum, while the wide flat cranial part, which largely covers the *M. gluteus medius*, arises from the fascia which covers the latter muscle. Distally it continues entirely into the fascia latae. The *M. gluteus medius* has its origin from the entire lateral surface of the broad iliac wing and it strongly inserts on the trochanter major. The *M. piriformis* is well developed and largely fused with the *M. gluteus medius*. The *M. gluteus profundus* consists of 3 separate heads.

The well-developed *M. gluteofemoralis* has its origin from the first caudal vertebrae and its tendon of insertion runs along the cranial border of the *M. biceps femoris* to the patella. The caudal fibres of the broad *M. biceps femoris* run in distal direction and insert on the calcanean tendon. The *M. abductor cruris caudalis* is shaped as in the dog, but inserts together with the caudal fibres of the *M. biceps femoris* on the calcanean tendon. The *M. semimembranosus*, which consists of 2 heads, is notably less-developed than in the domestic dog and cat.

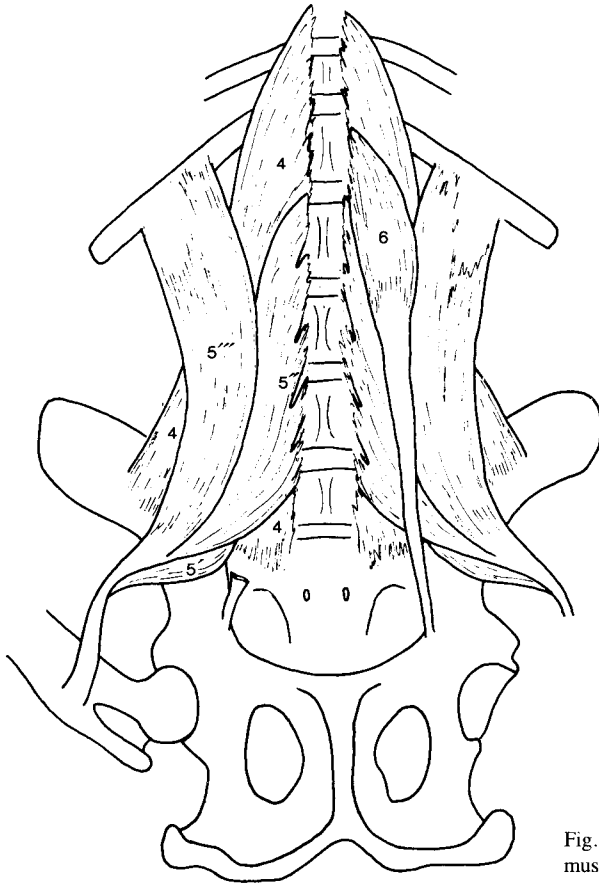


Fig. 1. Ventral aspect of the sublumbar muscles.

The 2 heads of the *M. sartorius*, one inserting on the patella and 1 on the tibial crest, are entirely separated. The weakly developed *M. gracilis* comes from a relatively small part of the symphysis pelvis. The subdivision of the *M. adductor magnus et brevis* is relatively clear. This muscle has a horseshoe-shaped origin on the os coxae around the *M. obturator externus*. The *M. quadratus femoris* is very weakly developed.

*H. hyaena* lacks the *M. extensor digiti I longus*. The *M. extensor digitorum brevis* has 3 heads. The tendon of the lateral head goes to digit IV, that of the middle head to digit III and that of the medial head to digit III in the right foot and to digits III and II in the left foot.

The distal tendon of the *M. flexor digitorum superficialis* does not comprise muscular fibres of the *Mm. flexor digitorum breves*. The distal tendon of the *M. flexor digiti I longus* consists of 2 flat tendons which fuse after passing the sustentaculum tali of the calcaneus. The superficial tendon is the continuation of the strong tendinous sheet covering the muscular belly, which itself ends in the deep tendon. There are 2 *Mm. interflexorii* with tendons to digits III and IV. Some additional tendonless muscle fibres on the medial side of the tendon of the deep digital flexor probably represent a third head. The left hindlimb has 3 *Mm. lumbricales*, which are lacking in the right hindlimb. The *Mm. adductores II and IV*, especially the former, are weakly developed.

