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Abstract: Elongated canines exclusively evolved in carnivores, which are able to stabilize their victims with their anterior extremities. It was shown that power and agility of the front limbs are strongly correlated with the development of sabers. Limb- and skull proportions of the extinct cat *Smilodon fatalis* were therefore compared with those of six extant species of large felids and those of *Canis lupus*. Furthermore, differences in hunting behavior and locomotory capabilities were analyzed. Ratios of limb segment lengths have been shown to relate to functional and locomotory differences (e.g., cursoriality) in both extinct and extant felines. *S. fatalis* is equipped with relatively short and sturdy limbs. Moreover, it possessed a great angle of inclination of the olecranon fossa relative to the long axis of the humerus, in addition to a wide and laterally oriented radial notch. The radial head was more circular than in any other extant cat member. Additionally, the Teres major muscle inserts further away from the shoulder joint and the joints are more powerfully built and demonstrate a great amount of strength and flexibility. It is very likely that *Smilodon* preyed on the large contemporary megafauna because of its overall more powerful anatomy compared to that of modern felines. Nevertheless, it is still a matter of dispute exactly, which hunting method *S. fatalis* applied. It is suggested that its massive forelimbs were employed to grasp and hold large prey, which was then pulled down and finally killed or fatally wounded with a canine shear bite applied to the throat or abdomen. In contrast, the lightly built *Acinonyx jubatus* is found exclusively in low structured habitats, consequently it has the relatively longest limbs of all large felids, the smallest angle of inclination of the olecranon fossa and an insertion of the T. major closer to the joint. Its prey usually weighs less than its own body weight. Bivariate regression analyses on log-transformed limb segment lengths were employed to test overall differences and scaling variations in limb proportions. Multivariate factorial- and discriminant analysis were performed on a number of limb dimensions of all the examined species. Results reveal that cats can accurately be distinguished into three different categories upon these ratios (even across taxonomic boundaries): 1. Highly cursorial felines like the cheetah, 2. Pantherine cats, including the puma, 3. Dirk-toothed cats such *S. fatalis*, and *X. hodsonae* (scimitar-toothed felid with the morphology of dirk-toothed cat).

DIPLOMARBEIT

KILLING BEHAVIOR IN *SMILODON FATALIS* (MAMMALIA, CARNIVORA, FELIDAE) BASED ON FUNCTIONAL ANATOMY AND BODY PROPORTIONS OF THE FRONT- AND HIND LIMBS

BY

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JULY 2000

Hiermit versichere ich, die vorliegende Arbeit selbständig und nur unter Zuhilfenahme erlaubter und angegebener Hilfsmittel angefertigt zu haben.

Tübingen, August 2000.

(Jens Schmieder)

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Bivariate regression analyses on log-transformed limb segment lengths were employed to test overall differences and scaling variations in limb proportions. Multivariate factorial- and discriminant analysis were performed on a number of limb dimensions of all the examined species. Results reveal that cats can accurately be distinguished into three different categories upon these ratios (even across taxonomic boundaries):

1. **Highly cursorial felines** like the cheetah,
2. **Pantherine cats**, including the puma,
3. **Dirk-toothed cats** such *S. fatalis*, and *X. hodsonae* (scimitar-toothed felid with the morphology of dirk-toothed cat).

CONTENTS

1 INTRODUCTION

The purpose of this study is to compare limb proportions, different adaptations of limb anatomy, and features of the skull morphology in seven large living and extinct cats in order to determine whether functional differences due to morphological variation can be correlated with different hunting behavior. Statistical studies should shed light on the relationship between development of the sabertooth canines and their forelimbs. Furthermore, by means of statistical analysis, proportional differences are used to separate the various representatives into three distinct guilds.

To begin with, a scant summary will be given of different theories proposed by a selected number of authors to clarify the problematic hunting behavior found in saber-toothed cats, which are based mainly on the morphology of the skull and cervical vertebrae.

In many species of saber-toothed felines, in particular *Smilodon*, the upper canines had evolved into long, curved and laterally flattened sabers. These more or less serrated canines were used for killing comparatively large prey, but opinions vary as to exactly how they were employed. WARREN (1853) was one of the first to study behavioral implications of the saber-toothed morphology. He concluded that the elongated canines were used on prey in a stabbing mode with a following cut and tear action as the predator's head was pulled backwards. MATTHEW (1901, 1910) supported and elaborated the idea that the canines were used for stabbing. He assumed that the specific action of the canines was to strike and then rip or gash so that the prey bled to death. This hunting method was supposed to allow sabertooths to kill large, thick-skinned prey such as adult proboscideans.

SIMPSON (1941) further polished this theory, and proposed a combined action of the head depressor and neck depressor musculature, supported by the inertia of the predators leaping body, to maintain the needed force for stabbing. MILLER (1969) and SCHULTZ et al. (1970), who considered saber-toothed cats as active predators that used their canines in a stabbing mode as well, speculated that the powerful front limbs of these felines were used to immobilize their victims while the long sabers were applied to stab the prey animal.

Some authors such as MARINELLI (1938) or BOHLIN (1940) on the other hand have rejected the stabbing theory and have tried to show that the sabers were ill adapted for this kind of function and must have served primarily for slicing. Moreover, they both brought forth strong functional and anatomical arguments against a predator theory. In this regard, they presumed that the sabers were not developed to withstand lateral forces, which would surely have occurred in the stabbing of a struggling prey.

However, in spite of all various proposed hypotheses the most plausible and recent theory suggests that saber teeth were used to deliver a fatal shearing bite to the belly or throat of a prey animal causing considerable loss of blood (AKERSTEN, 1985). Thereby the mandible played an active role in killing by providing anchorage for a downward movement of the upper canines, which in turn was primarily powered by the atlanto-mastoid musculature. Further support for AKERSTEN'S model provided a recent analysis (BRYANT, 1996) of the jaw-adductor mechanics in *Smilodon*, suggesting that the strength of the neck muscle was necessary to compensate for a relatively low-out force of the jaw adductors at large gapes. DUCKLER (1997) interpreted the typical occurrence of parietal depressions found in skulls of *Smilodon* as a consequence of repeated strain on the temporalis muscle, which proposes an active task of this muscle in the killing, supporting a biting rather than a stabbing mode. Moreover, ANTÓN & GALOBART (1999) intensify the canine shear-bite theory on the basis of the neck function in *Homotherium latidens*.

Behavioral investigations have shown that the method employed by carnivorans in catching and killing prey varies considerably between species (GONYEA, 1976). Unlike most other carnivorans, the primary organ of prehension used to capture prey in felids has been found to be the claw equipped forelimbs. In this regard, the jaws and thus the canines are usually not involved in capturing prey, but function exclusively for killing. In addition, many felids are capable of killing prey larger than their own body weight (LEYHAUSEN, 1965; SCHALLER, 1967; KLEIMAN and EISENBERG, 1973); a behavior that would be atypical for most other solitary hunting carnivorans, in which the jaws and not the forelimbs operate as the primary organ of prehension.

Due to its importance in hunting behavior, the proportions of the extremities are mainly stressed in this study. Skull proportions are compared with that of the anterior limb length in order to understand anatomical and allometric correlations of the post-cranial skeleton with that of the cranium.

In addition, the elbow and wrist anatomy is analyzed, based on the studies of GONYEA (1978), of extant felids with that of *Smilodon fatalis* in order to clarify habitat preferences.

Conclusions and interpretations are to some extent based on the author's own research but rely heavily on an assessment of the literature as well.

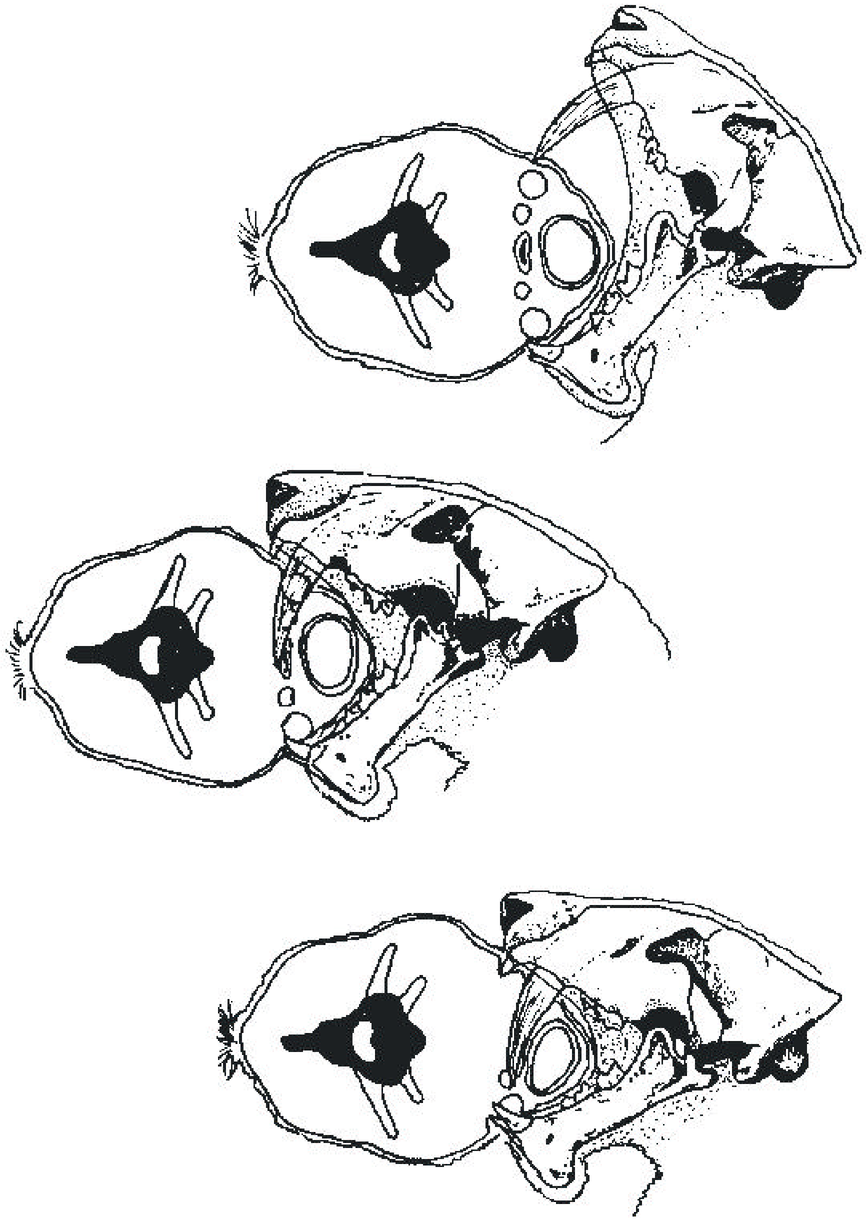

Figure 1.1 (after Turner & Antón)**:** The illustration shows a schematic section through the neck of a typical horse, with the skull of *Megantereon* biting at the throat. Notice how the vertebrae of the horse are arranged toward the back of the neck, and how near the surface of the throat are the windpipe and major blood vessels. With the animal held immobile by the strong forequarters, even relatively superficial slashes into the neck would produce considerable blood loss and induce shock, and choking off the air supply would be relatively easy. Such a technique would avoid the need for the violent and rather inaccurate stabbing implied by some older ideas about how sabertooths dealt with their prey.

2 PREVIOUS WORK

The large body of literature on sabertooths deals mainly with systematics, while functional studies primarily focuses, with a few exceptions, on cranial morphology in particular on whether the elongated canines were used for stabbing, slicing, or active biting and whether saber-toothed cats were more likely to have been active predators or scavengers (see above).

Post cranial morphology, in turn, particularly limb anatomy and limb proportions, are restricted to a handful of studies (GONYEA, 1976, 1978; V. VALKENBURGH, 1987). Although most of the works that deal with sabertooth morphology point to the striking forelimb anatomy and its probable implicated function[1], it is primarily the studies of V. VALKENBURGH (1987), TURNER & ANTÓN (1996) and especially GONYEA (1976, 1978) that focus exclusively on this matter of subject.

GONYEA (1976a) compared body proportions of eight extant species of large felids in order to demonstrate the tied relations implicated between their morphology, habitat structure and habitat utilization. The results indicate that cats found preferably in highly dense structured habitats[2] have relatively, the shortest front limbs and lumbar spine and are capable to bring down prey that exceeds their own body weight. The cheetah, in turn, is found in low structured habitats. It has the relatively longest limbs and lumbar spine of the large felids and its prey is usually smaller than itself. In other works GONYEA (1976b & 1978) compared the claw retractile mechanism for extant cats with that of saber-toothed felids and equated body proportions between living cats and extinct sabers. He concluded that the claw retraction for saber-toothed felids was the same as that of modern felids. The relative body proportions of *Smilodon* were found to be similar to modern felids of high structured dense forests. GONYEA also introduced an elegant model of the elbow and wrist anatomy of different living felid species, particularly the shape and position of the olecranon fossa, which enabled him to conclude habitat preference. His studies, in fact, have inspired much of this analysis.

V. VALKENBURGH (1987) on the other hand, tried to assess the correspondence between locomotor function (climbing, digging, and running) and skeletal morphology in living and extinct carnivores. He assigned four broad locomotor categories by means of olecranon size and orientation, astragalar shape, and manus and hind limb proportions, etc. His results demonstrate that osteological indices are good predictors of locomotor behavior among living carnivores. In an earlier study from 1985 he determined locomotor behaviors and diversity

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[1] See BOHLIN (1940); MARINELLI (1938); MARTIN (1980); MERRIAM & STOCK (1932); SCHAUB (1925); etc.

[2] Especially *Panthera onca* and *Neofelis nebulosa*

within past and present guilds from data of body weight, ungual shape, elbow shape and limb proportions of extinct and extant large predatory mammals. Nevertheless, despite of the presented detailed studies, almost all of the authors who have worked with saber-toothed felids called attention to the extremely strong and sturdy front extremities (e.g. MERRIAM AND STOCK, 1932; ABEL, 1914; MARINELLI, 1937; MARTIN, 1980; et al.) concluding that they almost certainly ambushed their victims from concealment rather than pursuing them as cheetahs do.

Analysis of cranial measurements from EMERSON & RADINSKY revealed several differences in skull morphology between saber-toothed cats and conical toothed felines, which mainly represent modifications for an increasing maximum gape. Distinctions for sabers include: relatively narrow zygomatic arches, a shorter distance between mandibular condyles and carnassials, relatively shorter and narrower temporal fossae, longer tooth row lengths, smaller orbits, smaller masseter and temporalis moment arms, reduced coronoid process, lower canines reduced and incisors more pointed and procumbent, and more upwardly rotated facial skull relative to braincase, etc.

VAN VALKENBURGH & RUFF (1986) in turn compared canine lengths in different cat species, both modern and extinct, with skull lengths and discovered that felids, as a group, possess longer canines than do canids and hyaenids and that saber-toothed cats evidently have long canines relative to all living felids except for the clouded leopard (*Neofelis nebulosa*). They concluded that the relative skull length is a good predictor of stress felt at the canines because of its close correlation with muscle size and moment arms.

3 OVERVIEW OF THE EVOLUTION OF LARGE CATS

In order to improve the overall picture of the cat family it would be beneficial to the reader to have a short introduction in the fossil history of the felines and to present one reasonable way to classify their rather complex interrelationships. The phylogeny of felids recently published by TURNER and ANTÓN (1996) is adopted here, and summarizes the views of previous authors (BEAUMONT 1978, 1990; TEDFORD 1978; MARTIN 1989). Moreover, the recently discovered *Xenosmilus hodsonae*, found in Florida, appears to be a new design of saber-toothed cat and forces taxonomists to add a third category to the already existing two groupings.

Neofelids, also known as modern or true cats, are not recognized with certainty until around 30 Ma ago in Oligocene time (TURNER & ANTÓN, 1996) and the fossil record improves around 10 Ma ago close to the end of the Miocene. Between their first emergence towards the end of the Miocene, a number of species enter the scene that are clearly catlike in their morphology. These were formerly considered to be ancestral to true cats and thus were classified as the Paleofelids, or ancient cats.

More recent studies however, suggest that these catlike animals differ enough from the modern cats to be considered a separate family, the Nimravidae (BRYANT, 1991). The main anatomical characteristic used in making this distinction is the formation of the external auditory bulla. In true cats the interior of the bulla is separated into two chambers by a septum, but Nimravids either lack the septum or the entire bulla, implying only a cartilaginous housing for the middle ear that has not fossilized (TURNER & ANTÓN, 1996). Despite this distinction the Nimravids already possessed well-developed basic adaptations such as retractile claws, sectorial carnassials, reduction of the posterior molars, etc. Nonetheless, the taxonomic position of the Nimravidae within the carnivore-family still remains a problematic issue.

Modern or true cats first appear around 30 Ma ago in the Upper Oligocene of France with the genus *Proailurus lemanensis*. This relatively small animal was very much cat-like in its appearance especially in terms of the skull shape and the form of its teeth. However, the skull carried a much larger number of teeth compared to more modern cats[3]. In America the first recorded finds of felines are from Nebraskan Miocene deposits of about 16 Ma ago (HUNT, 1989).

Approximately 20 Ma ago a feline named *Pseudaelurus* first appears in French Miocene deposits and forms the basal stock from which the group quickly diversified into a series of

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[3] A primitive feature in comparison with the reduced number of teeth seen in the dentition of more recent fossil specimen and in living species.

conical- and scimitar toothed cats (MARTIN, 1989). The conical toothed cats include all modern true cats as well as their fossil ancestry. The scimitar toothed cats on the other side lead to the now extinct saber-toothed species, the machairodonts. However, TURNER & ANTÓN (1996) point out that the genus *Pseudaelurus lorteti* and *P. transitorius* exhibit a more gracile and slender appearance than those of the genus *P. quadridentalis*, which is built more robust. Hence they suggested a split in the tree of relationships at that point, with one line placed in the subgenus Schizailurus leading through to the fossil and living conical-toothed species of true cats, and another placed in the subgenus Pseudaelurus leading to the saber-toothed species of the machairodonts.

Figure 4.1 schematically demonstrates the relationships of the Felidae after TURNER & ANTÓN, (1996). In this pedigree the conical toothed cats are split in the subfamily Felinae, whereas the extinct saber-toothed cats are classified in the subfamily status of the Machairodontinae. The latter is divided into three tribes: 1. Homotheriini, 2. Metailurini, and 3. Smilodontini.

It should be noted however, that a very recent discovery, studied by BABIARZ, MARTIN et al. (1999) added a new intermediate member[4] to the Machairodont subfamily, which combined scimitar-toothed canines with short, massive limbs of a dirk-toothed predator.

Nonetheless, the first tribe of the subfamily the Homotheriini, also known as the scimitar-toothed cats, are comparatively long-legged and slender and give the animal a particularly unusual appearance, somewhat reminiscent of a hyena. Their canines are relatively short and coarsely serrated. In some forms they may even have cheetah-like skeletal proportions (MARTIN, 1989). They include the North American species of *Nimravides catacopis* found in Hemphilian deposits of Texas, Florida and Kansas, the Eurasian genus *Machairodus* of the Mio-Pliocene as well as the genus *Homotherium* of Europe and Asia, after which the subfamily is named.

The questionable tribe of the Metailurini continues to be a source of confusion and disagreement regarding composition of the group and reconstruction owing to the fact that no complete skeletons nor intact skulls are yet known (TURNER & ANTÓN, 1996). The specimens applied to this tribe are of later Miocene to earliest Pleistocene in age with a predominantly Eurasian distribution. The majority was about the size of a modern leopard, with the upper canines moderately elongated and flattened (TURNER and ANTÓN, 1996). Important genera include *Adelphailurus*, *Metailurus* and *Dinofelis*.

The tribe of the Smilodontini, to which the genus *Smilodon* belongs and towards which this study is focused, became famous through numerous individuals excavated in the Rancho la Brea tar pits in California, making them among the most well known of the ancient predators. Bones from at least 1,200 individuals have been recovered there, and scattered

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[4] *Xenosmilus hodsonae*

about in museums throughout the world. These dirk-toothed cats all possess finely serrated and long canines coupled with short legs built for power rather than speed (BABIARZ, MARTIN, et al., 1999). Cats of the genus *Smilodon* were restricted to North and South America and have never been found in Eurasia.

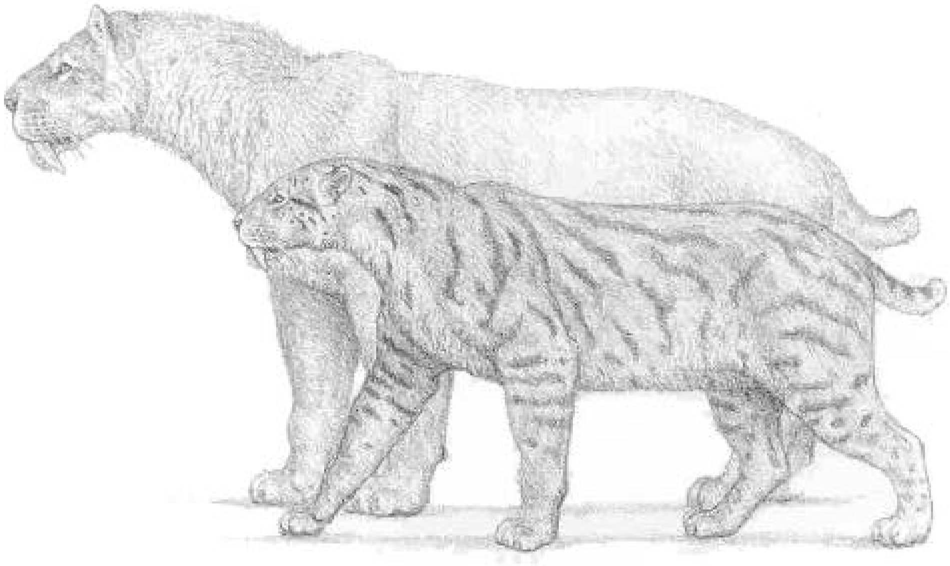

Figure 3.1: Size comparison between S. fatalis (foreground) and S. populator (background). The S. fatalis specimen is a subspecies found in Florida and is slightly smaller than the average Rancho La Brea samples (after TURNER & ANTÓN, 1996).

