Anat. Anz., Jena 160 (1985) 215—220

# Body Proportions in Hyaenidae

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With 12 Tables (Received April 29, 1985)

*Key words:* body proportions, hyaenidae

## Abstract

Indexes of skeletal measurements are used to compare body proportions in Hyaenidae, Canidae and Felidae. *Hyaena* and *Crocuta* are characterized by a long neck and long forelimbs. The humerus is relatively short and the radius and metacarpal bones are long. In the hindlimb the os femoris is long and the tibia short. The proportions are adapted to carry large and heavy prey and provide maximum static stability. *Proteles cristatus* which mainly feeds on termites and insects has the long neck and forelimb in common with the other Hyaenidae, but its hindlimbs are longer and the length of the limbsegments reveals more canid proportions.

## Introduction

When discussing the locomotion of hyenas, Howell (1944) remarked: "They are of real interest in any study of locomotion because of the fact that the forequaters are much heavier than the hinder ones ... The proportions are noteworthy among all carnivores."

Ehrenberg (1940); Howell (1944); Davis (1964) and Savage (1977) give some data on limb proportions of hyenas but these are either incomparable or inaccurate. The present analysis of body proportions was made as a background study for further research on the myology and locomotion of the Hyaenidae. Therefore, it is primarily descriptive, but incidentally the relation between the body proportions and the way of life is discussed.

Skeletal material of the Spotted Hyena (*Crocuta crocuta* [Erxleben 1777]), the Striped Hyena (*Hyaena hyaena*, [L. 1758]) and the Aardwolf (*Proteles cristatus*, [Sparrman 1783]) has been studied. The skeleton of the Brown Hyena (*Hyaena brunnea*, Thunberg 1820) is represented by a single incomplete specimen.

## Material and Methods

Body proportions are analysed by comparing the length of the limb bones and of the cervical and thoracolumbar region of the spine with those of Canidae and Felidae. Members of these families have about the same size and they share cursorial locomotion with the hyenas.

The skeletal material of the Hyaenidae includes all adult specimens of the Rijksmuseum van Natuurlijke, Historie, Leiden, the Zoologisch Museum Amsterdam, the Koninklijk Museum voor Midden Afrika, Tervuren (Belgium) and the British Museum (NH), London. The skeletal material of the Canidae and the Felidae is of the Rijksmuseum van Natuurlijke Historie, the Zoologisch Museum Utrecht, the Zoologisch Museum Amsterdam and the British Museum (NH), London. The material is listed in Table 1.

Table 1. Skeletal material. Number of specimen in parentheses

| | |
|---|---|
| Hyaenidae: | *Crocuta crocuta* (14), Cc |
| | *Hyaena hyaena* (9), Hh |
| | *Hyaena brunnea* (1), Hb |
| | *Proteles cristatus* (6), Pc |
| Canidae: | *Canis lupus* (5), Clu |
| | *Canis latrans* (2), Cla |
| | *Cuon alpinus* (3), Ca |
| | *Lycaon pictus* (3), Lp |
| Felidae: | *Panthera pardus* (5), Pp |
| | *Panthera onca* (2), Po |
| | *Uncia uncia* (1), Uu |
| | *Felis concolor* (2), Fc |
| | *Neofelis nebulosa* (1), Nn |
| | *Profelis temmincki* (1), Pt |

The lengths of the left limb bones were measured to the nearest millimeter with Vernier Calipers, that of the regions of the spine with a measuring tape, following the method of Hildebrand (1952).

Indexes were calculated for the Hyaenidae and for Canidae and Felidae comparable in size to *Crocuta* and *Hyaena*, for which the length of the thoracolumbar spine was taken as a criterion. This restriction avoids misinterpretation of the indexes due to the effects of different body sizes. Since the contribution of the cervical part to the total length of the spine varies largely among the 3 families, the length of the thoracolumbar spine was taken as a standard to calculate relative lengths instead of the total length of the presacral spine (Hildebrand 1952; Gonyea 1976). The observed differences for the various indexes are statistically tested using one-way analysis of variance and the Student-Newman-Keuls test as described by Sokal and Rohlf (1969).