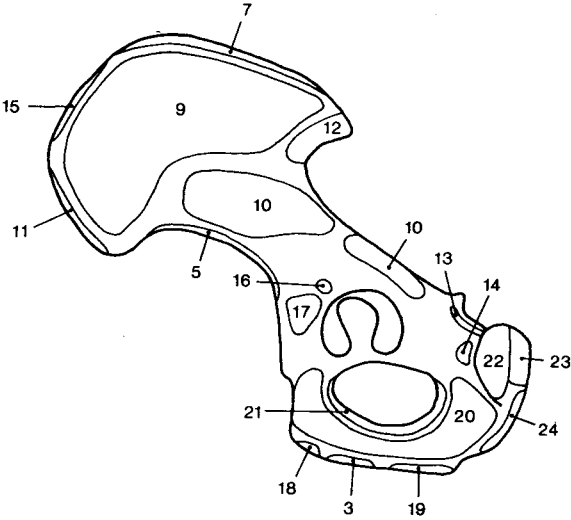


Fig. 2. Lateral aspect of the left os coxae showing areas of muscle attachment.



Fig. 3. Superficial muscles of the thigh, lateral aspect.

## Discussion

### 1. The Back

The trunk of the hyenas is characterized by the wide and long thoracic cage. All cursorial carnivores have 20 thoracolumbar vertebrae, of which seven are lumbar in Canidae and Felidae, while *C. crocuta* has 5 and *H. hyaena* 4 or sometimes 5 lumbar vertebrae. The relative length of the lumbar spine expressed as a percentage of the length of the thoracolumbar spine is therefore considerably smaller in the Hyaenidae (29–30 and 23–25 for a specimen of *H. hyaena* with 4 lumbar vertebrae) than in the Canidae (41–44) and the Felidae (44–49). Even if the relative length of the lumbar spine is calculated in the Hyaenidae on the basis of 13 thoracic and 7 lumbar vertebrae it is smaller (39–40) than that in the Canidae and Felidae. Therefore both the number of thoracic and lumbar vertebrae as well as the relative small width of the vertebral bodies (and intervertebral disks) contribute to the short lumbar region in the Hyaenidae. The relatively long thoracic cage in the Hyaenidae with 2 or 3 more ribs than in the Felidae and Canidae increases the stability of the trunk. The relative length of the lumbar spine is correlated to its action during locomotion. Since a considerable part of the sagittal bending occurs in the thoracolumbar transition zone (SLIJPER 1946), a relatively long lumbar region is more effective to increase the stride length and acceleration than a short one. The Felidae reveal considerable flexion and extension of the spine during jumping and the leaping gallop used in short sprints. In Canidae and Hyaenidae the locomotion is more characterized by endurance than by extreme speed and the spine movements are less impressive than in Felidae. SPOOR and BELTERMAN (1986) mention the lack of sagittal bending movements in the spine of hyenas during the gallop, but this statement is largely based on analysis of the gallop of zoo specimens which do not run at maximal speed. The silhouettes of a galloping spotted hyena given by KINGDON (1977) show sagittal flexion of the spine, which will be, however, less effective than in Canidae and especially Felidae due to the relatively short lumbar region.

Anatomical comparison of vervet monkeys, which increase the range of sagittal motion of the spine during galloping, and patas monkeys, which do not so, showed that the former possess relatively thicker intervertebral discs and relatively smaller dorsoventral diameter of their thoracic cage than the latter (HUROV 1987). The anatomical characters of the vervets are interpreted as adaptation to the increased sagittal mobility of the back. Both in the cheetah and the striped hyena the total length of the intervertebral discs is about 24% of the length of the thoracolumbar spine, despite the large differences in sagittal mobility of the back. The ratio transverse/dorsoventral chest diameter measured at the level of the fifth rib is 94 in *H. hyaena*, 85 in a Danish dog and 64 in the cheetah, which demonstrates a reverse correlation with sagittal mobility of the back when compared to Hurov's results. In the cursorial carnivores the thoracic part of the spine plays a minor role in the sagittal mobility of the back and the shape of the thoracic cage is adapted to the movements of the forelimbs. In the cheetah the transversely flattened thoracic cage promotes the extreme freedom of movement of the scapula in the sagittal plane. In the hyenas, however the mode of attachment of the forelimbs to the trunk is primarily related with obtaining stability and lifting power (SPOOR, BADOUX 1986).