Despite a complex history of names, three species are generally recognized. The earliest is *Smilodon gracilis*, primarily known from the eastern part of the USA and dated between about 2.5 and 0.5 Ma. It is the smallest of the species and thought to be most closely related to *Megantereon* (see below), its likely ancestor.

Smilodon populator on the other hand was the largest of the three species and approximated in size a modern African lion. It possessed enormously elongated upper canines that protruded well below the mandible: the total length of large tooth specimens approaches 28 cm, perhaps 17 cm of which would have protruded from the upper jaw (TURNER & ANTÓN, 1996). *S. populator* is a species found in the eastern part of South America (see Figure 3.1).

Smilodon fatalis[5] of the Rancho la Brea asphalt beds was a relatively recent saber tooth, known mainly from the later Pleistocene of North America until the end of the last glaciation around 10,000 years ago when it finally went extinct. It is generally intermediate in size, but with important differences from the South American species in skull and body shape and proportions (TURNER & ANTÓN, 1996). In comparison to the African lion, the body of *S. fatalis*

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[5] Also known as *Smilodon californicus*

was about a foot shorter and the hind limbs appear relatively light while the front limbs are strong and powerful extremities. The sturdiness and strength is likewise shown by the rib basket and breastbone (Stock, 1972). The lower segments of the limbs are relatively short in contrast to those in modern big cats. It can therefore be assumed from an analysis of the structural features that these animals were not fleet-footed carnivores like the lion or the tiger. They were probably ambush hunters that stalked their prey such as the slow-moving mammals with which they were associated during Pleistocene time.

Other members of the tribe Smilodontini include the disputable genus of Paramachairodus as well as the genus Megantereon, which has been found in Africa, Eurasia and North America.

The saber-toothed morphology has appeared independently among the Felidae, the Nimravidae, as well as in the extinct order of the Creodonta, and in the suborder of the Marsupialia. Thus the saber-tooth morphology is an excellent example of convergent evolution, since it appeared independently in several evolutionary lineages.

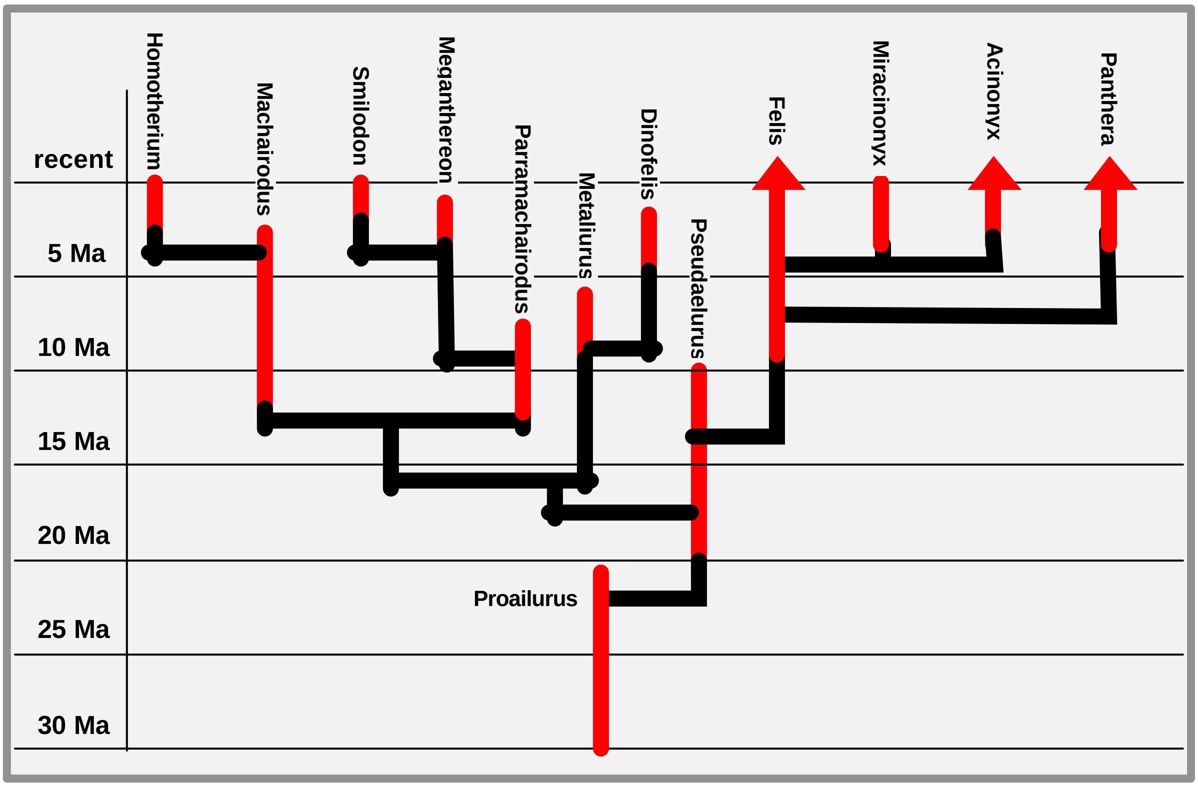

Figure 3.2: Phylogeny of the Felidae after Turner and Antón (1996). See text for further explanation.

With the exception of the genus *Homotherium*, all these various types of sabers had very robust and short limb structures in common [6], a feature that clearly points towards the same

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[6] Although the Creodont *Machaeroides* and the Marsupial *Thylacosmilus* lacked retractable claws.

evolutionary function, namely to subdue and hold prey in a very catlike manner (RIGGS, 1934; TURNER & ANTÓN, 1996).

The following chapter is dedicated to summarizing different kinds of habitats, which cats prefer and how body proportions and limb anatomy are tied to habitat choice and hunting behavior. Moreover, problems involved in making a concrete statement as to precisely how canine shape and forelimb anatomy are related to each other, are demonstrated.

4 MATERIALS AND METHODS

2.1 Measurements

Measurements in the present study are mainly based on the work of Angela von den Driesch (1976). Total skull length (SL) was measured as the distance between akrokranion and prosthion, total dental length (DL) as the distance between the condyle process and the infradentale. Maximum skull width (SW), or the zygomatic breadth, extends from zygion to zygion. The distance between the upper two canines (CD) is equal to the breadth at the canine alveoli. Upper canine shape[7] is characterized by three different measurements: 1. crown height (CH) measured from dentine-enamel junction at alveolar margin to tip; 2. antero-posterior diameter (CX) at base of the dentine-enamel seam; and 3. medio-lateral diameter (CY) at base of the dentine-enamel seam.

The overall length of the humerus (GL) is identical to its greatest length; (Li) stands for the ratio to the inner lever of the attachment of the Teres major[8]; (Bd) is equivalent to the greatest breadth of the distal end of the humerus, whereas (Bt) stands for the greatest breadth of the trochlea. The muscle attachments of the Teres major on the inside of the humerus and on the distal edge of the scapula were somewhat hard to define and precise measurements specifically on the fossil specimen cannot be guaranteed.

The radius was measured in its total length (GL), its greatest medio-lateral breadth of the distal end (Bd) and in its greatest antero-posterior breadth (Qr).

Measurements of the ulna include the greatest length (GL), the greatest medio-lateral breadth (Bd) as well as the total antero-posterior breadth (Qr), and finally the length of the olecranon.

The greatest length of the femur (GL) is often exceeded by the greatest length from the proximal caput femoris (GLC) by a few millimeters. (Bp) is the greatest breadth of the proximal end and (Bd) corresponds to the maximum breadth of the distal end of the femur.

Tibia measurements include the greatest length (GL) and the maximum transversal depth of the distal end (LT).

The length was measured for the astragalus and the calcaneus as well as for the metacarpus and metatarsus. Of the latter two, exclusively the third phalanges were taken.

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[7] Compare to V. VALKENBURGH, B and C.B. RUFF (1987)

[8] See HILDEBRAND, M. (1988)

Finally, two measurements were taken from the scapula: 1. the height along the spina scapulae (HS) and 2. the greatest length of the processus articularis[9] (GLP).

A caliper with vernier scale and a smaller dial caliper served as measuring instruments on the skeletons.

One should bear in mind that for most osteological characters within species, coefficients of variation (*V* s) usually fall between about 4-6 % (MAC FADDEN, 1989).

Since the number of specimens for this study was limited the data inevitably may lead to less representative results (see Statistical Analysis).

Where more than one specimen was available from a species, mean values were calculated for each species so it was possible to work with one figure.

X-ray computer-tomography was applied on the humerus, ulna, and femur for *Smilodon*, in order to determine strength and cross sectional outlines; for the ulna shape and position of the radial notch was established, and for the distal portion of the humerus the angle of the olecranon fossa was examined on the tomographic sections. The X-ray tomography was done in the Röntgen-Zentrum of the Universität Tübingen.

2.2 Material

Measurements were taken on six extant great cat species including the tiger (*Panthera tigris*; SZ3728, SZ3796), lion (*Panthera leo*; SZ3280, SZ7497, 6805), jaguar (*Panthera onca*; Mam.199), leopard (*Panthera pardus*; Mam.203, SZ4227, SZ7301), cougar (*Felis concolor*; Mam.198), and the cheetah (*Acinonyx jubatus*; Mam. 202, SZ3797) in addition to the wolf (*Canis lupus*) [10]. The material was provided by the osteological collection of the University of Tübingen. The fossil material on the other hand, which is primarily restricted to *Smilodon fatalis* of the Rancho la Brea tar pits, was taken from the GPI in Tübingen.

Published discriptions of *Homotherium ischyros, H. serum* and *Xenosmilus hodsonae* (BABIARZ, MARTIN et al., 1999) were employed for morphological comparisons.

Descriptions of musculature anatomy and muscle insertions in extant carnivores (NICKEL; SCHUMMER; SEIFERLE, 1977) were used as a guide for the reconstruction of certain muscles in *Smilodon*.

Due to time constraints and the limited number of skeletons available the measurements on the specimens could not exclusively be carried out on one sex. However, only adult

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[9] glenoid process

[10] see chart in appendix

individuals[11] were measured, and where possible, only the limb elements from the right side were measured.

GONYEA (1976) pointed out that there is a significant added variance component among species for the relative lengths of both the anterior and posterior limb bones. Moreover, sexual dimorphism in cats is markedly high. In addition, various individuals of the same species living in a different habitat can vary considerably in size and to a lesser degree in their proportions as well. If not explicitly labeled on the specimen, I was unable to identify possible occurring subspecies status in the material, although differences in morphology and lifestyle can reach tremendous differences regarding morphology, etc.

This study is restricted to metric measurements, superficial features and X-ray CAT scans and does not attempt to be definitive or comprehensive. The taxonomic breadth, sample sizes, and number of features examined are small. However, it does suggest possible patterns and raises concerns that need to be addressed in future investigations.

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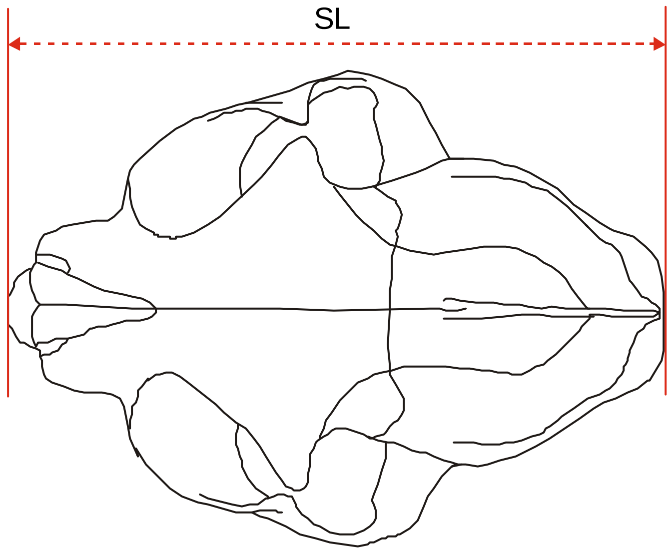
[11] Judged by closed epiphyses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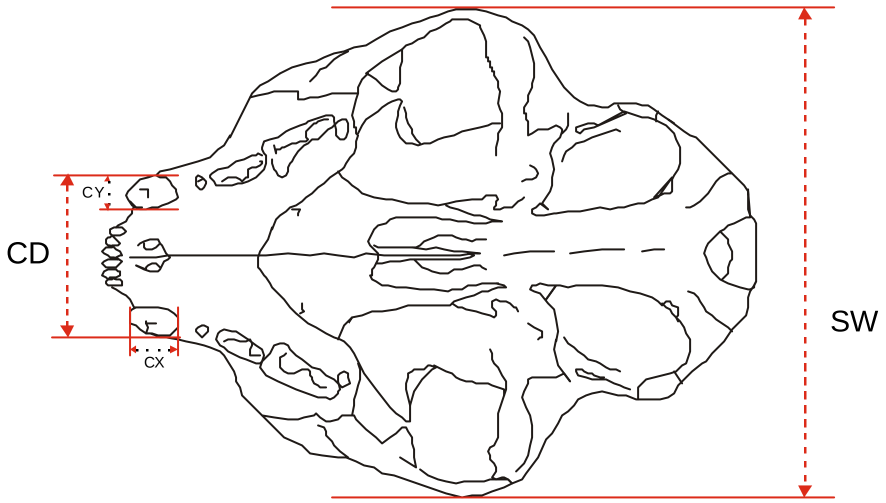
CY
CD
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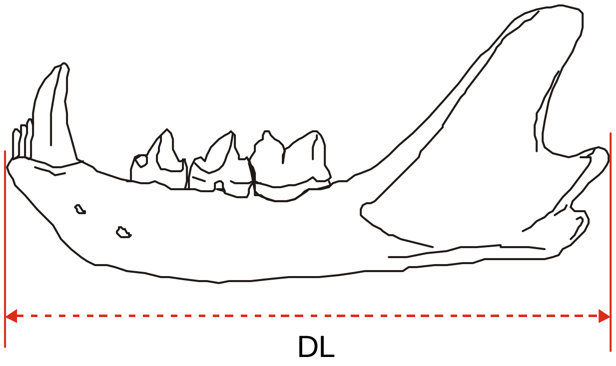
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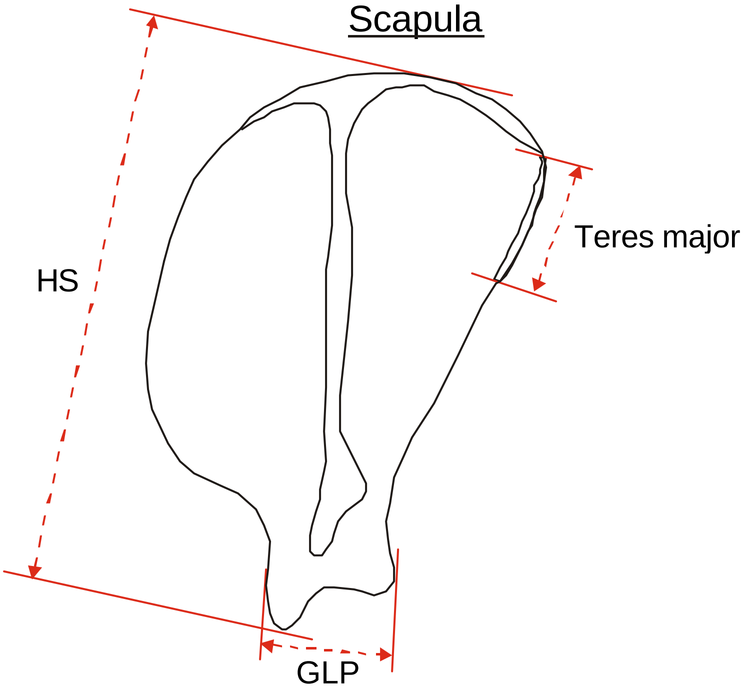
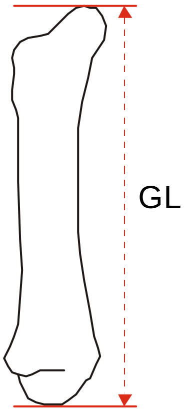
Scapula



Mtc.



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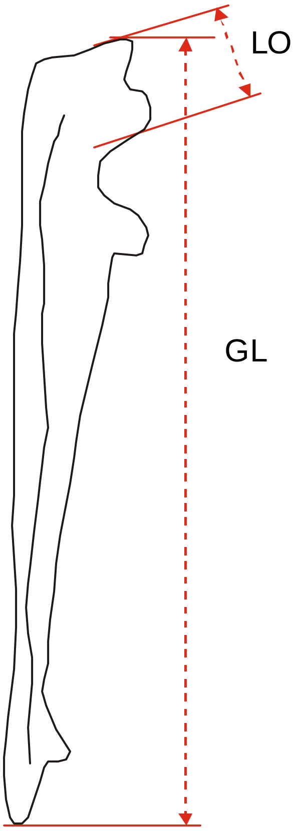
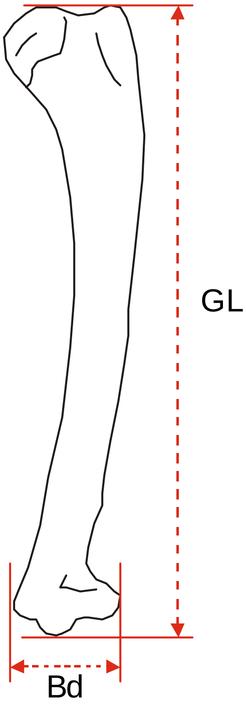
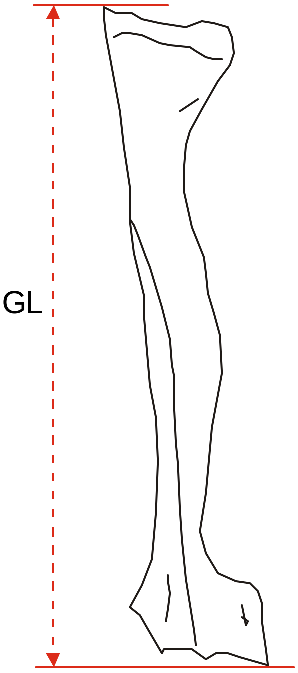


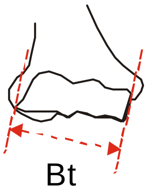
Humerus



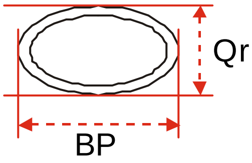
Radius



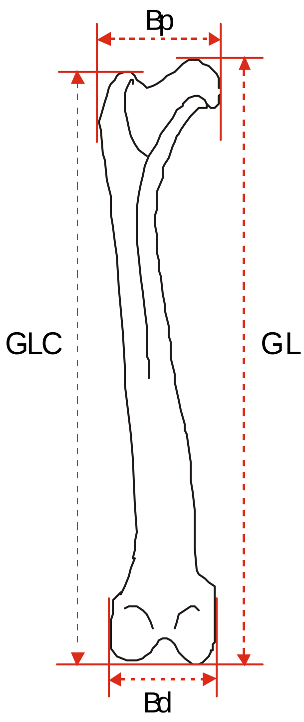
Humerus (dist.)



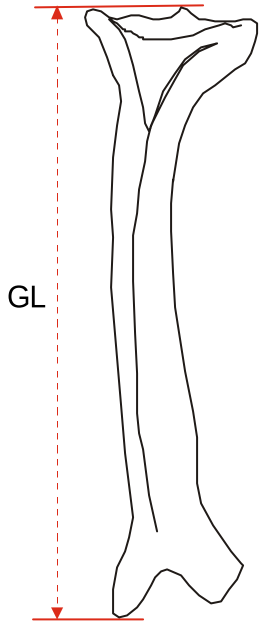
Radius head (prox.)