## Results

In Tables 2—11 the indexes of the relative lengths of the cervical spine, limbs and limb segments of the Hyaenidae and a selected number of Canidae and Felidae species are compared and the differences are statistically tested. For the 10 indexes there is a significant added variance component among the tested species ($p < 0.001$). In Table 12 the length of each limbsegment is given as a percentage of the total length of the limb for the 13 species.

The neck of all Hyaenidae is notable longer than that of the Canidae and Felidae. The forelimb (humerus + radius + longest metacarpal bone) of the Hyaenidae is longer than that of the Canidae and Felidae. All 3 limbsegments contribute to this difference but the radius provides the largest share. The hindlimb (os femoris + tibia + longest metatarsal bone) of the Hyaenidae is either longer or equals the length in Canidae. The difference in length between the hindlimbs of these 2 families is always less than that between the forelimbs, hence the intermembral index (length forelimb/hindlimb $\times$ 100%) is larger in the Hyaenidae. The hindlimb of *Hyaena* and *Crocuta* is characterized by a long os femoris and a short tibia. *H. hyaena* differs from *C.* crocuta by having longer limbs due to a longer radius, tibia and metapodial bones, their intermembral index however, is not different. The proportions of *H. brunnea* have an intermediate position between those of *H. hyaena* and *C. crocuta*. The length of the neck and the forelimb of *P. cristatus* is about the same as that of *H. hyaena*

Tables 2—4, 6—11. Means of lengths given as percentage of the thoracolumbar spine length. Table 5: Means of the intermembral index. Abbreviations of species see Table 1. *: the smallest significant difference between means ($p < 0.05$), ns: not significant. Species represented by one specimen are not tested (—)

Table 2. Forelimb

| | | Pc | Hh | Cc |
|---|---|---|---|---|
| Pc | 111.8 | — | | |
| Hh | 110.0 | ns | — | |
| Cc | 102.5 | * | * | — |
| Cla | 94.5 | | | ns |
| Lp | 91.8 | | | * |
| Clu | 91.2 | | | |
| Uu | 81.2 | — | — | — |
| Pp | 77.0 | | | |
| Po | 76.2 | | | |
| Ca | 75.2 | | | |
| Pt | 74.8 | — | — | — |
| Nn | 74.4 | — | — | — |
| Fc | 72.4 | | | |

Table 3. Hindlimb

| | | Pc | Hh | Cc |
|---|---|---|---|---|
| Pc | 113.8 | — | | |
| Hh | 107.0 | * | — | |
| Cla | 104.4 | | ns | ns |
| Lp | 101.0 | | ns | ns |
| Cc | 100.7 | | * | — |
| Clu | 100.6 | | | ns |
| Uu | 95.4 | — | — | — |
| Pp | 94.1 | | | * |
| Pt | 91.2 | — | — | — |
| Fc | 90.1 | | | |
| Ca | 89.7 | | | |
| Nn | 89.4 | — | — | — |
| Po | 89.3 | | | |

Table 4. Cervical spine

| | | Pc | Hh | Cc |
|---|---|---|---|---|
| Pc | 55.8 | — | | |
| Hh | 54.3 | ns | — | |
| Hb | 54.3 | — | — | — |
| Cc | 51.6 | * | ns | — |
| Cla | 44.6 | | * | * |
| Lp | 40.8 | | | |
| Clu | 40.6 | | | |
| Ca | 40.5 | | | |
| Nn | 32.3 | — | — | — |
| Pt | 32.1 | — | — | — |
| Po | 31.7 | | | |
| Pp | 30.7 | | | |
| Fc | 29.1 | | | |
| Uu | 26.9 | — | — | — |

Table 5. Intermembral index

| | | Hh | Cc | Pc |
|---|---|---|---|---|
| Hh | 102.6 | — | | |
| Cc | 101.8 | ns | — | |
| Pc | 98.3 | * | * | — |
| Lp | 90.9 | | | * |
| Clu | 90.6 | | | |
| Cla | 90.5 | | | |
| Po | 85.3 | | | |
| Uu | 85.1 | — | — | — |
| Ca | 83.8 | | | |
| Nn | 83.2 | — | — | — |
| Pp | 82.0 | | | |
| Pt | 82.0 | — | — | — |
| Fc | 80.4 | | | |

but the hindlimb is longer, resulting in an intermembral index intermediate between the other Hyaenidae and the Canidae. Apart from the long metapodial bones, the contribution of the length of the limb segments to that of the whole limb length of *P. cristatus* resembles that of the Canidae.