The vertebrae of cursorial carnivores show remarkably few morphological characters that are related to the differences in the flexibility of the spine. According to SLIJPER (1946) neither the position of the articular processes, nor the presence or absence of accessory processes gives a satisfactory explanation of these differences.

The *M. psoas minor* and *M. quadratus lumborum*, which are flexors of the lumbar spine, are relatively small in *H. hyaena* (Table 2), while they (and especially the *M. psoas major*) are very impressive indeed in the cheetah. The relative weight of the *M. iliopsoas* in *H. hyaena* is comparable to that in the Canidae and Felidae since this muscle is a flexor of the hipjoint and in *H. hyaena* it has an additional head to the last (15th and 16th) ribs (Fig. 1). This head together with the *M. obliquus internus abdominis*, which extends from the tuber coxae to the last ribs firmly bridges the relatively small distance between the pelvic girdle and the thoracic cage and therefore contributes to the intrinsic stability of the trunk.

Table 2. Relative weight of the muscles of the hindlimb of *Hyaena hyaena* and their relation to various species of Canidae and Felidae after GAMBARYAN (1974). > larger, < smaller, = equal

	<i>H. hyaena</i>	in relation to	
		Canidae	Felidae
<i>M. iliopsoas</i>	4.7	=	=
<i>M. psoas minor</i>	0.6	<<	<<
<i>M. gluteus superficialis</i>	3.2	>>	>>
<i>M. gluteofemoralis</i>	2.8	>	-
<i>M. gluteus medius</i>	8.0	>>	>>
<i>M. gluteus profundus/M. piriformis</i>	2.2	>	≥
<i>Mm. obturatorius int./ext.</i>	2.4	=	=
<i>Mm. gemelli</i>	0.2	=	=
<i>M. quadratus femoris</i>	0.1	<<	<<
<i>M. sartorius</i>	5.2	>	=
<i>M. rectus femoris</i>	3.9	=	=
<i>Mm. vastus lat./int./med.</i>	14.5	=	=
<i>M. pectineus</i>	0.8	=	=
<i>M. gracilis</i>	3.1	<	=
<i>Mm. adductores</i>	10.0	<	<
<i>M. biceps femoris</i>	14.0	≥	≥
<i>M. semitendinosus</i>	4.0	≥	=
<i>M. semimembranosus</i>	5.3	<<	<<
<i>M. tibialis cranialis</i>	2.1	>	=
<i>M. extensor digit. longus</i>	0.8	<	<
<i>M. peroneus long./brev./</i>			
<i>M. extensor digit. lat.</i>	0.9	=	=
<i>M. gastrocnemius</i>	4.5	=	<
<i>M. flexor digit. superficialis</i>	2.0	=	=
<i>M. flexor digit. profundus/</i>			
<i>M. tibialis caudalis</i>	2.2	=	=

## 2. The Hindlimb

Table 2, which compares the relative weight of the muscles of the hindlimb of *H. hyaena* with those of various Canidae and Felidae (GAMBARYAN 1974), shows that the former has remarkably well-developed gluteal muscles. This phenomenon is largely correlated with the broad iliac wings in the Hyaenidae (Fig. 4). The length of the ilium expressed as a percentage of the thoracolumbar spine is 21–26 in Hyaenidae, 18–21 in Felidae and 18–22 in Canidae (about 22 according to Hildebrand 1952). The breadth of the ilium, perpendicular to the direction of the fibres of the *M. gluteus medius*, expressed as a percentage of the ilium length is 83–90 in *H. hyaena*, 73 in *C. crocuta*, 31–41 in the Felidae and 50–56 in the Canidae. The breadth of the ilium provides a large cross-sectional area to the fibres of the *M. gluteus medius*, which makes it a very powerful muscle. As a result of experimental resection, CERMAK et. al. (1972) found that the *M. gluteus medius* plays an important role in stabilizing the hip joint, i.e. by preventing unwanted adduction. However, electromyographic studies of the activity of this muscle in the dog (WENTINK 1976) strongly points to its function as extensor of the hip.

The tendon of the large *M. gluteus superficialis* (Table 2) does not insert on the trochanter major, but fades into the fascia lata cranial of the os femoris, and is therefore an abductor and flexor of the hip and, indirectly, an extensor of the knee. The origin of this muscle, extending from the cranial border of the ilium to the sacrum provides it with a large moment arm about the hip joint. Since the *M. gluteus superficialis* partly replaces the position and function of the *M. tensor fasciae latae* in the Canidae and Felidae the latter muscle is small in *H. hyaena*.