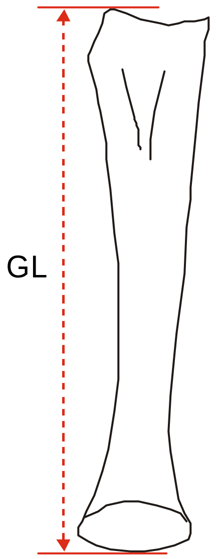
Femur



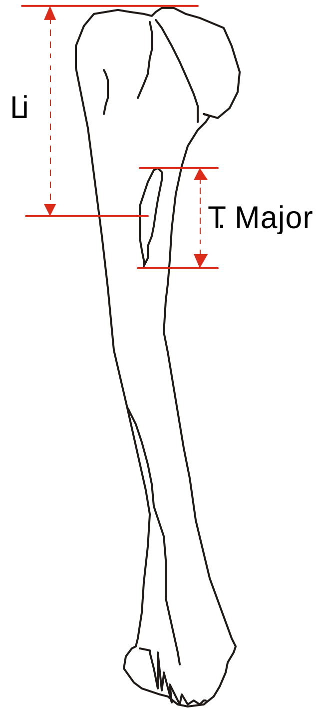
Tibia



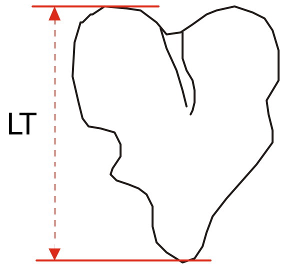
Metatarsal



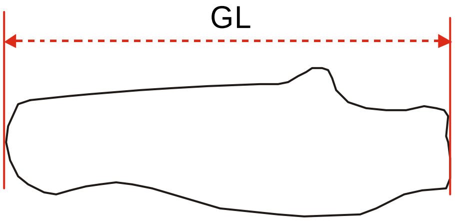
Humerus (medial)

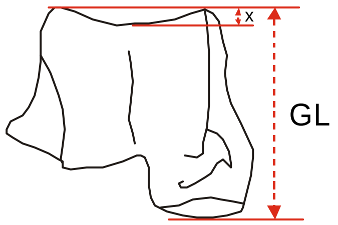


Tibia prox.



Calcaneus





Astragalus

5 RESULTS

5.1 Limb Proportions

Limb proportions are strongly correlated with hunting behavior and locomotion, which in turn is often expressed by the choice of habitat (GONYEA, 1976). Furthermore, it is presumed that the development of long saber-like canines is dependant on strong and sturdy front limbs that would provide a larger insertion area for important muscles.

In order to testify these theories it is necessary to compare various limb segments of different species with each other. The table provided in the Appendix lists all measurements of the examined species.

Humerus, Ulna, Radius, Metacarpus III: Figures 5.2.1, 5.2.2 & 5.2.3 (top)

The cheetah forms one extreme in having the longest and most lightly built limb bones of all the big cats, which enables it to run at very high speeds. [12] It should be noted that the relative length of its anterior limbs are significantly longer and less massive than it is for those felids that inhabit a more dense terrain (e.g., *P. onca*). The cheetah has a radius/ humerus length ratio of ca. 1.0 and an ulna/ humerus ratio of about 1.16, which is almost as high as for the highly cursorial wolf (1.02 and 1.20). This facilitates the animal a longer "forearm" in relation to its size. In contrast, *S. fatalis* exhibits the shortest relative limbs with a radius/ humerus ratio of around 0.79 and an ulna/ humerus ratio of about 0.97. The jaguar displays the shortest humero-radial and humero-ulna ratios among the living big cats with 0.82 and 1.01 closely followed by the tiger, the cougar and the leopard, respectively.[13] The lion has proportions that fall somewhat in between those of the cheetah's and those of the other pantherine cats with ratios of approximately 0.90 and 1.04.

Unfortunately, no data are available for the lengths of the radius of the fossil species of *H. ischyros, H. serum, and X. hodsonae.*

The proportions between the humerus and the ulna however, are comparable to the humero-radial ratios. The segment ratios of the humero-ulna lengths in *H. ischyros* approximate 1.10 and its relative *H. serum* reaches 1.05. The recently discovered saber-toothed cat from the Irvingtonian of Central Florida *Xenosmilus hodsonae* on the other hand (BABIARZ et al., 1999) possessed an even shorter ulna relative to the humerus than *S. fatalis* with an index of ca 0.89.

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[12] See Table 1

[13] See Figure 5.2.1 and 5.2.4

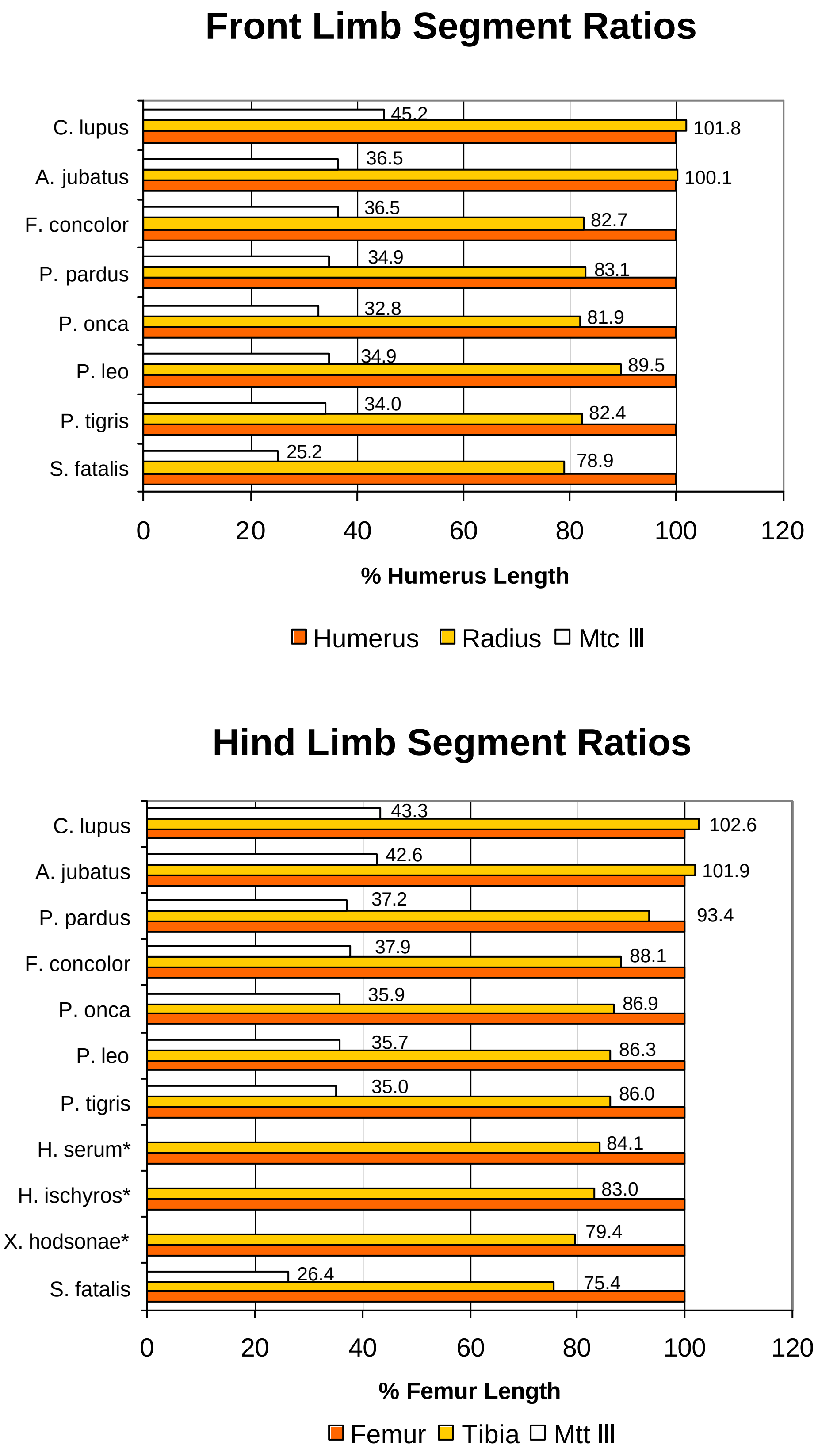
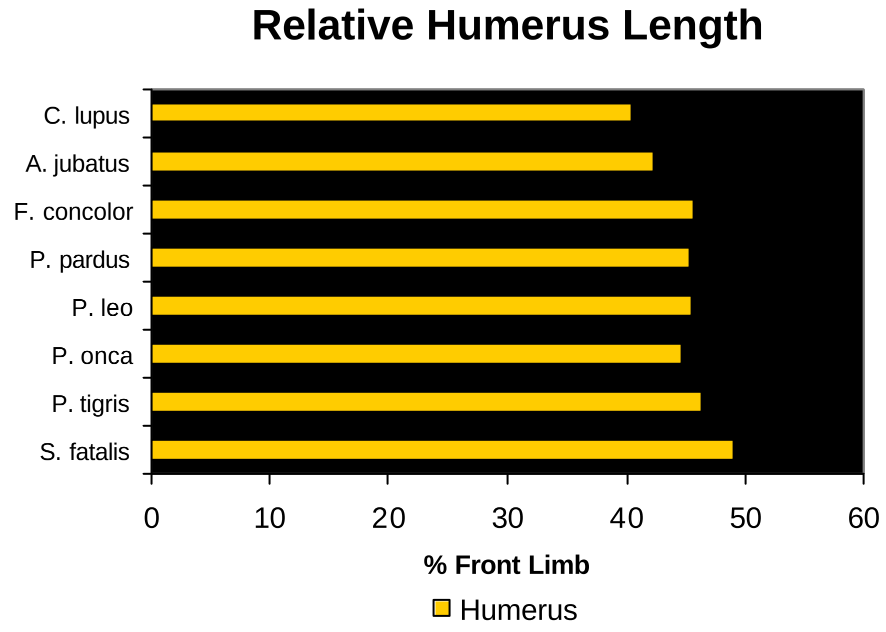


Figure 5.2.1: diagrams illustrating the relative proportions of the humerus/ radius/ metacarpus (top) and femur/ tibia/ metatarsal (bottom) of the measured specimen plus fossil data (*) taken from the studies of BABIARZ et al. (1999). Each species is shown with the humerus and femur scaled to the same length (100%), and the radius/ metacarpal - and tibia/ metatarsal length expressed as a percentage of the humerus- and femur measurements, respectively.



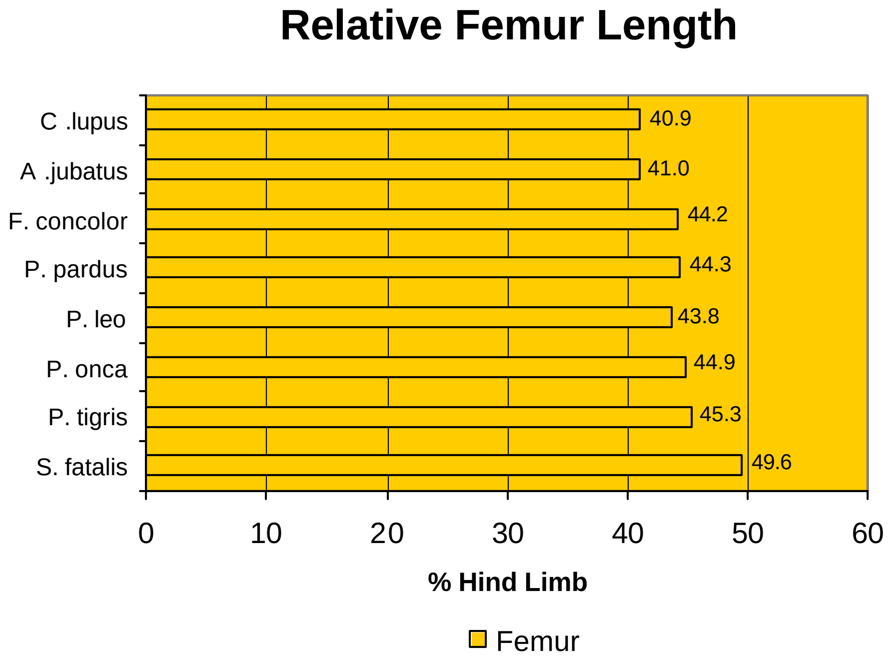
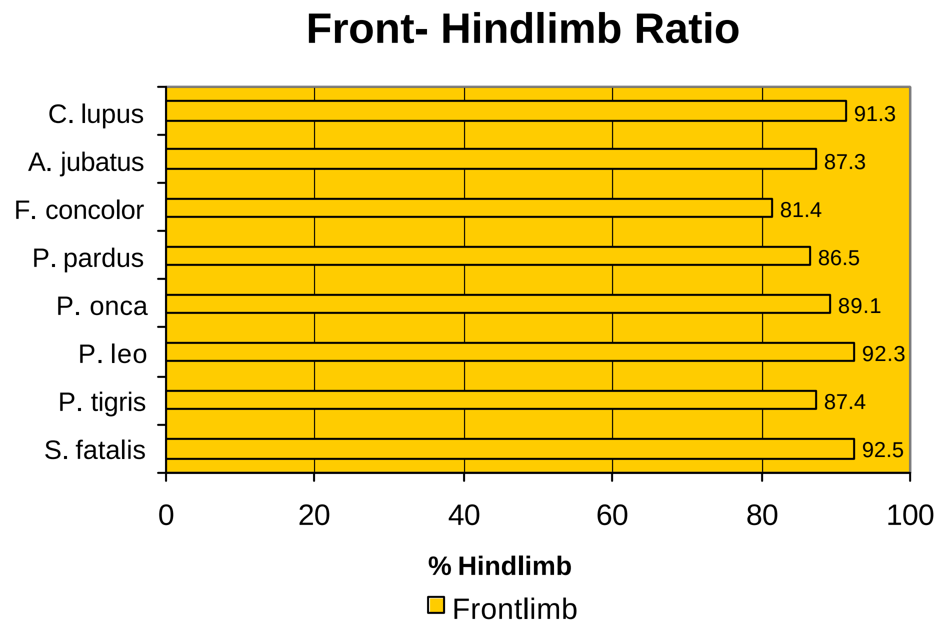


Figure 5.2.2: relative length of both the humerus and the femur scaled to the limb length (100%), which is consisted of the humerus, radius, and metacarpal for the anterior limb and the femur, tibia, and metatarsal bones for the posterior extremity.



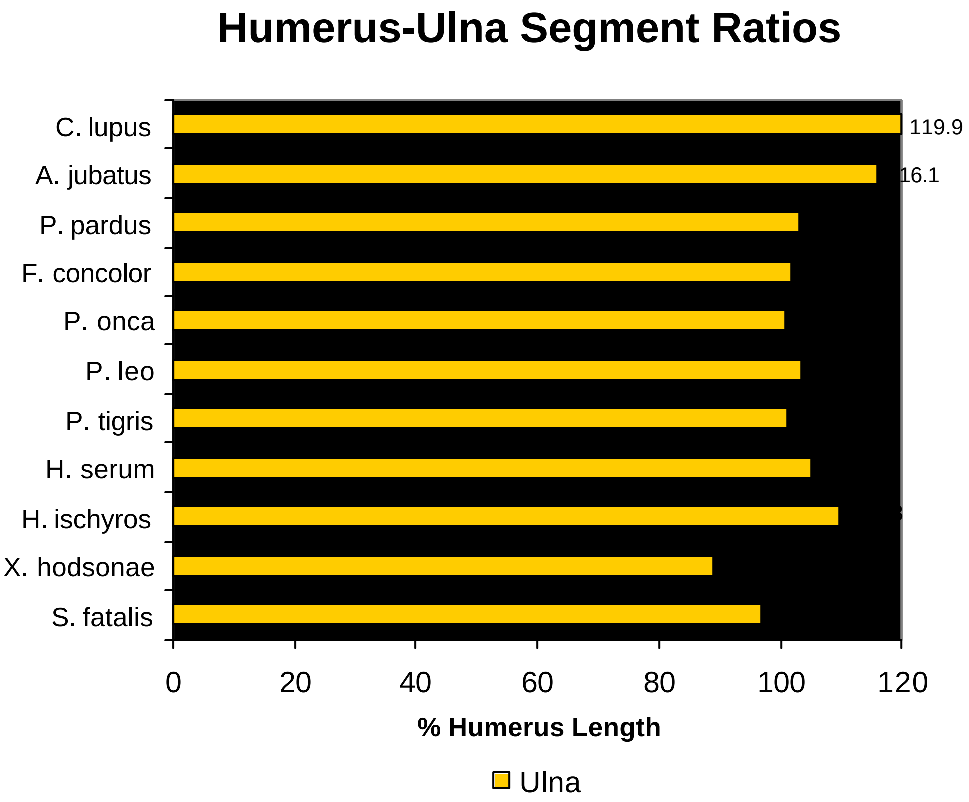


Figure 5.2.3: Front limb section proportions between ulna and humerus (top). Humerus scaled to the same length (100%). Length comparison between hind- and front-limbs at bottom. The hind limb is scaled to the same length (100%) and the front limbs are expressed as a percentage of the latter. The anterior limb is calculated of the maximum lengths of the 3rd metacarpus, the radius, plus the humerus. The posterior limb is the sum of the 3rd metatarsus, the tibia, and the femur.

Figure 5.2.2 shows the relative length variations of the humerus to the overall length of the anterior limb. It is conspicuous that *Smilodon's* humerus takes up almost half (49%) of the length of the entire forelimb, whereas the cheetah's humerus length is relatively short in comparison with 42.3%. Among the living big cats, *Panthera tigris* comes closest to *S. fatalis* with a humerus length of 46.3%, followed by *P. pardus*, *Felis concolor, P. onca* and *P. leo* of which the humerus encompasses a length between 45-46%.

Calculations showed that *Smilodon,* which has a radius-metacarpus ratio of 0.32, is very similar to the cheetah's index of ca. 0.36. *P. onca*, has an index of 0.40 similar to the lion's (0.39), leopard's (0.42) and tiger's (0.41) proportions. *F. concolor* in turn, exhibits a ratio of 0.44 and thereby falls slightly behind *C. lupus*.

Comparisons between metacarpal length and humeral length revealed (see Figure 5.2.1), that in all of the extant cats studied, there is only a minimal deviation of the metacarpus length, which lies in between ca. 0.33 in the jaguar and 0.365 in the puma and cheetah. *Smilodon* again forms an exception in having a metacarpus/ humerus ratio of 0.25.

Femur, Tibia & Metatarsus III: Figures 5.2.1 & 5.2.2 (bottom)

The cheetah exhibits the relatively highest posterior limb ratio of almost 1.01 followed by the leopard with 0.93, the puma with 0.88, the jaguar closer to 0.87, and the lion and tiger both with a femur/ tibia index of 0.86. On the opposite, the two fossil genders of *Homotherium* have even smaller ratios closer to 0.83 – 0.84, and *X. hodsonae* and *S. fatalis* show tendencies of extreme shortening of the tibia bone against the femur, in which *S. fatalis* has a ratio of 0.75 and *X. hodsonae* one of 0.79.

On the other hand, if the proportions between the femur and the metatarsus are compared, as shown in Figure 5.2.1, it is striking that the cheetah, although having a relatively short metacarpus for the extant cats, exhibits the longest metatarsus with a ratio of almost 0.43, which is very close to the wolf's femur/ metatarsus ratio of 0.433. The mountain lion's quotient of 0.38 is only slightly higher than its humerus/ metacarpus ratio and is followed by the leopard (0.372), the jaguar (0.359), the lion (0.357), and the tiger (0.35). *Smilodon* once more shows the lowest extreme with a ratio of approximately 0.26. In addition, the proportions between tibia and 3rd metatarsal (not illustrated) also display eloquent dissimilarities among the studied felids, but with different stresses in the species when compared with the anterior limb. The puma is observed in having the highest ratio of 0.43 equal to the wolf's proportions, in contrary to *Smilodon*, which exhibits an index of 0.35. The remaining species rank relatively close together in the following order: cheetah (0.417), jaguar (0.414), lion (0.413), tiger (0.407), and leopard (0,398).

Equivalent to the relative length of the humerus with its corresponding anterior limb length, the relative portion of the femur against the posterior limb length, is also greatest in *Smilodon* with 49.6%, followed by the tiger (45.3%), jaguar (44.9%), leopard (44.3%), the puma

(44.2%), and lion (43.8%). Likewise, *A. jubatus* has the shortest relative femur length, which makes up only 41 % of the whole extremity equal to those of the wolf.

Figure 5.2.3 indicates that the anterior extremities of *F. concolor* are comparatively shorter (81.4%) than the length of the posterior limb. This difference is relatively greater than that of the other large felids investigated: *P. tigris* (87.4%); *P. leo* (92.3%); *P. onca* (89.1%); *P. pardus* (86.5%); *A. jubatus* (87.3%); *S. fatalis* (92.5%). Nonetheless, all of the specimen studied, are characterized by longer hind limbs than front limbs.

Calcaneus: Figure 5.2.4

Smilodon possesses the longest relative length for the calcaneus with a percentage of 35.1. The lion (33.3%), tiger (32.5%), and jaguar (31.6%) all range within close boundaries followed by the leopard, which has a calcaneus that makes up 29.2% of the tibia. The puma on the other hand exhibits a rather short calcaneus (30.5%). For the cheetah it makes up only 27% of the tibial length, whereas for the wolf the calcaneus has an index of 27.9%.

Olecranon: Figure 5.2.5 (top)

The cheetah was observed in having a relatively short olecranon compared to the ulna with a ratio of 10.4, followed by *H. serum* (13.2) and the wolf (13,7). The pantherine cats on the other hand, like the lion, the olecranon makes up to 18 % of the entire ulna length. The jaguar and the puma exhibit percentages that are closely together with ratios of approximately 0.19, followed by *Smilodon* and *X. hodsonae* both with a ratio in the vicinity of 0.17. At last the tiger and leopard both have ratios of ca. 0.16.

Caput Radii: Figure 5.2.5 (bottom)

Canis exhibits the lowest approximation to a circular shape of the proximal radial head with a ratio of 0.69, the cheetah is only little behind the wolf with 0.74%. The tiger and jaguar are followed closely by the cheetah with ratios of about 0.73. The cougar in turn falls only slightly behind *Smilodon* with an index of ~ 0.77. The leopard surpasses the lion with a quotient of approximately 0.77 in contrast to 0.75. In general can be said that the radial head within the Felidae was found to vary arbitrarily for different species except for the cheetah, but at the same time shows tendencies for a more elliptical shape than that of the canids (see also GONYEA, 1978).