## Discussion

Long limbs are usually considered as an adaptation to cursorial locomotion (Howell 1944), but the long and massive limbs of *Hyaena* and *Crocuta* are certainly not primarily specialized for speed.

Table 6. Humerus

| | | Pc | Hh | Cc |
|---|---|---|---|---|
| Pc | 43.7 | — | | |
| Hh | 41.7 | ns | — | |
| Hb | 41.1 | — | — | — |
| Cc | 40.0 | * | * | — |
| Cla | 38.2 | | | ns |
| Clu | 37.5 | | | * |
| Lp | 37.0 | | | |
| Po | 36.0 | | | |
| Pp | 35.6 | | | |
| Uu | 35.0 | — | — | — |
| Nn | 34.8 | — | — | — |
| Pt | 33.1 | — | — | — |
| Fc | 32.7 | | | |
| Ca | 32.6 | | | |

Table 7. Radius

| | | Hh | Pc | Cc |
|---|---|---|---|---|
| Hh | 48.3 | — | | |
| Pc | 46.1 | ns | — | |
| Hb | 44.3 | — | — | — |
| Cc | 44.1 | * | ns | — |
| Cla | 39.6 | | * | * |
| Lp | 39.3 | | | |
| Clu | 38.4 | | | |
| Uu | 33.7 | — | — | — |
| Pp | 30.0 | | | |
| Pt | 29.5 | — | — | — |
| Ca | 29.4 | | | |
| Po | 29.1 | | | |
| Nn | 29.0 | — | — | — |
| Fc | 27.7 | | | |

Table 8. Longest metacarpal bone

| | | Pc | Hh | Cc |
|---|---|---|---|---|
| Pc | 22.0 | — | | |
| Hh | 19.9 | * | — | |
| Cc | 18.5 | | * | — |
| Cla | 16.8 | | | ns |
| Lp | 15.5 | | | * |
| Clu | 15.5 | | | |
| Ca | 13.2 | | | |
| Uu | 12.5 | — | — | — |
| Pt | 12.1 | — | — | — |
| Fc | 12.0 | | | |
| Pp | 11.4 | | | |
| Po | 11.2 | | | |
| Nn | 10.6 | | | |

Table 9. Os femoris

| | | Cc | Pc | Hh |
|---|---|---|---|---|
| Cc | 46.6 | — | | |
| Pc | 46.3 | ns | — | |
| Hb | 46.3 | — | — | — |
| Hh | 46.2 | ns | ns | — |
| Lp | 41.8 | * | * | * |
| Clu | 41.8 | | | |
| Po | 41.5 | | | |
| Pp | 41.0 | | | |
| Cla | 40.8 | | | |
| Uu | 39.6 | — | — | — |
| Nn | 39.6 | — | — | — |
| Pt | 39.3 | — | — | — |
| Fc | 38.7 | | | |
| Ca | 37.9 | | | |

The long neck and forelimbs enable the hyena to lift and carry large prey without dragging it over the ground. Since competition with other carnivorous animals is large, hyenas developed a strategy of fast laceration and transport of kills. Moreover the long neck gives space for powerful musculature. A short humerus and a long radius and metacarpal bones usually go with speedy locomotion. In the Hyaenidae, the relative short humerus is favourable since the bodyweight acting on the humeral head has a relatively small moment arm about the elbow joint; this is important for an animal carrying heavy load by mouth.

The length of the hindlimbs is a compromise between 2 conflicting demands. On one hand they must have a minimum length in relation to the forelimbs to enable normal locomotion, on the other both long fore and hindlimbs decrease the transverse static stability of the body. The proportion of the hindlimb segments (long os femoris, short tibia) is unusual for carnivores which exclusively live on plains. The Canidae (for instance *Cuon*) and Felidae (Gonyea 1976) which have identical proportions are