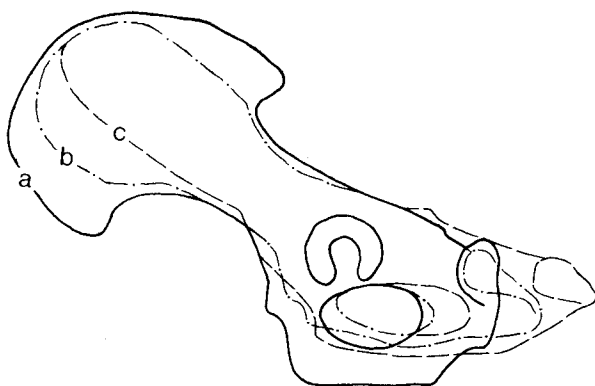


Fig. 4. Circumference of the left os coxae of a) *Hyaena hyaena*, b) *Canis familiaris* and c) *Panthera pardus*. Scaled to the same thoracolumbar spine length.

Fig. 4 shows the differences between the post-acetabular part of the os coxae of the Hyaenidae, Felidae and Canidae. These differences largely exceed those caused by sexual dimorphism in each species. Although the ischium of the Hyaenidae is notably shorter than that of the Felidae and Canidae, the ischiatic tuberosity has the same relative position as in the Canidae. In the Canidae the ischiatic table is much more developed, hence the medial angle of the ischiatic tuberosity projects more caudad than in Hyaenidae. Consequently the *M. biceps femoris* and *M. semitendinosus* have about an identical moment arm about the hip joint in Hyaenidae and Canidae while that of the *M. semimembranosus* is smaller in the hyenas. Since the latter muscle is also weakly developed in *H. hyaena*, it is a less important extensor of the hip compared to the situation in Canidae and Felidae. In the Felidae the hamstrings have a larger moment arm about the hip joint and are therefore potentially more powerful, which reflects their action in the leaping and sprinting type of locomotion.

The symphysis pelvis is situated more ventral in Hyaenidae than in Canidae and Felidae (Fig. 4), hence the *M. pectineus*, *M. gracilis* and the *Mm. adductores* have a relatively large moment arm about the hip joint. The surface of the origin of the latter muscle on the os coxae of *H. hyaena* is notably larger than in the dog and cat. In combination with the relatively long os femoris (SPOOR 1985) these muscles and the hamstrings are powerful stabilizers and extensors of the hindlimb. It is not clear yet if there is a relation between the morphology of the os coxae in the hyenas and the characteristic difference in length of the forelimb and hindlimb (SPOOR 1985).

The insertion of the caudal fibres of the *M. biceps femoris* on the calcanean tendon (instead of an accessory tendon as in the Canidae and Felidae), promotes the action of this muscle as an extensor of the ankle joint. The length of the calcanean tuber (i.e. the actual moment arm of the extensors of the ankle joint) expressed as a percentage of the longest metatarsal bone (i.e. the actual moment arm of the normal force) in Hyaenidae (35–42) is hardly different from that in Canidae (36–45) and somewhat smaller than that in Felidae (42–46). The observed variation of this ratio is mainly caused by the differences in length of the metatarsal bones among cursorial carnivores (SPOOR 1985).

The *M. quadratus femoris* and the *M. gluteus medius* are both "high-gear" extensors (HILDEBRAND 1974), they have a small moment arm about the hip joint. The large size of the gluteal might be correlated with the poorly developed *M. quadratus femoris* (Table 2), while the small origin of the latter provides additional surface for the origin of the *Mm. adductores*. Previous descriptions of the *M. quadratus femoris* do not mention a weak development in Hyaenidae. WATSON and YOUNG (1879) pictured a dog-sized *M. quadratus femoris* in the spotted hyena (*Crocuta crocuta*) and YOUNG and ROBINSON (1889) mention that this muscle in the striped hyena is arranged as in the spotted hyena. In this respect, our specimen may show individual variation.