Radial Notch: Figure 5.2.7

The figure illustrates diagrammatic cross-sections of the radial notch for the right ulna and demonstrates that the cursorial cheetah exhibited a lateral position of the radial notch whereas the dog's is facing more anteriorly. *Smilodon* exhibited the largest angle of inclination of around 65?, whereas the rest of the big cats more or less range within 50?.

Olecranon Fossa: Figure 5.2.8

P. onca and *N. nebulosa* were recorded with the largest angles for the olecranon fossa with 14? of the large living felids, whereas the degree of inclination for the cheetah has the lowest angle (3?) of any felid. Both the lion and leopard were observed with angles of ca. 13?. Unfortunately, no data are available for the tiger and cougar. Figure 5.2.7 illustrates the various angles of the olecranon fossa for the dog, cheetah, margay, and *Smilodon.* The latter is observed in having the greatest angle of approximately 20? to the long axis of the body.

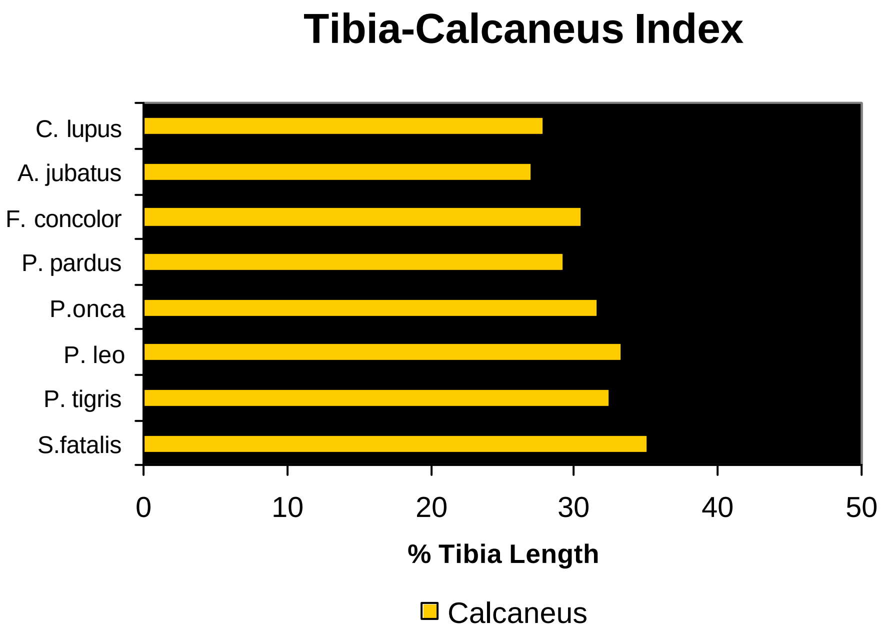
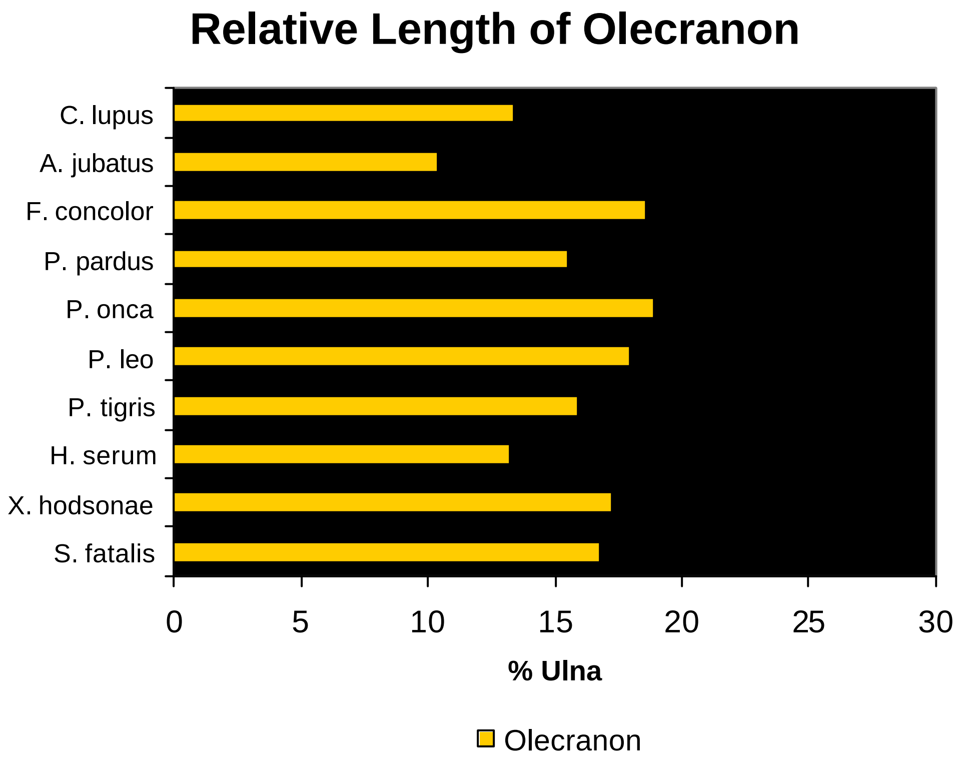


Figure 5.2.4: Relative length comparison between tibia and calcaneus. Tibia is scaled to 100%, but only calcaneus is shown on this chart.



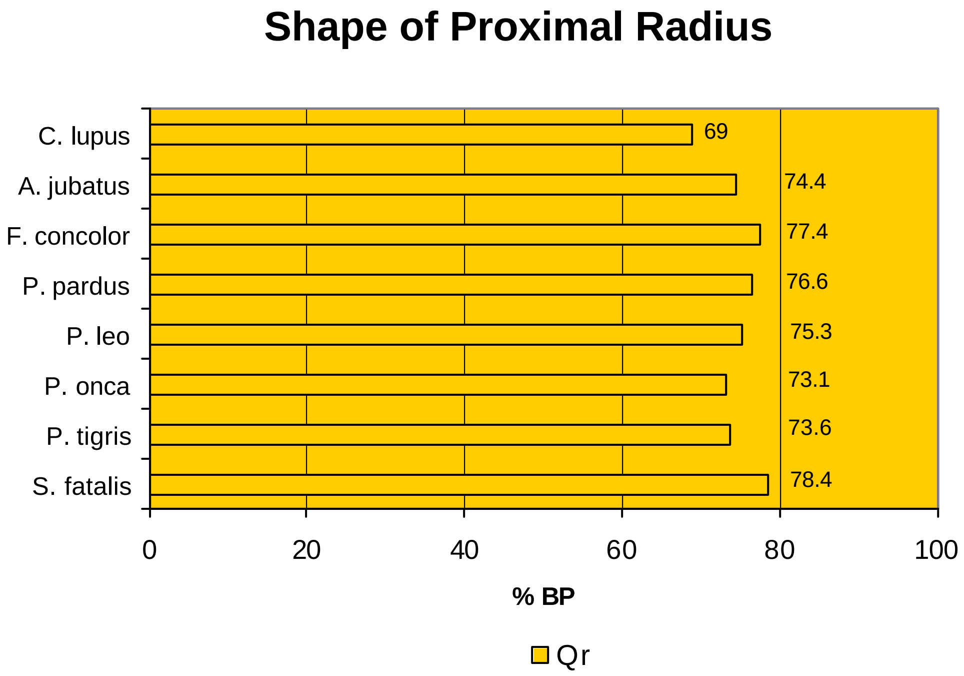


Figure 5.2.5: Relative length comparison between the total ulna length and its corresponding olecranon length (top) and the cross-section of the Caput radii (BP = 100% versus Qr).

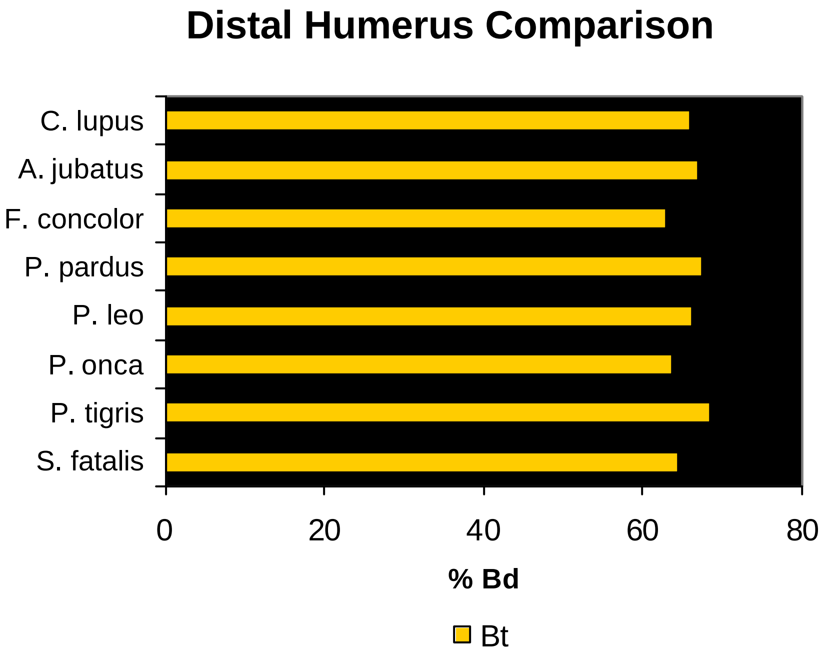


Figure 5.2.6: Proportions between the Condylus of the humerus (Bt) and its distal breadth (Bd). Bd scaled to the same length (100%), while Condyli are expressed as a percentage of the latter.

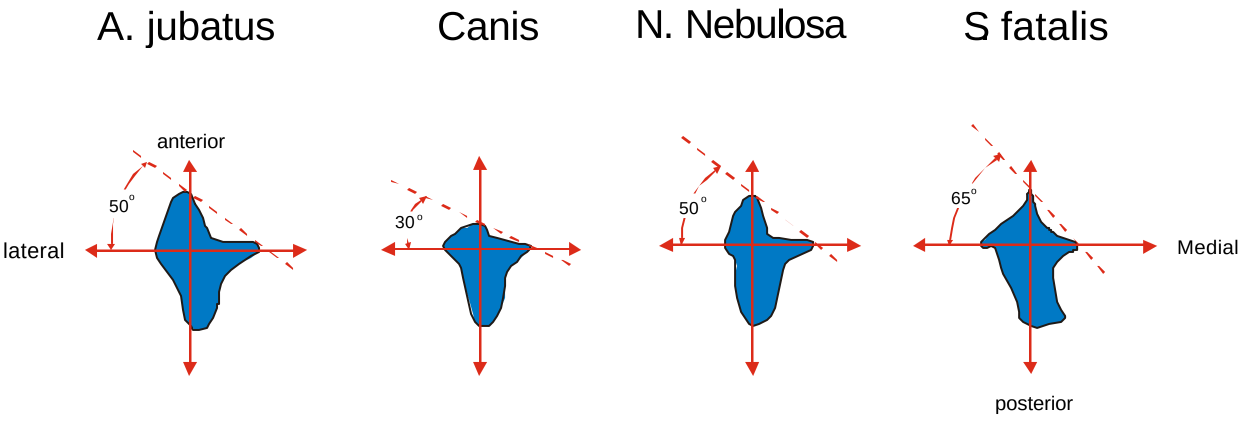


Figure 5.2.7: Diagrammatic cross-sections of the right ulna illustrating the orientation of the plane of the radial notch. All figures are reduced to the same size (after GONYEA, 1978).

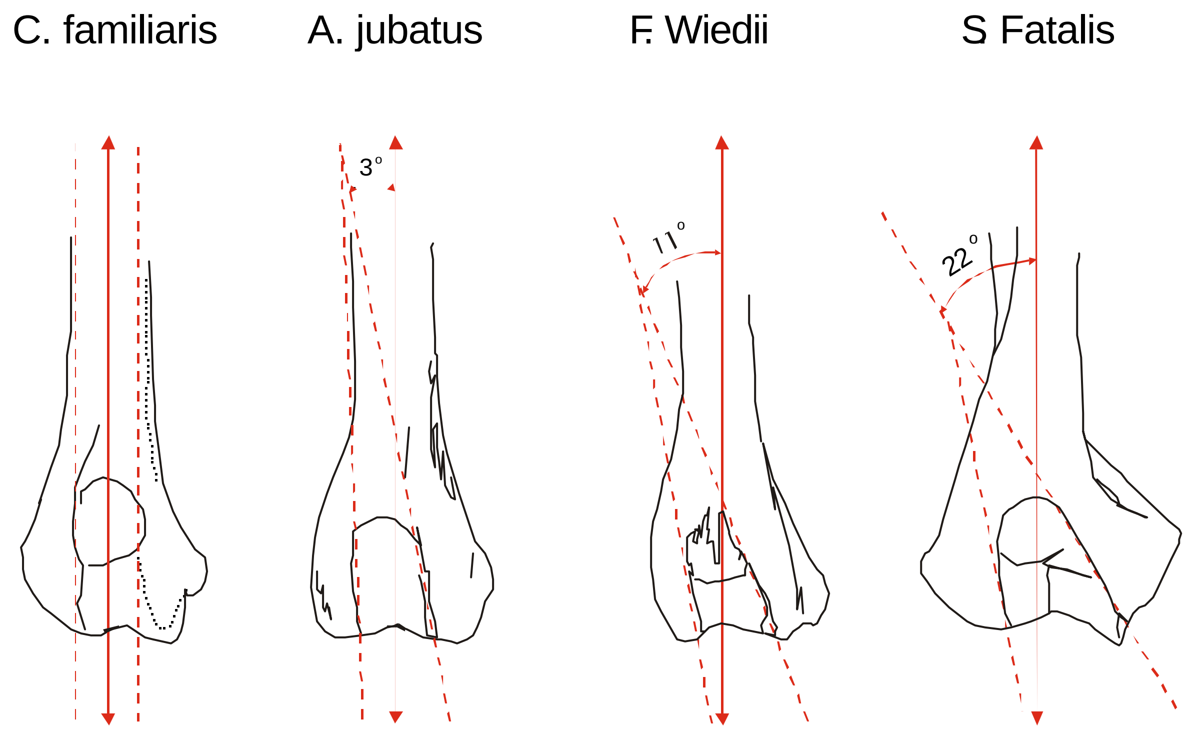


Figure 5.2.7: Illustrations of the posterior surfaces of the left humerus of representative carnivorans demonstrating the position of the olecranon fossa relative to the long axis of the humerus. For comparative purposes, all figures are reduced to the same size (after Gonyea).

Humerus, Distal: Figure 5.2.6

Measurements of the distal humerus include its greatest width against the maximum extension of the Condylus humeri[14]. The latter is one of actually three joints that form the elbow joint, which builds a hinge-like articulation with the trochlear notch of the ulna. The differences regarding the relative strength of the humeral trochlea against its distal width show only slight variation between species. However, the cougar is shown to have the lowest ratio of 0.63 falling right behind the jaguar, which has an index of 0.637. *S. fatalis* has a relatively narrow epicondyle as well (0.645), which is even smaller than that of the wolf (0.66) and the cheetah (0.67). The tiger is observed in having the highest ratio (0.684) before the leopard (0.675) and the lion (0.662). The wolf, which broadly resembles the cheetah in habitat preference and limb proportions, has an index of 0.66 in comparison but rather shows similarities to the leopard and lion.

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[14] trochlea

Tibia, Proximal: Figure 5.2.8 (top)

The proximal portion of the tibia (condylus lateralis and medialis), which forms the knee joint and articulates with the corresponding distal femur (condyli femoris), is shown in Figure 5.2.8. Its length was compared with that of the tibia length. It is *S. fatalis* (29.5%), *P. leo* (27.2%), and *P. onca* (27.0%), which have ratios that clearly exceed those of *A. jubatus* (21.0%) and *C. lupus* (21.8%). The exception is found in *P. pardus* (22.5%), which is only little above the index of the wolf. *P. tigris* (24.6%) and *F. concolor* (24.0%) are intermediate in their proportions.

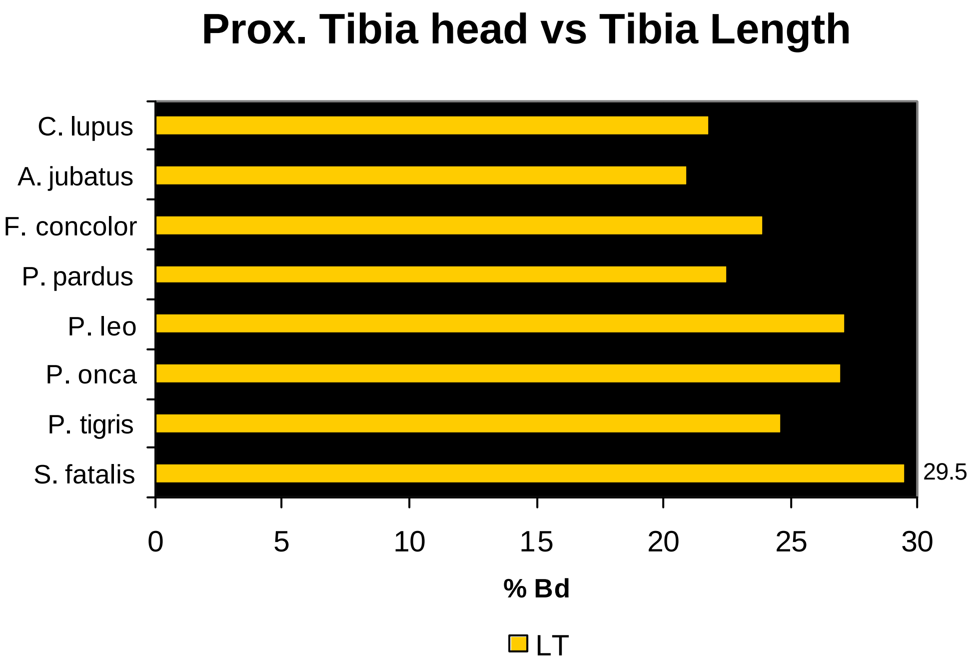
Femur, Proximal: Figure 5.2.8 (bottom)

Positioned laterally of the Caput femoris lays the Trochanter major. The results indicate that the Trochanter major exceeds the opposing Caput femoris with only a lightly by about 0.05 cm in the jaguar and 0.65 cm in the cougar. The wolf and *S. fatalis* in turn, exceed the opposing femoral joint with around 0.2 cm (see Appendix).

The overall width of the proximal head of the femur between Trochanter femoris and Caput femoris is plotted in Figure 5.2.8 together with the ratios of its distal ends. It is measured against the femoral length. *Smilodon* is observed in having a relatively long proximal head with a percentage of over 26%, followed by the lion with almost 25%. The jaguar's proximal end takes in 23.5%, the wolf's 23.4%. The tiger, leopard, puma, and cheetah show a relatively low percentage compared to the femur with ratios between ca. 0.22 and 0.20, respectively.

Scapula: Figure 5.2.9

A most apparent feature seen in this chart is that the wolf exhibits the relatively broadest glenoid process compared to its shoulder length of all the investigated species. The cheetah on the opposite shows the lowest degree of enlargement, whereas the rest of the cats more or less move within the same range between the wolf and cheetah. The problematic insertion area of the T. major muscle on the lower distal margin of the scapula is best developed in fast running cats of a more open terrain such as *F. concolor* (0.41), *A. jubatus* (0.381), and *P.leo* (0.353), but also the tiger shows ratios identical to the lion. Forest dwellers as *P. onca* have ratios that range in between 0.27 – 0.28. *P. pardus* is a little above this figure compared to the latter two with an index of 0.302.



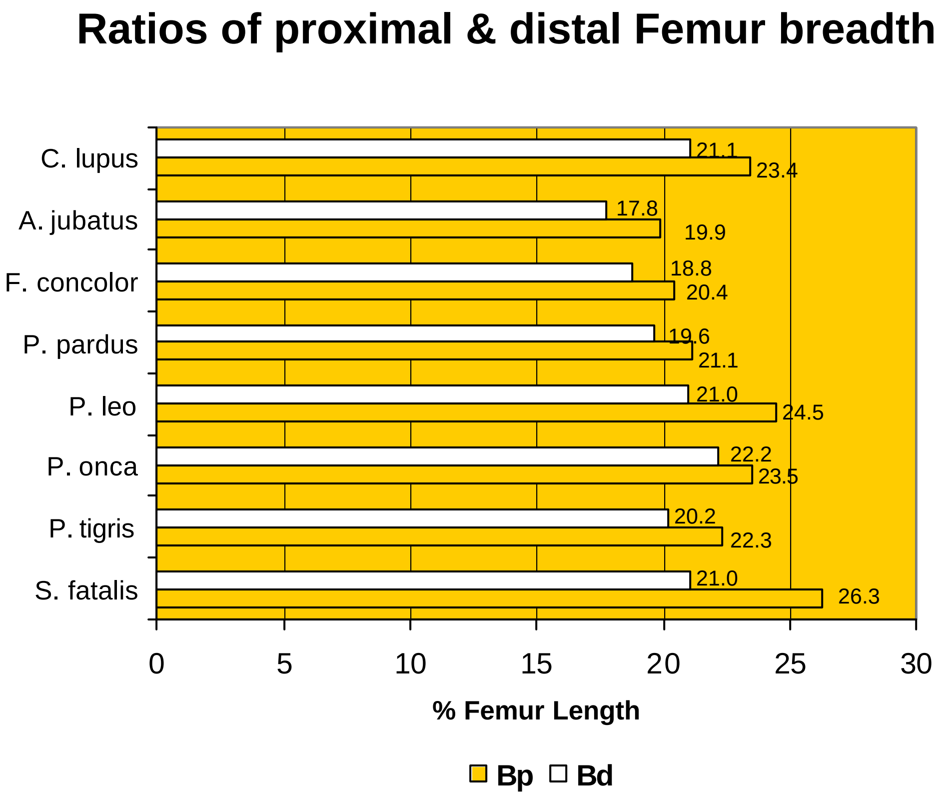


Figure 5.2.8: ratio between the width of the proximal tibia, which is part of the knee joint, and the tibia length (above). Comparison between distal-and proximal maximum breadth of the femoral joints (below) scaled against femur length.