Table 10. Tibia

| | | Pc | Hh | Cc |
|---|---|---|---|---|
| Pc | 46.0 | — | | |
| Cla | 44.5 | ns | ns | |
| Hh | 42.0 | * | — | |
| Clu | 41.7 | | ns | |
| Lp | 41.6 | | ns | * |
| Uu | 39.8 | — | — | — |
| Cc | 37.4 | | * | — |
| Pp | 37.3 | | | ns |
| Ca | 36.4 | | | ns |
| Hb | 36.3 | — | — | — |
| Fc | 35.8 | | | ns |
| Nn | 35.8 | — | — | — |
| Pt | 35.7 | — | — | — |
| Po | 33.9 | | | * |

Table 11. Longest metatarsal bone

| | | Pc | Hh | Cc |
|---|---|---|---|---|
| Pc | 21.5 | — | | |
| Hh | 18.8 | * | — | |
| Cla | 18.5 | | ns | ns |
| Lp | 17.6 | | ns | ns |
| Clu | 17.1 | | ns | ns |
| Cc | 16.9 | | * | — |
| Pt | 16.2 | — | — | — |
| Uu | 16.0 | — | — | — |
| Pp | 15.7 | | | ns |
| Fc | 15.6 | | | ns |
| Ca | 15.4 | | | ns |
| Nn | 14.0 | — | — | — |
| Po | 13.9 | | | * |

Table 12. Percentages of limbsegments to total limblength

| | hum. | rad. | mc. | Ofe. | tib. | mt. |
|---|---|---|---|---|---|---|
| *C. crocuta* | 39 | 43 | 18 | 46 | 37 | 17 |
| *H. hyaena* | 38 | 44 | 18 | 43 | 39 | 18 |
| *P. cristatus* | 39 | 41 | 20 | 40 | 41 | 19 |
| *C. lupus* | 41 | 42 | 17 | 41 | 41 | 18 |
| *C. latrans* | 40 | 42 | 18 | 40 | 42 | 18 |
| *C. alpinus* | 43 | 39 | 18 | 42 | 41 | 17 |
| *L. pictus* | 40 | 43 | 17 | 41 | 41 | 18 |
| *P. pardus* | 46 | 39 | 15 | 44 | 40 | 16 |
| *F. concolor* | 45 | 38 | 17 | 43 | 40 | 17 |
| *P. onca* | 47 | 38 | 15 | 46 | 39 | 15 |
| *U. uncia* | 43 | 42 | 15 | 41 | 42 | 17 |
| *N. nebulosa* | 47 | 39 | 14 | 44 | 40 | 16 |
| *P. temmincki* | 44 | 40 | 16 | 43 | 39 | 18 |

typical forest dwellers. The long os femoris renders a large moment arm to the extrinsic muscles which increases the stability necessary in a long-legged animal handling a heavy load.

The differences in size between the species of Hyaenidae contribute to the differences in body proportions (comparable to the differences between *C. lupus* and the smaller *C. latrans*) and both are related to different feeding habits. *H. hyaena* is a real scavenger which sometimes hunts small animals (Rieger 1979) while *C. crocuta* is both a scavenger and an active hunter which, living in clans, chases even large ungulates (Kruuk 1972). Consequently the latter is larger and more massive, as is expressed in the proportions. The much smaller *P. cristatus* has a different way of life and feeds mainly on termites and insects which is reflected in the largely reduced teeth. Therefore the intermembral index and proportions of limb segments of this animal differ sharply from those in the "true" hyenas. *P. cristatus* shares the long neck and long limbs with the other Hyaenidae. They possibly stress the strategy of this defenceless species to mimic *Hyaena* (Gingerich 1975), but on the other hand these proportions can be looked upon as adapatations to hunt small prey in the high

grass as can be seen in the Maned Wolf *(Chrysocyon brachyurus)* (Hildebrand 1952).

## Acknowledgements

I thank Drs. Th. Belterman and Prof. Dr. A. v. d. Stelt (University of Amsterdam) for "introducing" me to the hyenas and for their support during the study and Prof. Dr. D. M. Badoux (State University Utrecht) for his valuable comments on the manuscript. I am grateful to Dr. J. Clutton-Brock (British Museum NH), Dr. C. Smeenk (Rijksmuseum van Natuurlijke Historie), Dr. D. Meirte (Koninklijk Museum voor Midden Afrika, Tervuren), Dr. P. v. Bree (Zoologisch Museum Amsterdam) and Drs. D. v. d. Tooren (Zoologisch Museum Utrecht) for their permission to study skeletal material.

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