The morphology of the hip joint in the Hyaenidae was studied with special attention to the characteristics observed by JENKINS and CAMAZINE (1977). Both the femoral head and the lunata surface of the os coxae are flattened in the transverse plane (Fig. 5), which restricts the hip

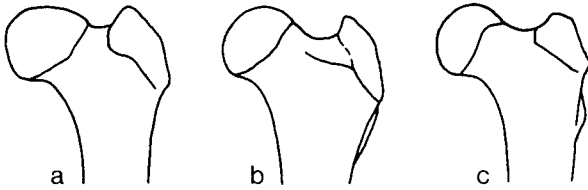


Fig. 5. Proximal left femora in cranial view, a) *Hyaena hyaena*, b) *Canis familiaris* and c) *Panthera pardus* (to scale).

movements mainly to the sagittal plane. The fovea is situated at the same position as in the Canidae. The shaft of the os femoris is slightly bent as in Canidae, while that in Felidae is straight. The biomechanical importance of this curvature is not clear (HOWELL 1944; KUMMER 1959). However, the fact that the os femoris in the non-cursorial canid *Speothos* (HILDEBRAND 1954) and the Felidae is straight while that in the cursorial Canidae is slightly bent, indicates a relation between femoral shape and locomotion pattern. The femoral trochlea is not as long and narrow as in the Canidae, but broad and flat like than in the Felidae. Both condyles of the os femoris are relatively broad and flat in the transverse plane and the intercondylar fossa is narrow. The tibial condyles are also flat. The articulation between the tibia and the talus is wide and flat in transverse direction and the trochlear ridges of the talus are less pronounced than those in Canidae and Felidae. The calcaneal tuber of the Hyaenidae is very solid. The relative wide and flat articulation surfaces (in transverse direction) of the hip, knee and ankle joint in the Hyaenidae contribute to an efficient distribution of stress in the joints.

### Conclusions

The conformation of the body of the hyena is a compromise between adaptations to lifting power, stability and cursorial locomotion. The osteology and myology of the neck and forelimb show various adaptations to tearing, seizing, lifting and carrying large and heavy prey (SPOOR, BADOUX 1986). The trunk and hindlimbs are adapted to provide stability and powerful propulsion during these actions. The well-developed *M. biceps femoris*, gluteal muscles and *Mm. adductores* are, in combination with the relatively long os femoris, powerful stabilizers and retractors of the hindlimb. The morphology of the joints enables the transmission of large forces between the limb-segments. The trunk is characterized by its robustness. The long and wide thoracic cage is firmly connected with the ilia. Since the thoracic cage is wide, the forelimbs stand relatively wide apart, which increases the transverse stability of the body. The relatively short lumbar spine and the weakly developed sublumbar flexors of this region suggest that sagittal spine movements are of less importance to increase the stride length and acceleration during the gallop in the hyena than in Canidae and Felidae. Despite the various adaptations to power and stability, which are supposed to have a noncursorial character (like the relatively long os femoris and short tibia), the hyenas are able to run at considerable speed over long distances (SPOOR, BELTERMAN 1986). The relative shortness of the lumbar region and the large breadth of the ilium are less explicit in *C. crocuta* than in *H. hyaena* which may be related to the more hunting and less scavenging way of life of the latter.

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## Abbreviations

- |                                     |                               |
|-------------------------------------|-------------------------------|
| 1 – M. erector spinae               | 13 – Mm. gemelli              |
| 2 – M. obliquus internus abdominis  | 14 – M. quadratus femoris     |
| 3 – M. rectus abdominis             | 15 – M. sartorius             |
| 4 – M. quadratus lumborum           | 16 – M. articularis coxae     |
| 5 – M. iliopsoas                    | 17 – M. rectus femoris        |
| 5'. M. iliacus                      | 18 – M. pectineus             |
| 5''. M. psoas major, vertebral head | 19 – M. gracilis              |
| 5'''. M. psoas major, costal head   | 20 – M. adductor              |
| 6 – M. psoas minor                  | 21 – M. obturatorius externus |
| 7 – M. gluteus superficialis        | 22 – M. biceps femoris        |
| 8 – M. gluteofemoralis              | 22' its caudal fibres         |
| 9 – M. gluteus medius               | 23 – M. semitendinosus        |
| 10 – M. gluteus profundus           | 24 – M. semimembranosus       |
| 11 – M. tensor fascia latae         | 25 – M. gastrocnemius         |
| 12 – M. piriformis                  |                               |

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