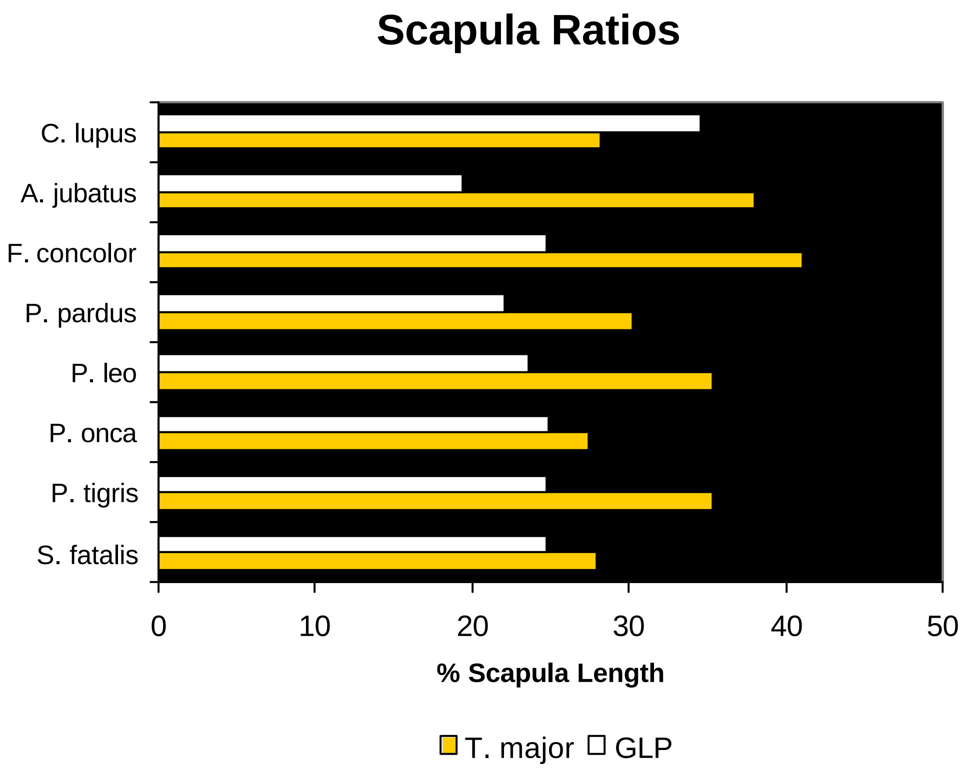
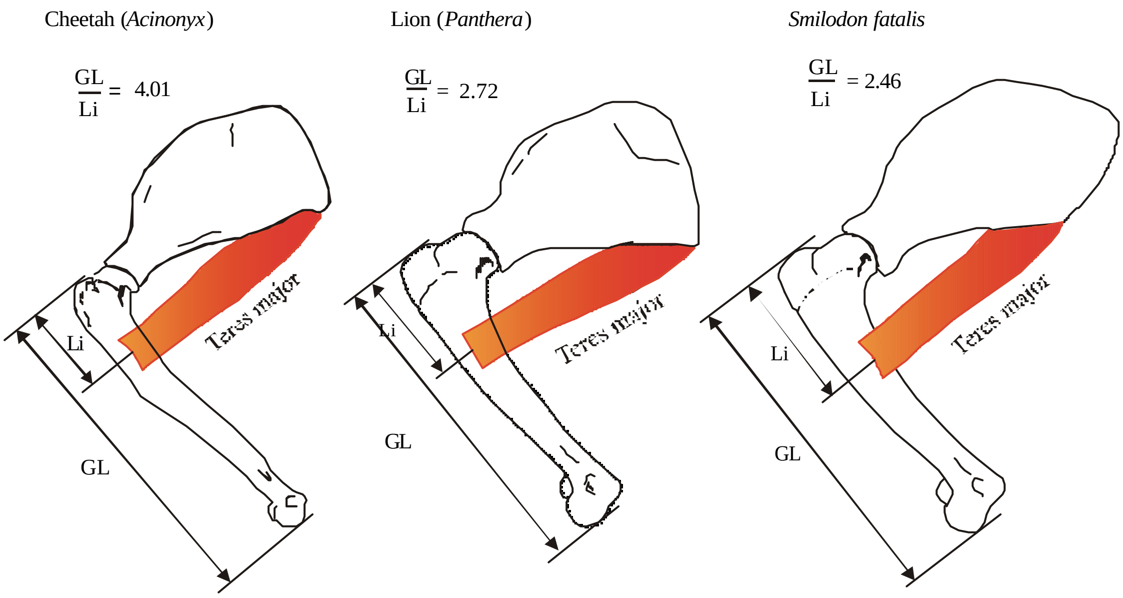


Figure 5.2.9: proportions of glenoid process and assumed Teres major muscle attachment area of the scapula. Scaled to the maximum length of the scapula (compare Figure 3.2.2).

Teres major:

Figure 5.2.10 demonstrates the reconstructed insertion areas of the T. major muscle on both the scapula and the humerus inferred on the basis of superficial scars or delimitable surfaces. The results indicate, that *A. jubatus*, as the fastest land animal, exhibits a T. major attachment scar closer to the joint than any other cat or the wolf (see Figure 5.2.10 and Table 5.2). *S. fatalis* in comparison, is shown to be the exact opposite with a T. major muscle attaching far away out from the shoulder joint. The pantherine cats range relatively close within 2.68 and 3.00 between the latter two, while the cougar goes towards the cheetah and wolf with a T. major attaching relatively close to the joint.



Cheetah (*Acinonyx*) Lion (*Panthera*) *Smilodon fatalis*

	GL/ Li	GL/ T. major
S. fatalis	2,42	13,9%
P. onca	2,68	13,6%
P. leo	2,77	17,0%
P. tigris	2,69	15,2%
P. pardus	3,00	15,9%
F. concolor	3,32	15,4%
A. jubatus	4,02	14,4%
C. lupus	3,35	14,6%

Figure 5.2.10: Contrast between insertion of the Teres major on the humerus of A. jubatus (left), P. leo (middle), and S. fatalis (right). The ratio of the out-lever (GL) to the in-lever (Li) is greater for cursors (after Hildebrand).

Table 5.2: Ratios for all of the studied carnivores (left) and percentage of T. major insertion area against humerus length.

Humerus Cross-Section: Figure 5.2.11

An index for the ellipticity of the shaft is obtained by dividing the minimum diameter by the maximum diameter at midshaft (Taylor, 1974). Thereby a figure of 100% indicates a circular cross-section or zero ellipticity. The shaft of the humerus in *Smilodon* was x-rayed in order to exemplify its cross-sectional outline and the strength of its bone wall (see Figure 5.2.11). It is striking that the midshaft cross-section is distinctly laterally compressed in *Smilodon* (76%). The bone wall of the femur in turn, doesn't seem to be extraordinarily massive, except in the y-plane it appears to be stronger in thickness.

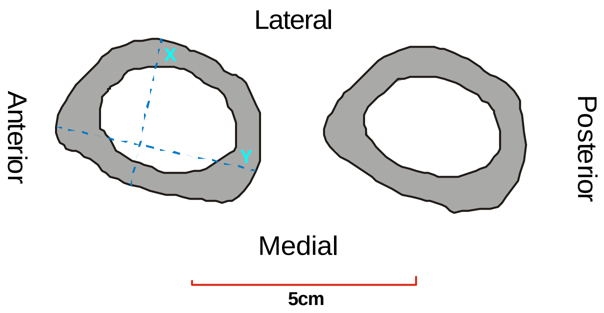


Figure 5.2.11: Cross section through the midshaft of the humerus of S. fatalis. Note the laterally compressed outline in the antero-posterior plane.

Y = 4,62 cm; x = 3.33 cm (= 72.1 %)

5.2 Skull Proportions

The proportions of skull characteristics are restricted to a handful of comparisons in the present study, since a lot of studies especially those of EMERSON & RADINSKY (1980) concentrated exclusively on the cranial morphology also by means of morphometric length collations.

However, it is beneficial for this work to add cranial to post-cranial length proportions since length increase or decrease of sections in both body portions seem to some extent be strongly correlated with each other.

Studies from EMERSON & RADINSKY (1980) exemplified various adaptations in skull morphology between saber-toothed cats and conical toothed felines, which mainly represent modifications for an increasing maximum gape (see Chapter 2).

VAN VALKENBURGH & RUFF (1986) compared canine lengths in different cat species with skull lengths. They concluded that the relative skull length is a good predictor of stress felt at the canines because of its close correlation with muscle size and moment arms.

Measurements in the present study include comparisons between skull length against skull width and canine length, skull width with canine distance (Figure 5.3.1), skull length against dental length, and cross-section of canines with canine height (Figure 5.3.2).

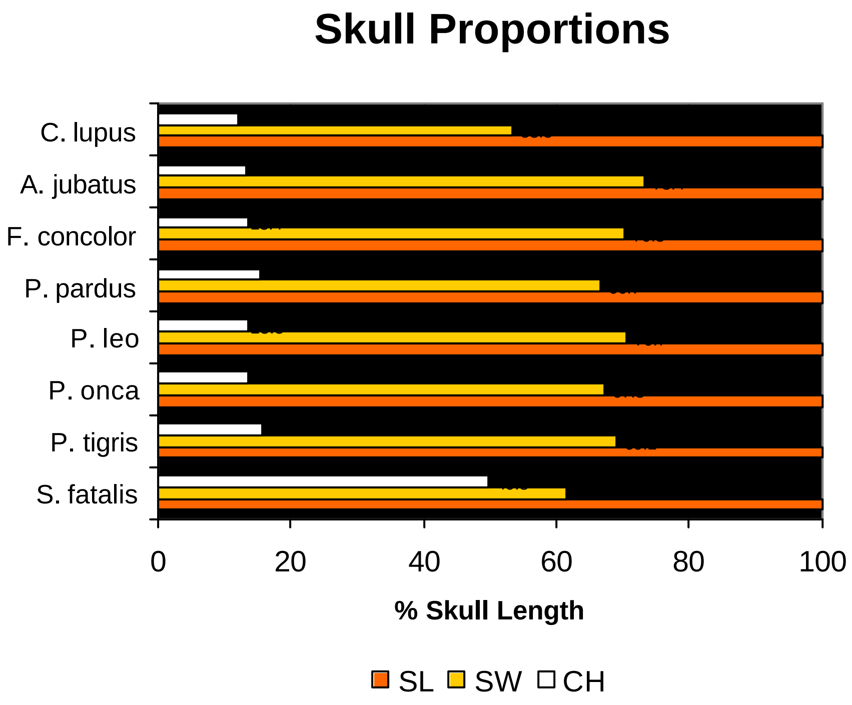
Canine Length & Skull Width: Figure 5.3.1 (top)

Of course, it is easy to recognize that *S. fatalis* has the longest canine teeth relative to the skull length, thus its name, while *C. lupus* has the shortest ratio of 0.122 in comparison. The rest of the modern cats range in between 0.132 in the cheetah up to 0.156 in the tiger.

The relative skull width was also correlated with the skull length. Thus results may be broadly similar for one or the other study objects. This is true at least for the wolf, which exhibits the relatively narrowest skull, which takes in only little more than the half of the skull length with a ratio of about 0.54. As EMERSON & RADINSKY already pointed out in their studies, my results confirm a relatively narrow skull for *Smilodon* in contrast to the conical toothed modern cats. For the cheetah with its shortened skull, the zygomatic arches make up more than 73% of the length, whereas the tiger, puma and lion range in between 69-71%. The jaguar and leopard reach about 67%.

Canine Distance: Figure 5.3.1 (bottom)

This chart expresses the relations between the upper canine-distance to the width of the skull. For *Smilodon* the clearance of the upper two canines makes up around 47% of the skull width, whereas for the wolf it is close to 36%. For modern big cats relative canine distance more or less correlate with the proportions of the skull width and usually ranges in between 38-41%. Only the cheetah is observed with a lower figure in this proportion of around 34%.



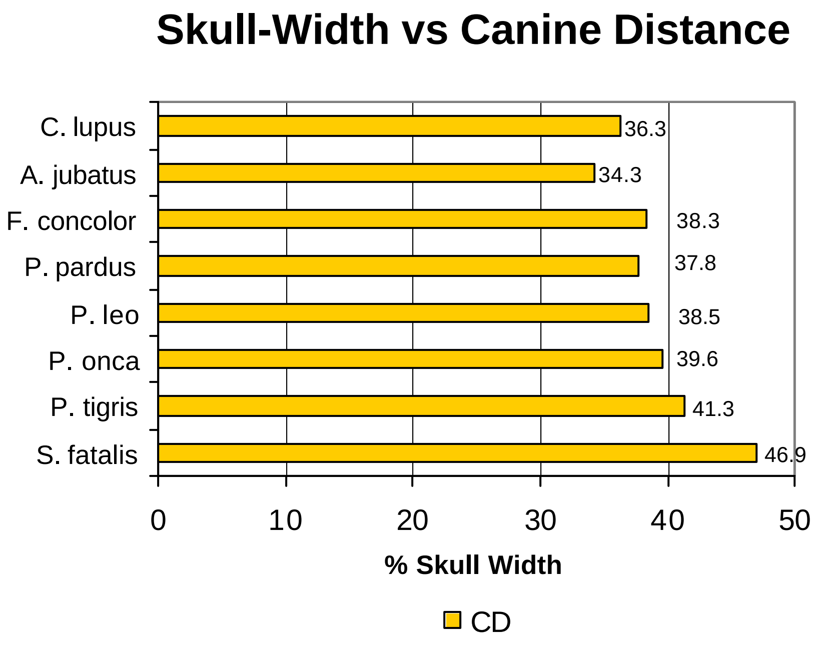


Figure 5.3.1: length ratios between skull width (SW) and canine height (CH) against skull length (SL) in top figure. The bottom figure illustrates the percentage of the canine distance (DC) to that of the skull width.

Canine Shape: Figure 5.3.2 (bottom)

The chart illustrates the shape of the canine teeth, which were measured after the same principal as Van Valkenburgh and Ruff (1986). The antero-posterior (x) and the medio-lateral diameters are plotted against the canine height. Only *C. lupus* and *S. fatalis* exhibit medio-lateral flattened canines, of which the antero-posterior breadth is more than twice as long as the medio-lateral breadth in the wolf (50,1%) and even higher in *S. fatalis* (51,2%).

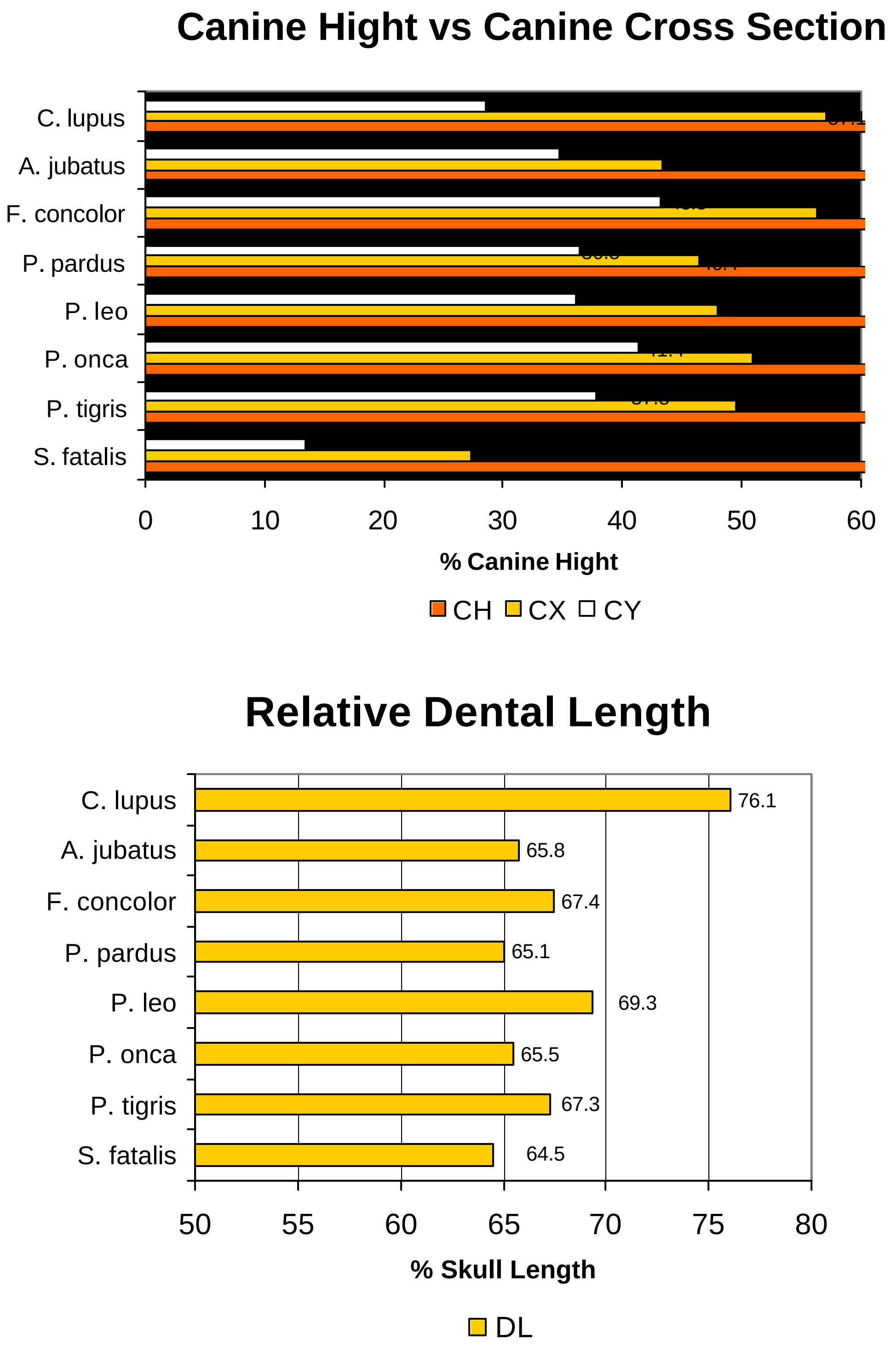


Figure 5.3.2: proportions between the antero-posterior (x) and medio-lateral (y) extensions of the upper canines against canine height (top). Bottom: dental length against skull length, the latter is scaled to the same length (100%).

Therefore, saber-tooth cats are shown to be more similar in shape and strength characteristics of the canines to those of living canids than felids (see also VAN VALKENBURGH & RUFF, 1986). Conical toothed cats, as their name suggests, have canines that are more round in shape, which was confirmed through my investigations. Usually the antero-posterior diameters exceed the medio-lateral diameters of around 20-25% in all of the modern representative cat species.

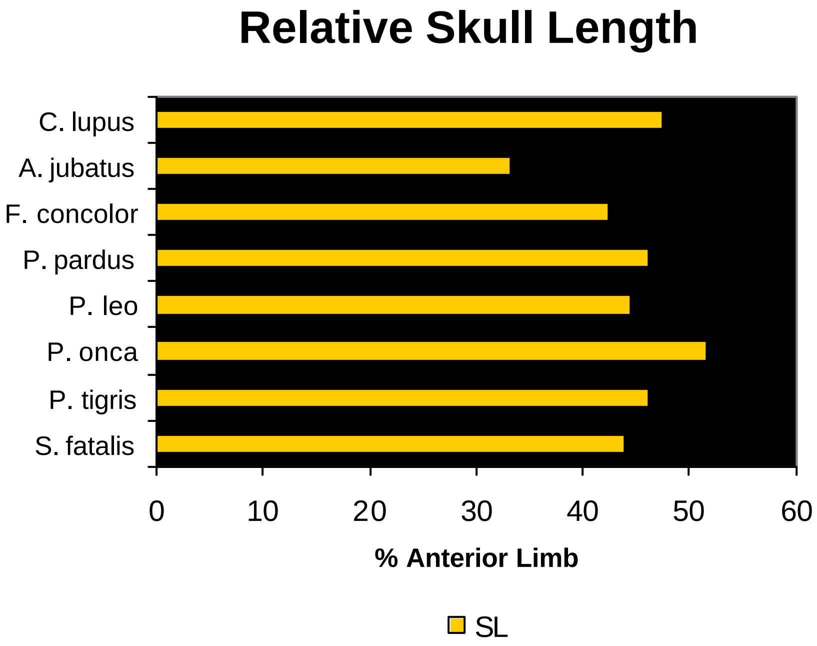


Figure 5.3.3: Segment ratios between total skull length against overall anterior limb length. Each species is shown with the skull length expressed as a percentage of the forelimb measurements. Note that the length of the jaguar's skull makes up more than half of the forelimb, whereas it in *Smilodon*, with its extremely shortened anterior limbs, makes up only 44%.

Dental Length: Figure 5.3.2 (bottom)

Apparently the wolf with its large array of teeth, possess the relatively longest dental bone compared to the skull length. The lion has the relatively longest dental bone for all of the big cats with a percentage of around 69%. The dental bone of the tiger and puma both make up ca. 67%, while the cheetah, leopard and jaguar fall slightly behind with about 65-66%. The dental of *S. fatalis* is observed in having the lowest percentage of 64.5% of the total skull length.

Skull Length to Anterior Limb Length: Figure 5.3.3

Comparisons between skull length and the overall anterior limb extent, is shown in Figure 5.3.3. It is striking that the skull length of the jaguar is comparatively long against its forelimb measurement, whereas it in other species ranges between around 42% for the puma and 46% in the tiger and leopard. In the cheetah however, the skull makes up only about 33% of the anterior limb length. *Smilodon* in turn was shown to possess the relatively shortest distal limb elements, but the skull still appears to be comparatively short when scaled against the front extremity (~44%).

5.3 Statistical Analysis

A primary objective of this study is to produce a database for future morphological comparisons between extinct and extant feline species.

The numerous illustrations on length comparisons in the last chapter describe differences in proportions and morphology among the living big cats, the saber-toothed cat *Smilodon* and the wolf as the only member of the canids. Knowing the ecological and behavioral background of extant representatives, the data sets and diagrams can be used to demonstrate correlations associated with habitat utilization and killing behavior. The very distinct body proportions in *Smilodon* and *X. hodsonae* from their modern relatives clearly show a type that is much different from the generalized basic phenotype [15]. Hence, sabertooths must have utilized a modified hunting technique, which is certainly obvious by the sheer size of the upper canines. The cheetah on the other hand also exhibits body proportions that are undoubtedly divergent from the basic phenotype, but in a much different way than that of *Smilodon*, namely in being more similar to those of the highly cursorial wolf.

By means of bivariate plots and factorial- and discriminate statistical analysis, groups are characterized through the differences in morphology and body proportions for all specimens studied.

For the following plots, log-values of the same data were calculated in the same order as for the first illustrations of Chapter 5.2, however, only for the long bones of the anterior and posterior limbs, which are directly related to cursoriality. The specimens have to be roughly subdivided into three different categories before, which are based upon characteristic deviations from the general phenotype (see Chapter 6.2, p. 47).

1. Basically, the first group (?) is characterized by elongated, slender distal limb elements, non-retractile claws, etc. These are features, which are typical for fast running felines of low structured habitats.

2. The second guild (?) more or less equals the basic “felid phenotype,” which will be further explained in the following Chapter. It is somewhat intermediate in its features between the first and third category.

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[15] See following chapter for explanation

3. The third guild at last (?) possesses short and sturdy anterior limbs with powerful muscles attaching and elongated canines in conjunction with an array of peculiarities in the skull anatomy [16].

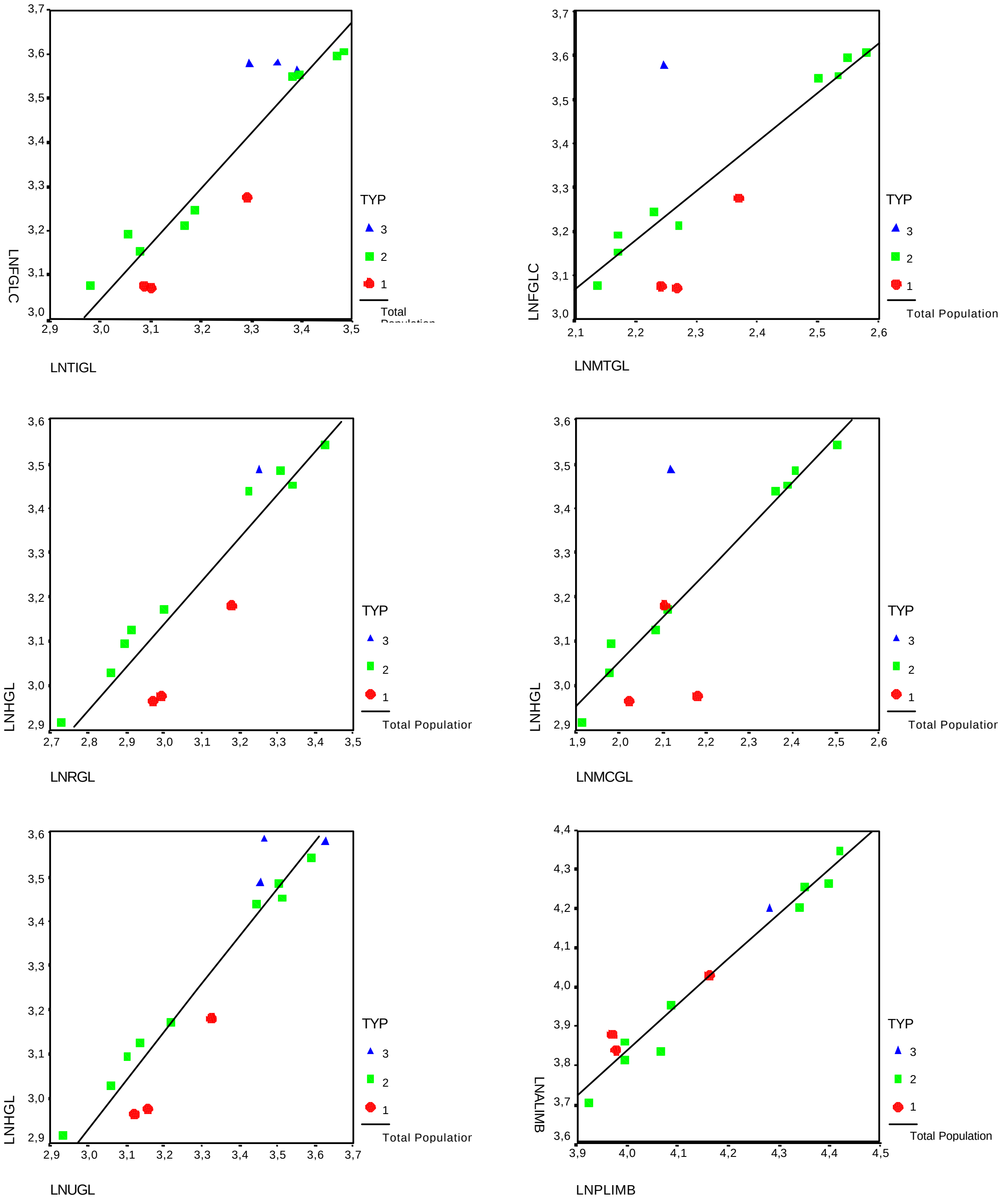

Table 5.4.1: Log/ log plots of various limb lengths for all three groups in the same order as in Chapter 5.2, respectively.

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[16] An exception forms Homotherium, which is somehow intermediate between pantherine- and smilodontine cats. Thus it is often clustered together with the former.

In Table 5.4.1 these tendencies are further illustrated for the anterior and posterior limb segments. It is clearly visible that the values for species of category one (wolf & cheetah) fall below the regression line, whereas those of group three (*Smilodon, X. hodsonae* & *Homotherium*) fall above it. Although *Homotherium* is intermediate in its features, particularly its elongated limbs show resemblance to pantherine felines and thus can be found within guild two. Guild two includes all the pantherine cats plus *F. concolor*, which all assemble closer

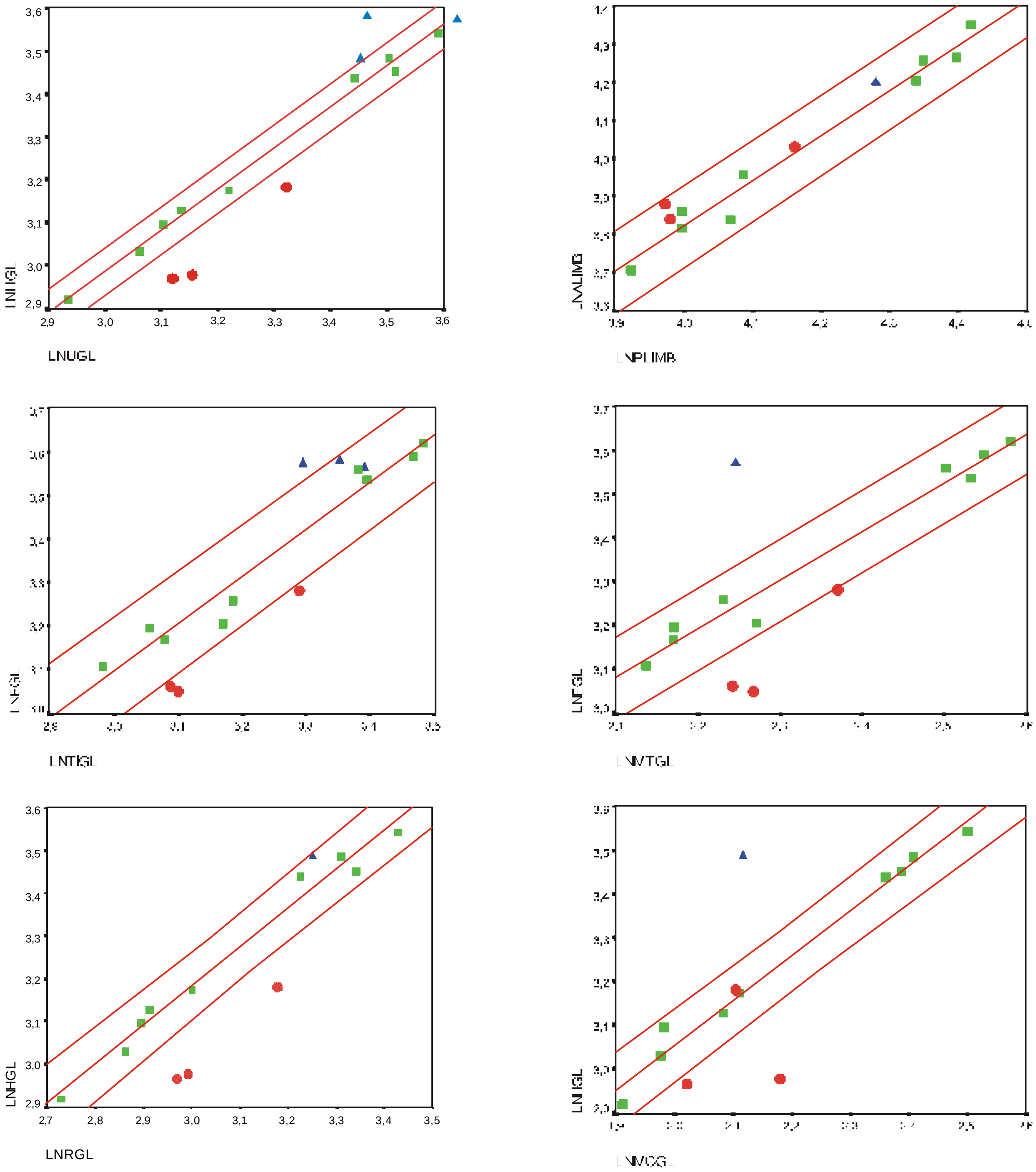


Table 5.4.2: Log/ log plots of the same limb length ratios as in Table 5.4.1. Confidential intervals (red lines) are fitted to the data for the pantherine cats of guild two. Every plot that falls out of this interval is distinguished clearly in proportion and function from guild two.

around the regression line. The basic meaning of the observed pattern is, that the distal limb elements, in both posterior and anterior limb seem to grow faster than their proximal counterparts (femur and humerus) during physical maturity.

For the total limb lengths (top right), which is collated between posterior and anterior extremities, growth rates switch within different limb segments in a similar fashion for all three guilds, thus they all gather closely around the regression line.

The wolf is characterized by higher values than for the cheetah, hence it is always placed relatively far away from the latter.

1. Factorial Analysis

A factorial analysis is applied to the data set in order to find out if groups of variables can be shown to be correlated to factors like cursoriality or strength. Hence the factorial analysis reduces the data set and the factors determine the behavior of the all variables.

Descriptive Statistics

	Mean Value	Standard Deviation	Analysis N
LNSL	3,2031	,2640	8
LNDL	2,8237	,2707	8
LNSW	2,7894	,2701	8
LNCD	1,8620	,3305	8
LNSCH	1,4215	,6007	8
LNCX	,6273	,4294	8
LNCY	,2671	,3767	8
LNHGL	3,2263	,2368	8
LNLI	2,1310	,3549	8
LNHBD	1,8742	,3370	8
LNHBT	1,4326	,3472	8
LNTM	1,3955	,3592	8
LNRGL	3,0873	,2241	8
LNRBP	1,0655	,3533	8
LNRQR	,7637	,3697	8
LNUGL	3,2782	,2159	8
LNUBD	,3301	,2637	8
LNULO	1,4503	,3001	8
LNUQR	-4,54E-02	,2804	8
LNMCGL	2,1582	,1923	8
LNFGL	3,3314	,2212	8
LNFGLC	3,3252	,2210	8
LNFBP	1,8463	,2827	8
LNFBD	1,7402	,2539	8
LNTIGL	3,2199	,1733	8
LNTILT	1,8296	,2440	8
LNFIGL	3,1389	,1683	8
LNASGL	1,3744	,2649	8
LNCALGL	2,0424	,2177	8
LNSCGLP	1,5916	,3239	8
LNSCHS	2,9801	,3169	8
LNSCTMAJ	1,8742	,3387	8
LNMTGL	2,3097	,1594	8

Rotated Factor Matrix [a]

	Factors	
	1	2
LNCX	,971	,152
LNUBD	,920	,241
LNRQR	,901	,404
LNRBP	,889	,429
LNCY	,877	,308
LNHBT	,876	,472
LNSCGLP	,875	,356
LNLI	,872	,468
LNSCH	,866	,213
LNHBD	,842	,516
LNUQR	,819	,469
LNFBP	,810	,568
LNFBD	,807	,581
LNCD	,806	,513
LNASGL	,796	,476
LNSL	,791	,489
LNSCHS	,777	,545
LNULO	,755	,527
LNTM	,720	,655
LNDL	,703	,498
LNSW	,694	,595
LNMTGL	,115	,960
LNTIGL	,337	,935
LNFIGL	,365	,901
LNRGL	,386	,882
LNUGL	,470	,857
LNMCGL	,291	,847
LNSCTMAJ	,455	,766
LNHGL	,655	,739
LNFGL	,644	,731
LNFGLC	,659	,726
LNCALGL	,676	,724
LNTILT	,696	,701

Extraction Method: Principal Components Analysis.
Rotation Method: Varimax with Kaiser-Normalization.

a. Rotation is converged in 3 Iterations.

Table 5.4.3: The standard deviation coefficients of the left chart range in between 1.6 - 6 % for the whole data set. A high deviation is seen mainly in the canine teeth, which are strongly influenced

through the extremely elongated canines of the sabertooth *Smilodon*. Low values are found primarily t in the long bones, which are related to cursoriality.
Right side: The first factors load high on skull measurements and the articular ends of the long bones as well as for the Teres major muscle and the astragalus. They all are relatively well correlated. The second factors in turn focus on the long bones of the anterior- and posterior extremities. They are strongly correlated with the growth of the animal and cursoriality.

Declared Total Variance

	Initial Eigenvalue			Rotated Sum of square loads		
Factors	Total	% of Variance	Cumulated %	Total	% of Variance	Cumulated %
1	27,576	83,564	83,564	17,612	53,371	53,371
2	2,701	8,185	91,750	12,665	38,379	91,750
3	1,427	4,324	96,073			
4	,853	2,586	98,659			
5	,224	,678	99,337			
6	,134	,405	99,742			
7	8,514E-02	,258	100,000			
8	1,468E-15	4,450E-15	100,000			
9	9,937E-16	3,011E-15	100,000			
10	6,935E-16	2,102E-15	100,000			

Extraction Method: Principal Components Analysis

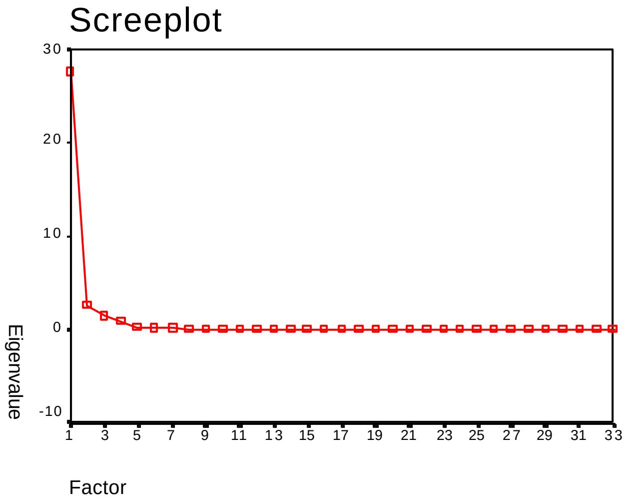


Table 5.4.4: The screeplot on the left side illustrates the ordered factors after the size of their Eigenvalues. Each factor shows the corresponding size of the Eigenvalue. The first factors explain approximately 84% of the variables and have an Eigenvalue of about 27. Factor 2 explains about 8 % of the entire variables and its Eigenvalue is 2,7 (See also Table above).

A factorial analyses was applied in order to test the extend to which the development of the variables between each other correlate, and if the variability can be traced back to only a few factors.

Primarily two factors are to be expected for the correlation between the variables: growth after allometric conformities and speed. The growth factor will likely explain the main part of the correlation between variables. On the other hand, another expected factor would be adaptations within the limb skeleton relating to speed.

At first, after the dispersion of the factor loadings, the factorial analyses only extracts one factor after the Kaiser-criteria, which can be attributed to allometric growth. But because the Eigenvalue of the second factor was only slightly below the threshold of extraction in addition to the small number of investigated individuals, the extraction of two factors was given. As shown in the screeplot and Table 5.4.4, the following factors do not contribute significantly to the explanation of the variability.

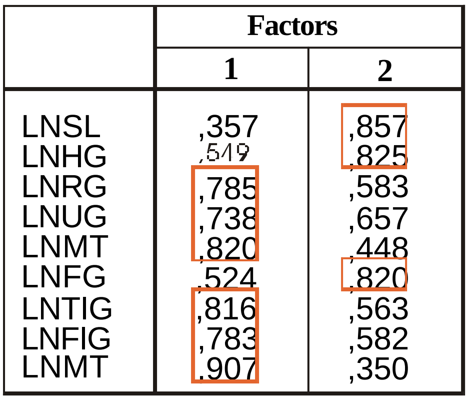
The pattern of the factor loadings on the variability shows that the second factors correlate negatively with the prolongation of the distal limb segments. This is particularly obvious, if the selection of the variables is minimized to the length of the limb bones (see Table 5.4.6). Thus the second factor can indeed be identified with the adaptation of the limb skeleton to strength versus cursoriality. The dispersion of the factor loadings stays the same, even if more or even all variables are added in the analyses.

The canine height is actually associated with adaptations to limb strength. Surprisingly, this association is obtained when *S. fatalis* is excluded from the analyses and exclusively recent big cats are taken into account.

Some measured parameters that correlate with the adaptation to strength:

1.) long canines
2.) short humerus
3.) short femur
4.) relatively broad joints, etc.

The stable dispersion patterns of the factor loadings make one expect, that a profound characterization of the affected variables into three guilds is possible. In order to prove this with the corresponding variables, that have high factor loadings on the second factor “strength”, a discriminant analyses was applied. This method actually proved that a profound separation into three guilds is feasible. A two-dimensional scatter plot of the factor values against each other clearly distinguishes these three guilds (see table 5.4.7). While the cursorial cats can be found in the upper left corner of the diagram, *Smilodon* settles in the lower right corner. The pantherine cats of the second guild all gather closer to the coordinates` origin. In comparison to the individual regression analyses and the scatter plots of the individual variables against each other, the three guilds are more clearly separated in the scatter plot of the factor values.



	Factors	
	1	**2**
LNSL	,357	,857
LNHG	,519	,825
LNRG	,785	,583
LNUG	,738	,657
LNMT	,820	,448
LNFG	,524	,820
LNTIG	,816	,563
LNFIG	,783	,582
LNMT	,907	,350

Table 5.4.6:

Extraction Method: Principal Components Analysis.
Rotation Method: Varimax with Kaiser-Normalization.
Rotation converted in Iterations.

Numbers in red frames underline the belongings to either Factors 1 or 2 of the various length measurements. Skull length, humeral length and femoral length (Factor 2) have a strong correlation to another and relations to strength advantages. The distal limb elements in turn (Factor 1) show correlations to speed.

Rotated Factor Matrix[a]

	Factors	
	1	2
LNSCH	,472	,857
LNHGL	,727	,675
LNHBD	,490	,861
LNLI	,394	,911
LNTM	,653	,721
LNRGL	,884	,416
LNRBP	,438	,881
LNRQR	,427	,898
LNUGL	,850	,501
LNMCGL	,727	,591
LNFGL	,714	,662
LNFBD	,487	,871
LNTIGL	,888	,454
LNFIGL	,912	,392
LNSCTMAJ	,812	,406
LNMTGL	,873	,459

Extraction Method: Principal Components Analysis.
Rotation Method: Varimax with Kaiser-Normalization.

[a] Rotation is converged in 3 Iterations.

Rotated Factor Matrix[a]

	Factors	
	1	2
LNSCH	,110	,956
LNHGL	,668	,735
LNHBD	,439	,889
LNTM	,584	,788
LNLI	,401	,894
LNRGL	,844	,479
LNRBP	,374	,906
LNRQR	,334	,933
LNUGL	,815	,552
LNMCGL	,893	,251
LNFGL	,652	,739
LNFBD	,530	,819
LNTIGL	,897	,426
LNFIGL	,849	,479
LNSCTMAJ	,655	,616
LNMTGL	,975	,140

Extraction Method: Principal Components Analysis.
Rotation Method: Varimax with Kaiser-Normalization.

[a] Rotation is converged in 3 Iterations.

Table 5.4.6: Relations between characteristics that correspond to strength of the forelimbs. The chart on the left side demonstrates the values for all the specimens except for *Smilodon*, which, with its elongated canines, clearly contributes to a greater deviation in the factorial analysis. The table on the right side in turn includes *Smilodon*.

2. Discriminant Analysis

The discriminant function can be mentally subdivided into two different steps. In the first step a discriminant function is to be guessed, the second step undertakes a classification of the cases and with it a subdivision in separate groups. The peculiarity of the discriminant function results from the second step however, which serves to calculate, from the constant values of the declared variables, discrete values and together with that group membership of the dependant variables.

High correlation coefficients in table 5.4.6 point towards a good correlation between the functional values and the values of the variables and the other way around for low or negative correlation coefficients.

Canonical correlation coefficients measure the severity of coherence between functional values of the discriminant function and groups of dependant variables. The latter also amounts the portion of the dispersion between groups of the entire dispersion. The values of coefficients range in between 0 and 1. The bigger the value, the higher the dispersion between groups in proportion to the dispersion within the groups. This way a high canonical correlation coefficient points towards a good separation between the groups and hence towards a high content of declaration of the model.

A dispersion diagram (Figure 5.4.7) illustrates group membership for each data values. The pantherine cats (green) are relatively close together and far apart from guild one (red) and three (blue). Guild two has low values for the first and second discriminant functions, where- as group one loads high on the second discriminant function and low on the first. For guild three the opposite is true. It is these different stresses of the values that separate the groups clearly apart from each other.

Structural Matrix

	Factor	
	1	2
LNSCH	,288	-,075
LNSCTMAJ	-,157	,034
LNRBP	,124	-,100
LNFIGL	,116	-,098
LNMCGL	,085	-,006
LNTIGL	,083	-,067
LNHBD	,007	-,204
LNLI	,111	-,186
LNRGL	,025	-,155
LNTM	,088	-,117
LNFBD	,040	-,103
LNRQR	,085	-,093
LNHGL	,072	-,082
LNMTGL	-,025	,079
LNFGL	,019	,041

Table 5.4.6: Common correlations within groups between discriminant variables and standardized canonical discriminant functions. Variables are ordered after their absolute size of correlation within the function.

* Highest absolute correlation between each variable and one discriminant function.
a This variable is not used in the analysis.

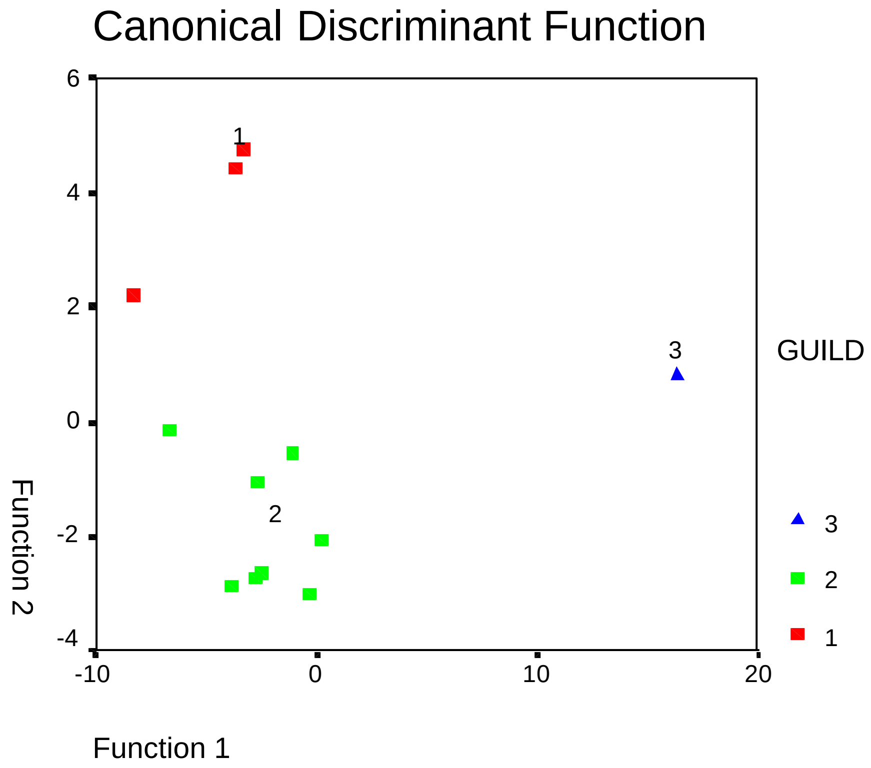


Figure 5.4.7: Dispersion diagram illustrating a clear separation between the three principal guilds.

6 DISCUSSION

6.1 Habitat Preferences

The behavior of any kind of mammal is in many aspects greatly influenced by the structure of its three-dimensional habitat (EISENBERG AND LOCKHART, 1972; GEIST, 1974). Several of the living large cats are found in high-structured habitats[17] almost exclusively. These species include the jaguar (*Panthera onca*) of the New World, which has a natural distribution that extends from South Argentina to the southern states of the US. In its northern most extensions however, the jaguar is forced to enter scrub country and even deserts (NOWAK, 1991). Nevertheless, it generally seems to require the presence of much fresh water, which is plenty available in tropical, dense forest habitats. The jaguar is an excellent swimmer and a good climber.

The tiger (*Panthera tigris*) in contrast, is known to be tolerant of a wide range of environmental conditions, its only requirements being sufficient cover, water, and prey. It is found in high-structured tropical rainforests, evergreen forests, mangrove swamps, but also in low structured grasslands, Savannah's, and even in rocky countrysides. As the jaguar, the tiger is a very good swimmer and likes the vicinity of water (NOWAK, 1991).

The leopard (*P. pardus*) has the largest known geographical distribution of any felid species, which inevitably implies a highly variable habitat tolerance. It can adapt to almost any habitat that provides it sufficient food and cover and its diet appears to be more varied than that of any other large felid (SUNQUIST, 1985). *P. pardus* inhabits the ecotone between forest and steppe, but has also been recorded in deserts and at elevations of more than 5,600 meters on Mount Kilimanjaro (NOWAK, 1991).

The American mountain lion (*F. concolor*) in turn holds the greatest natural distribution of any mammal in the Western Hemisphere except Homo sapiens (NOWAK, 1991). Although the cougar seems to prefer high relief, it is known to live in grassland communities such as the Midwest prairies of the United States, and the lowland tropical forests of Central and South America (GONYEA, 1976). The elevational range extends from sea level to 4,500 meters in Ecuador (NOWAK, 1991). In general, *F. concolor* is adaptable in any area with adequate cover and prey.

More dependent on a high relief is the snow leopard (*U. uncia*), which is found in the high Himalayan Mountains of Central Asia. In summer it occurs commonly at elevations of 2,700-6,000 meters. During winter it may follow its prey down into forests below 1,800 meters (NOWAK, 1991). The usual habitat of the snow leopard is the open woodlands on mountain

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[17] Dense forest

slopes, which provides only little cover to conceal the predator's movements (GONYEA, 1976).

The lion (*P. leo*) prefers low-structured habitats of grassy plains, open woodlands, and scrub country, although it sometimes enters semi-deserts and forests and it has even been recorded at elevations of up to 5,000 meters (NOWAK, 1991).

The cheetah (*A. jubatus*), exclusively occupies low-structured habitats such as semi-deserts, open grasslands and dense bush vegetation. It originally occurred from Palestine and the Arabian Peninsula to Tadzhik and central India, as well as throughout Africa, except in the tropical forest zone and the central Sahara (NOWAK, 1991).

In general, species of large living felids are found that preferably exploit either high- or low- structured habitats, while others show a greater diversity in their habitat choice (GONYEA, 1976). It should be noted however, that habitat choice of any cat species is strongly influenced from the composition of the carnivore guild (TURNER & ANTÓN, 1996). In a modern intact ecosystem such as the Kruger National Park of South Africa for instance, the coexistence of several species of large predators[18] coexist there to varying degrees and with somewhat overlapping diets, but direct competition and its effects are minimized because the animals tend to use distinctive habitats and hunt during different times of the day (PIENAAR, 1969).

Smilodon fatalis clearly shows the proportions of a typical forest felid and presumably favored high-structured habitats if living a solitary life (BABIARZ et al., 1999). However, if it was hunting in packs, which can be assumed from the large number of specimen found at Rancho la Brea, together with the evidence of healed injuries that would enable sick or injured animals to survive strenuous times, it might as well have favored a more open terrain comparable to that of modern lions. Beyond that, climatic conditions were suggested to be very much similar in type from those existing today in the Southwest of the United States, namely a semi-arid scrub country (STOCK, 1972). This should be evidence enough to prove that *Smilodon* actually did not prefer high structured habitats, but rather low structured areas like they still exist today in the Sonora desert.

In fact GONYEA (1976) suggested that lions, although having the body proportions of forest felids, also reside in low structured habitats, because the utilization of large prey limits the possibilities for morphological adaptations for speed. To balance this lack of speed, increase hunting efficiency, reproductive success, and territorial defense on the plains, lions form prides. *Smilodon* was probably facing similar problems during its time of existence. It might have solved these troubles in the formation of comparable arranged prides, especially in view of the fact that contemporary co-predators such as *Panthera atrox* or the hyena-like dire wolf *Canis dirus,* were fierce competitors that may have tried to take over a kill, which they

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[18] lion, spotted hyena, leopard, cheetah and wild dog

presumably could have if *Smilodon* happened to lead a solitary life. Furthermore, based on the sheer number of individuals recovered at Rancho la Brea, it seems likely that the felines became trapped in attempts to reach already mired herbivores or their carcasses (AKERSTEN, 1985). If the number of large herbivores entrapped in the tar pits represents an approximation to the maximum number of trapping incidents, then several individuals of *Smilodon* were also caught during their efforts to grab each of those herbivores. TURNER & ANTÓN (1996) point out that it would be very unlikely that every *Smilodon,* trying to reach a trapped animal, suffered the same destiny; the entangled number of animals in the vicinity at any one time is too high to support an argument for a solitary lifestyle, considering that such a lifestyle would imply individual territories which in turn would reduce the number of animals able to amass in the area.

Nevertheless, cats in general are not animals of totally open country[19], which is rather true for the highly cursorial canids that have filled this adaptive zone, nor are they generally arboreal as are many of the mustelids and viverrids. MARTIN (1980) suggests that cats combine some of both, areas where trees and open areas mix may be the real adaptive zones of the felines. Depending on body proportions, morphological characters, favored prey size and abundance of co-predators as noted above, some might tend to be more appealed by low structured habitats rather than high structured habitats. Thus it seems rather problematic to strictly separate habitat preferences in different cat species, by only studying their limb proportions as suggested by GONYEA (1976). The exceptions are seen in the cheetah and in those felines that live in prides.

6.2 Discussion

In order to understand the differences and anatomical variances expressed in the results of the species examined one has to be familiar with their individual behavioral and ecological characteristics by virtue of phylogenetic inheritance (MARTIN, 1989). Therefore it is substantial to examine some of these social and behavioral factors that go together and which in turn are greatly influenced by the structure of the habitat as elucidated in Chapter 5.1.

Generally, cats are said to be cursorial animals. They are sprinters and capable of very rapid acceleration, that can maintain high speeds for only short distances (TAYLOR, 1989).

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[19] except for the cheetah

Most cats, living and extinct, therefore evolved elongated and relatively slender long bones in addition to elongated foot bones in contrast with some other animals of comparable body size (e.g. bears).

The basic felid "phenotype set" [20] is large, carnivorous, and typically captures terrestrial prey at least half its own body weight (GITTLEMAN, 1985; PACKER, 1986). It forages over a large area and often exists at low densities (GITTLEMAN & HARVEY, 1982; ROBINSON & REDFORD, 1986). Females reproduce every two to three years and young spend a year to one and a half dependant on their mother while perfecting their hunting skills (GITTLEMAN, 1986). Prey are typically captured from ambush and/ or stalk and short rush or chase by means of the claw equipped forelimbs and are dispatched with a swift killing bite delivered by the large conical-like canines (EWER, 1973, LEYHAUSEN, 1979). Only the cheetah [21] and the sabertooths [22] differ radically from this generalized body plan and technique of prey capture. Cheetahs are specialized for high-speed pursuit of smaller prey and consequently exhibit a variety of morphological specializations often comparable to the wolf, while *Smilodon* is the less fleet footed feline, which probably stalked its usually large prey like thick-skinned proboscideans or other slow moving mammals. Its massive anterior limbs possessed retractile claws and aided in seizing and immobilizing prey. The elongated sabers were exclusively used for killing prey with a canine shear bite applied to the soft parts (see Chapter 1).

With the exceptions of the lion and probably *Smilodon*, all the large felids are typically solitary hunters and feeders, although all large cats are sometimes known to form smaller groups during particular times.

Since felid morphology is the result of the compromise between the potential to catch prey and to kill it, all cats, with the exception of the cheetah, use retractable claws to make primary contact and to pull down prey (LEYHAUSEN, 1965B), see Figure 6.2.1.

Hence, the cat foot cannot be perfectly digitigrade, but is on the other hand capable of a more or less restricted supine- prone movement in the distal anterior limb element. The cheetah has elongated dog-like ungual sheaths on digits II-V that extend well beyond the fur and give the appearance that the claws are not retractile (GONYEA, 1975). It is for this reason why *A. jubatus* knocks over its prey (Figure 7.3), while canids (Figure 6.2.2) depend on their teeth for biting prey and bringing it down (ZIEMEN, 1981). As a result both their feet do not perform the same dual function as those of the pantherine felids (TAYLOR, 1989) [23].

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[20] comparable to number 2 of the three proposed cat categories.

[21] comparable to category number 1 as the wolf.

[22] See category number 3.

[23] See chapter 5.2

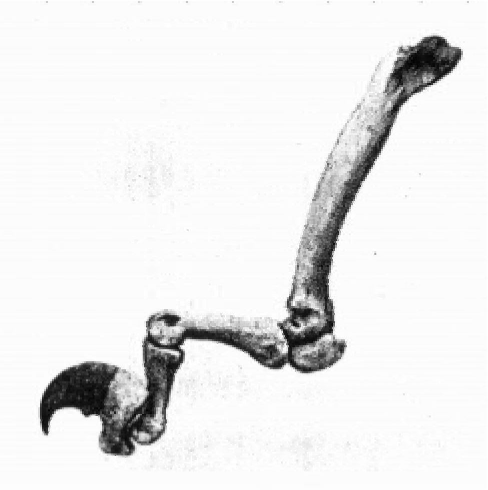
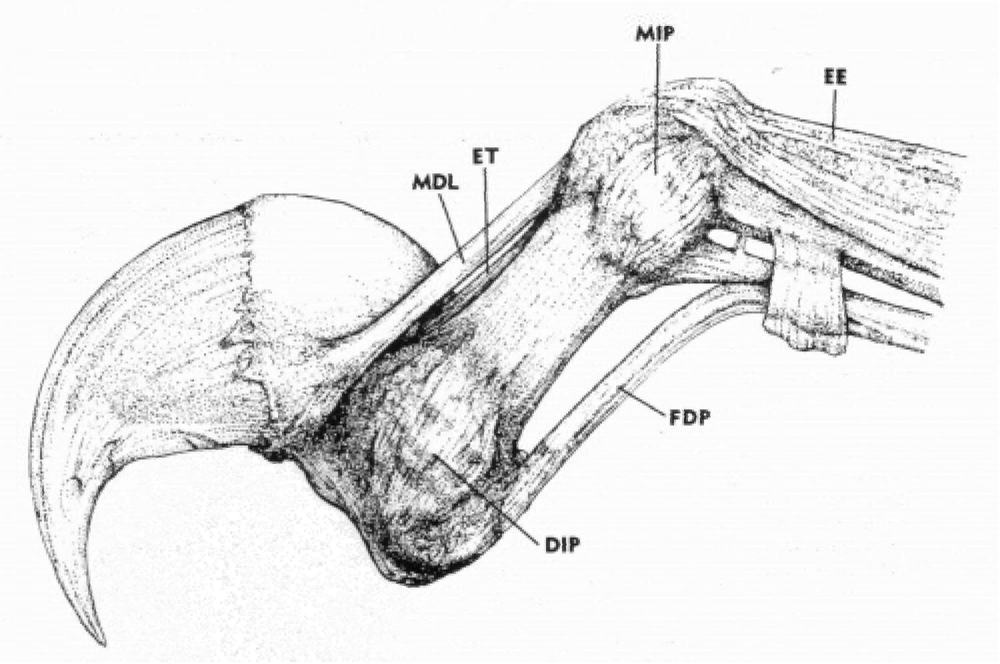


Figure 6.2.1 (right): Articulated 4^{tn} phalanx of the forefoot of *P. tigris* (after . ???, 19..).

(bottom): Anatomy of the claw retractile mechanism for *Felis catus* showing muscles and tendons. Medial view, partially protruted.

Abbreviations: DIP = distal interphalangeal joint; EE = extensor expansion; ET = extensor tendon; FDP = flexor digitorum profundus tendon; MDL = medial dorsal elastic ligament; MIP = middle interphalangeal joint (after GONYEA & ASHWORTH, 1975).



It is these behavioral variations that are also displayed in the body shape of the different cat species, which in turn is best reflected in skeletal proportions.

Humerus, Ulna, Radius & Metacarpalia:

The cheetah is evolved for speed over short distances, through which it is aided by its overall flexibility, its lean body, and long limbs that enables it to increase its stride length by flexing its back so that during maximum speed it covers about ten meters with a single leap (HILDEBRAND, 1959). Thereby its long tail plays an important role of maintaining balance

Figure 6.2.2: Killing bite of the wolf on medium sized prey (after ZIEMEN, 1981).

during the high-speed twists and turns of a typical chase. Therefore *A. jubatus* is strongly dependent on an open and flat terrain. In this regard, it is not surprising that the cheetah had the relatively longest extremities of all the large felids for the anterior limb ratios in the radius and ulna segments, but also the humerus was proven to be longer than in average as for many other taxa. TURNER & ANTÓN (1996) noted that the humerus is about ten times the average length of the thoracic vertebrae 3 to 8 in most pantherine cats, but in the cheetah the humerus is more than thirteen times that figure. The extremities of the lion in turn, which broadly occupies the same kind of habitat [24], exhibits only few changes in body proportions when compared to pantherine cats or “forest felids” such as the tiger. Although it was shown that the radius and the ulna in the lion were somewhat in between those of the cheetah and those of the rest of the examined modern species. However, GONYEA (1976) arguments, that the utilization of large prey limits the possibilities for morphological adaptations for speed. As noted in chapter 4.1, the formation of prides make up for this lack of speed, increase hunting efficiency, etc. The elongation of the radius and ulna may however reflect the first step towards an adaptation for a more cursorial life in low structured habitats.

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[24] See chapter 4.1

S. fatalis is expected to show the shortest anterior limb elements, which was verified through the results. It has the relatively shortest distal limb elements of all the felids: ulna, radius, and 3rd metacarpal. For *S. populator*, the relative radial length was even lower than that of *S. fatalis* with a ratio of only 0.73 (TURNER & ANTÓN, 1996).

Ratios of humero-ulna lengths in *H. ischyros* indicate, that with about 1.10, it had almost cheetah-like proportions in its anterior limbs, whereas its relative *H. serum* comes closer to the lion with 1.05. They both also exhibit a high scapula and a long neck. Together with short tibias (Figure 5.2.1) the animals must have shared a certain similarity to the appearance of a hyena (see Figure 6.2.2). TURNER & ANTÓN (1996) also point to the elongated radius, which was typically 91% of the length of the humerus, and a shortened calcaneum. It seems that such limb proportions would imply a selective advantage, although in general, these proportions are associated with a reduced ability to grasp and to jump. It has even been suggested that *Homotherium* falls into an intermediate position between pantherine cats and hyenas. If correct, and *Homotherium's* lifestyle was more similar to those of hyenas then they might as well have been able to sustain a chase for long distances. RAWN-SCHATZINGER (1992) elaborated this idea and pointed out that *H. serum* from Friesenhahn cave in Texas in conjunction possessed reduced claw retraction, features that in her view suggest a sprinting ability.

X. hodsonae, the newly introduced saber-toothed cat described by BABIARZ et al., 1999 combines scimitar-tooth canines with the short, massive extremities of a dirk-toothed cat like *Smilodon*, and hence presents a third way to set up a saber-toothed group of carnivores[25]. Because the data was obtained directly from the recent publication of BABIARZ et al. (1999) only few a relative length comparisons were made. There are comparisons between the humerus against the ulna, and between the femur and tibia. In spite of the scarce data available, they do indicate that *X. hodsonae* indeed is similar in habitus and proportions to *S. fatalis*. The tibia is shown to be almost as short in relation to the femur, while the ulna is extremely shorter than in *Smilodon* (compare Figure 5.2.1 & 5.2.3). Length variations for the ulna in pantherine cats and *Smilodon* were calculated to be 18% longer than the radius, leading to the estimate, that the radius of *X. hodsonae* must have been similar in proportions with a ratio of approximately 0.71 in contrast to *S. fatalis'* 0.79. However, BABIARZ et al. (1999) further pointed out that the postcranial skeleton is in fact as short and massive as in *Smilodon*, but resembles *Homotherium crenatidens* in detail.

Elongation of the distal limb elements is an indicator of cursorial specialization (HOWELL, 1944). This increase of the effective limb length is a characteristic for the cat family and is known as a digitigrate stance, which enables the animal to stand and move on its toes.

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[25] Compare Chapter 3.

In general, a shortening or elongation of the limbs primarily occurs in the distal segments of the limb, whereas the humerus and the femur change their length only to minimal amounts.

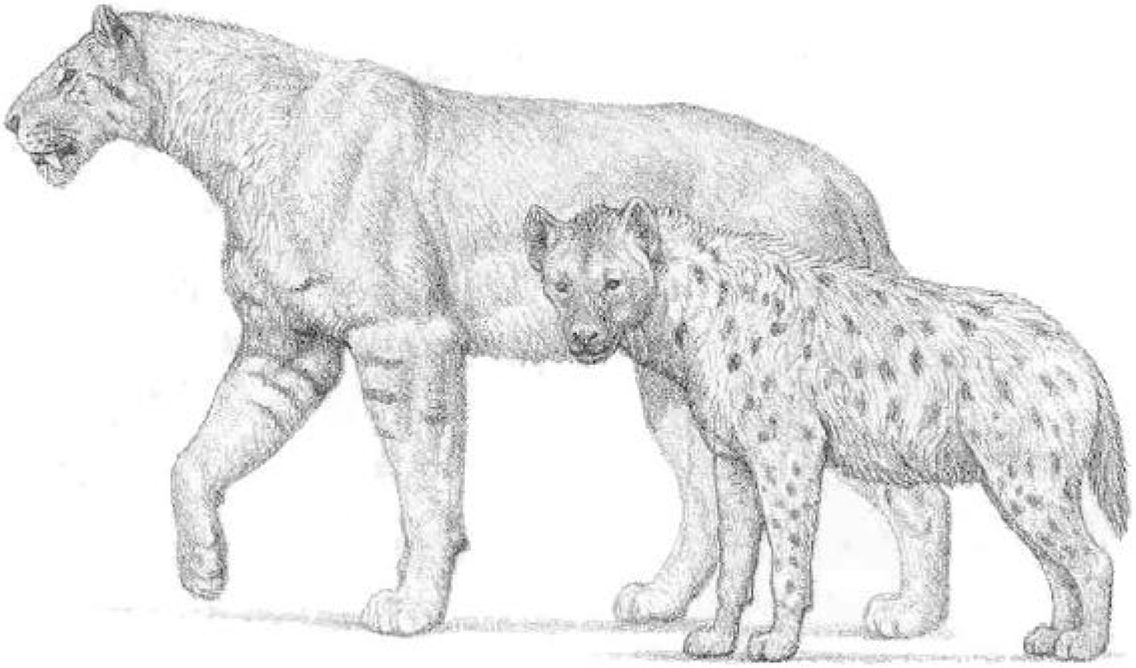

FIGURE 6.2.3: *Homotherium* and the spotted hyena (*Crocuta crocuta*). The slope-backed appearance of the hyena is seen to be paralleled in the cat.

Since the distal segments are considerably elongated in the cheetah and eminently shortened in *Smilodon* it is no coincidence that their corresponding proximal limb bones are relatively shorter for the cheetah and wolf and relatively longer in *Smilodon*. An elongation of the distal limb segments provides a longer leverage and enables a higher speed.

A short radius and short metacarpals provide better grasping strength than for those felids with longer proportions of these bone segments. Particularly for *Smilodon* and pantherine cats it is shown that strength is more important than speed in contrast to the cheetah or the canids. GONYEA (1976) showed that the relative lengths of the distal limb elements of the anterior limb differ significantly among the large felids. He also compared the relative lengths of the 3rd metacarpus against the radius and found the metacarpus surprisingly shorter in the cheetah than that of all the other large living felids. This in turn doesn't match with the latter idea, but in consideration of the cheetah's extremely prolonged radius it seems to be acceptable (compare Figure 5.2.1). Nevertheless, the ratios of the present study prove the opposite, namely that the metacarpal bones, exhibited in the cheetah and puma, are minimally longer, indicating a tendency towards a cursorial specialization and faster running. This proves to be true at least for the cheetah and points towards a closer relationship to the puma (see page 59). In contrast, the jaguar possesses the shortest metacarpal bones of the living cats, but in general no major difference was to be observed between the pantherine "forest felids".

Femur, Tibia, Metatarsalia & Calcaneus:

The hind limb segment ratios in cats may also reflect the animal's habitat preference and its implicated killing behavior. It is for this reason why it was found to be of great importance for this study in order to further elucidate GONYEA'S introduced model of habitat choice and body proportions. As can be expected, the posterior limb ratios between the femur and tibia are quite similar to the ratios of the humerus and radius of the front extremities in all of the studied cats. In this regard, pantherine cats that preferably inhabit dense forests have the relatively shortest posterior limb segments and felids that tend to inhabit a more open terrain have the relatively longest hind limb bones. The cheetah therefore exhibits the relatively highest ratio followed by the leopard, the puma, the jaguar, and the lion and tiger. On the opposite, the two fossil genders of *Homotherium* have even smaller ratios, and *X. hodsonae* and *S. fatalis* show tendencies of extreme shortening of the tibia bone against the femur.

The ratio of the femur to metatarsal length has often been used as an indicator of speed and cursoriality among mammals (GREGORY, 1912; OSBORN, 1929; HOWELL, 1944; BAKKER, 1983). Elongation and tapering of distal limb elements relative to the proximal section is thought to promote speed because limb length (and stride length) is increased without an unfavorable shift of the limb's moment of inertia, because muscle mass remains concentrated near the proximal joint (HILDEBRAND & HURLEY, 1985). Within the present specimens, there is a rough correspondence between speed and hind limb proportions. They again broadly resemble those of the front limb as expected, with the cheetah having the longest tibia and 3rd metatarsal bones and *Smilodon* having the shortest, whereas those of the other cats closely range together in between the latter two.

Moreover, relatively long posterior limbs have been found to be an indicator of good jumping skills, when compared to the length of the anterior limbs (HOWELL, 1944). Another important indicator for the leaping ability is said to be the length of the calcaneus (TURNER, 1996). Nevertheless, its relative length, compared with that of the tibia, shows some contradictions with the former model of HOWELL, 1944 [26].

The puma is agile and known to possess a great jumping power. It may leap from the ground to a height of up to 5.5 meters in a tree (NOWAK, 1991). Therefore its hind limbs should be relatively long compared to the front limbs and vice versa. This in deed was verified through the outcome, where *F. concolor* was shown to have the shortest anterior

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[26] See Figure 5.2.4 (bottom)

limbs and hence the longest posterior extremities (see Figure 5.2.3). The relatively short calcaneum in the puma doesn't seem to weaken its potential to leap. The tiger has been reported to cover 10 meters in a horizontal leap, the lion in turn 12 meters, and the leopard can jump over 6 meters horizontally and 3 meters vertically (NOWAK, 1991). No information was found for the jaguar and the cheetah. Of course, these numbers are also strongly dependant on the weight of individual species and many other factors and do not necessarily reflect the maximum jumping distance each would be capable of to cover. However, together with the hind- front limb ratios and the calcaneum length, it does provide a basic fundament for a categorization in good and less good jumpers. The tiger is a good jumper compared to the leopard, but both have similar proportions of the front limb ratios that are however, still notably longer than in the puma. However, *P. tigris* was shown to have a proportionately longer calcaneum than *P. pardus* giving it a better leverage at the ankle joint. The cheetah in comparison has similar ratios, but telling by the even shorter calcaneum (see Figure 5.2.4) it is presumably not able to cover such a large distance with a single leap as the other species. The jaguar and especially the lion exhibit rather long anterior limbs, but the long calcaneum in the lion seems to make up for this "disadvantage", whereas the calcaneum in the jaguar is only of average, indicating a weaker ability to jump and leap comparable to the leopard. In *S. fatalis* the elongated calcaneum seems to compensate for the long front extremity [27] as is likewise demonstrated in the lion, and in spite of its heaviness it must have had good jumping skills.

Astragalus:

Studies of ankle morphology among cursorial mammals have suggested that the functional consequence of a more grooved astragalus is a restriction of medial-lateral mobility at the tibia-astragalar joint (cf. OSBORN, 1929; GINSBURG, 1961; BAKKER, 1983; VAN VALKENBURGH, 1987). Cursorial mammals move their limbs primarily in a back and forth, rather than medial-lateral direction, meaning that the flexion and extension ability is favored over that of plantar eversion or inversion. Therefore, to advance joint stability while running, cursors have evolved a tighter interlocking of joint surfaces at almost every limb articulation (HOWELL, 1944; HILDEBRAND, 1974; BAKKER, 1983). This suggests that, within this sample, the higher cursorial species of group one should have the most deeply grooved trochlea. However, VAN VALKENBURGH (1987) concluded that the astragalar trochlea depth by itself says little about the locomotor abilities of a particular species. It rather reflects heritage than habitus. The felids are examined in having a relatively small range values.

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[27] or the relatively short posterior limb

Olecranon:

The olecranon on the proximal head of the ulna serves as the insertion area of the triceps muscles and hence its size is an indication for different velocity advantages at the distal epipodium (POUGH, HEISER, MCFARLAND, 1996). The triceps muscles arise from the humerus and scapula. Its most obvious action is to extend the forearm in the swing phase of the step cycle, but when the hand is maintained in fixed position on the ground during the stance phase, extension of the lower arm by the triceps helps push the body forward (WALKER, 1987). In general, the triceps is responsible for any pushing action away from the body. Faster and higher cursorial animals as the cheetah, *H. serum*, and wolf are shown to have a short olecranon with a smaller triceps attachment surface, while the sabertooths, are expected to exhibit the longest olecrani. Correspondingly, cats of group two must possess intermediate olecranon lengths. However, for group two and three there seems to be no notable differences for the length measurements, although the saber-toothed cats with their short and sturdy anterior limbs are expected to have more massive triceps muscles, that helped the animal to seize its prey thoroughly before the "delicate" canines were applied on the right spot to kill the victim. The puma, jaguar, and lion were shown to exceed the ratios of the sabers like *S. fatalis* and *X. hodsonae*, leading to the assumption that the olecranon length and thus the triceps insertion area is not necessarily stronger developed than in modern big cats. However, GONYEA (1978) showed that for category one the lateral tuberosity on the olecranon process was usually smaller than the medial tuberosity. Therefor, the medial head of the triceps muscle was relatively large for these species when compared with those of category two. Accordingly, the lateral tuberosities are larger than the medial tuberosities for category two, and the lateral head of the triceps is notably larger than that of group one. The exception forms *P. leo*, which has olecranon tuberosities of similar size. In *S. fatalis* the lateral tuberosities are comparatively larger than in modern pantherine cats indicating stronger muscle attachments, although the relative olecranon length retains rather small.

Caput Radii:

The shape of the proximal head of the radius (Caput radii) is found to be of great importance in terms of rotation of the radius around the ulna. The articular surface of the radial head moves on the capitulum and trochlea of the humerus, and its form is related to the shape of these surfaces (TAYLOR, 1974) as well as to the formation of the radio-ulnar joint. Figures 5.2.5 and 5.2.7 both illustrate the relative shape of the radial head and the cross-sectional areas of the radial notch and its orientation of the ulnae in various species. The prone and supine movements are possible through the articulation with the radial notch of the ulna, which forms part of the elbow joint. In the Felidae, the head of the radius has an elliptical outline, which allows it to act as a cam that transmits an aberrant motion to the radius during movements of pronation and supination (Gonyea, 1978). The eccentric motion of the rotating head has the effect of permitting rotation of the radius without stretching the interosseous ligament, which holds the radius and ulna together. Since the degree of forearm pronation-supination seem to depend on the shape of the radial head and the position of the radial notch, inferences for increasing or decreasing mobility in this section should be possible. In all probability, it is particularly *Smilodon*, from which is assumed to depend on a more flexible pronation- supination mechanism rather than concical toothed cats [28]. Because of that, the possession of a more circular-like shape in this section is supposed. The cheetah and wolf are both highly cursorial runners and do not seem to need a marked mobility in the forearm. Therefore, the species of group one should perform a radial head that is less elliptical in outline than those of group two and three. In addition, the orientation of the radial notch of the ulna should be placed more anteriorly for group one making a pronation of the forearm easier, but restrict supine movements. The results partially support this idea for the three groups, but exceptions for the radial shape form the cheetah, with an outline being slightly rounder than for the tiger and jaguar. *Canis* in turn was shown to have the lowest elliptical shape, while *S. fatalis* showed the highest. For the orientation of the radial notch the results confirm the postulated expectations.

Radial Notch:

Gonyea (1978) discovered that the orientation of the radial notch (proximal radio-ulnar joint) of the ulna was positioned laterally in all extant big cats, which have a relatively high degree of pronation-supination of the anterior limb. For those carnivores, which have the radial notch located more anteriorly like the canids, pronation of the forelimb would be made easier and supination would be restricted. The cross-sections in Figure 5.2.7 illustrate that basic pattern and also show that the angle for *Smilodon* surpasses those of the other species of approximately 15?. This further supports the interpretation that elbow movements in this saber-toothed cat allowed a greater flexibility than in modern pantherine felines.

Olecranon Fossa:

The sharp bony edges of the olecranon fossa help guide movements of the ulna on the trochlea of the humerus. Jenkins (1971) proved that the olecranon fossa possesses a greater angle of inclination in the felids than in canids. He argues that in non-cursorial mammals, the humerus is normally held at an angle to the sagittal plane of the body thereby requiring the elbow to flex and extend, while the long axis of the ulna is at an angle to the

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[28] Compare to Chapter 7

long axis of the humerus. However, a 'pendulum-like' flexion and extension during locomotion would result in there being no angle between the long axis of the humerus and ulna. This in turn would be reflected in the olecranon fossa having a vertical orientation; hence, the greater the deviation of the front extremity from a 'pendulum-like' motion, the greater the angle of the olecranon fossa in relation to the long axis of the humerus. With this in mind, GONYEA (1978) tried to correlate this morphological character with that of habitat preferences and concluded that the 'exclusive' forest dwellers have a greater olecranon angle and therefore a greater deviation of the anterior limb from a 'pendulum-like' movement than those felids that inhabit a more open country. Results of the present study confirm with his ideas and demonstrate that the inclination of the olecranon fossa in *Smilodon* is relatively high to modern pantherine cats.

Humerus, Distal:

Two articular joints on the distal end of the humerus are represented by the cylindrical trochlea, which links with the ulna, and the capitulum, which articulates with the radius. TAYLOR (1974) demonstrated that the shape of these two described segments limits movements in the antero-posterior plane between the humerus, radius, and ulna. Thus it is assumed that for group one the adaptive trend is toward restriction of elbow movement to flexion and extension in a sagittal plane providing additional elbow stability, while for cats of group two and three these trends should lead towards the other direction. Therefore, it is presumed that the trochlea would exhibit a greater relative breadth in higher cursorial carnivores, when collated to the maximum width of the distal humerus. However, results vary arbitrarily and do not confirm with any of the postulated ideas (see Figure 5.2.6). More relevant in this case seems to be the height of the trochlea rather than the width.

Tibia, Proximal:

Collations between the proximal sections of the tibial head against the tibial length should for one part demonstrate how limb bones primarily grow along the axis of the shaft in higher cursorial carnivores and that the proximal and distal ends are more or less neglected in this regard. To put it in other words, the diaphysis is expected to grow in length while the epiphysis more or less should stay at the same size. Secondly, cats of group two and three are believed to have bigger and stronger articular joints than runners like the wolf and cheetah. In fact, the results in Figure 5.2.8 indicate and further elaborate this interpretation. Group one is shown in having the smallest epiphysis, while group two is intermediate between the latter and group three, as expected.

Femur, Proximal:

The femur is the strongest bone in the mammalian skeleton, because of both, the supporting function and propulsion of the body. In respect of corresponding muscle performances for forward movements of the body and as an effect through the load applied onto this limb bone, the latter exhibits different stresses in terms of length, breadth, processes, etc. At the proximal end of the femur the Caput femoris forms the articular joint to the acetabulum of the pelvis. It is turned inwards and more or less perpendicular to the long axis of the shaft. Lateral to this joint lies the Trochanter major. This portion is usually situated below the articulating joint in cats, whereas in dogs it may reach equal height (NICKEL ,SCHUMMER, SEIFERLE, 1977).

Relations and comparisons between both, the proximal and distal heads of the femoral bone, as illustrated in Figure 5.2.8 on the bottom, should demonstrate length variances between these two segments. In much the same way as the trochlear ridge of the humeral elbow joint was thought to depend in size on the type of locomotion, the same principals are expected for the femoral knee joint. In this case however, it’s the medial and lateral epicondyles of the distal head that make up all the breadth. These epicondyles are insertion areas for muscles like the strong adductor magnus muscle on the medial- or the popliteus muscle on the lateral epicondyles. The former operates in unison with various other muscles moving the limb in an inward- and backward motion, while the latter is responsible for the flexion of the knee joint and for pronation of the shank (NICKEL ,SCHUMMER, SEIFERLE, 1977). The proximal head of the femur however, seems to be strongly dependent on the strength of the gluteus medius- and minimus attaching on the greater trochanter of the proximal end of the femur. These two muscles are responsible for abductions of the thigh at the hip joint. M. gluteus medius is furthermore involved in a backwards movement of the entire limb providing a forward propulsion of the trunk (NICKEL ,SCHUMMER, SEIFERLE, 1977). Moreover, a longer femoral neck, which is supposed to be shorter in runners of group one but longer in group two and three, obviously contributes to the overall width of the proximal head. Also, because the muscles attaching to the distal femoral portion are involved in propulsion of the body, pantherine cats are expected to have a somewhat larger greater trochanter, whereas for the muscles that insert on the distal segment seem to be more engaged for cursors of group one. Nevertheless, the results show that there seems to be no correlation whatsoever and a closer examination of muscles insertion areas would be more beneficial in this case.

In Figure 2.5.9 the proportions of the glenoid process and the muscle attachment size for the Teres major muscle were compared and scaled against the length of the scapula. The Teres major muscle inserts along the lateral axial border of the infraspinous fossa. Together with the M. subscapularis and Latissimus dorsi it rotates the humerus medially whereas alone, it acts as an adductor of the anterior limb. The lever arm of this muscle increases with the extension of the posterior angle of the scapula where the muscle attaches (HARVEY POUGH et al.,1996). This feature indeed is developed in the shoulder blades of group one and in the puma of category two, whereas the other cats have a more symmetrical scapula. It is for this reason why these muscles are expected to be stronger developed in the wolf and cheetah, and maybe in the puma as well, which is shown to be closer related to the latter (see below). The felids of group two and three in turn are thought to show relatively short muscles in this regard. The outcome of the data does confirm with these ideas for most species, except for the wolf and lion. However, the lion already showed affinities towards a more cursorial open terrain lifestyle, whereas the wolf, with a relative Teres major length that is almost as short as in *Smilodon*, may not rely heavily on such a well-developed muscle portion as in the cats or it simply uses different muscles for this action like the subscapularis muscle.

Scapula:

The scapula serves not only as an insertion area for all of the major muscles of the shoulder joint, it also plays an important role in contributing to the overall length of the anterior limb. If the scapula is aligned with and in the same plane as the other limb elements its rotation contributes to the length of stride (POUGH et al, 1996). For instance, if we take a look at the sloping back of modern hyenas or in the fossil scimitar-toothed cat *Homotherium*, a high scapula plus elongated forelimbs primarily lead to this distinctive posture. The scapula articulates with the Caput humeri of the humerus and allows rotation to varying degrees in different mammal species depending on an increasing specialization of the anterior limb towards a pure running mechanism.

The relative size of the glenoid process is strongly correlated to the Caput humeri, which allows rotation to different amounts in various cats also depending on specialization towards a strict running locomotion as in group one. Hence, the smaller, rounder and flatter the glenoid process the more mobile is the shoulder joint in a variety of planes and vice versa. In this regard, it is expected that pantherine cats of group two and particularly saber-toothed cats show great tendencies towards such developments, whereas carnivores of group one are thought to reduce features in this respect. Again, the data prove this for all to be similar except for the wolf, which has an extremely large glenoid process in comparison to the scapula length.

Teres Major:

The Teres major muscle is involved in the flexion of the shoulder joint and to a slight degree on the adduction of the front limb. In cats, the attachment area on the humerus is tendinous. Thus the approximate insertion area away from the joint could be estimated to a fairly profound degree. Inferences of muscle positions particularly in the shoulder and upper forelimb of carnivores with tendinous or aponeurotic attachments, is said to be generally associated with scarring or delimited osteological features, whereas direct attachments typically occur on smooth bone surfaces that are often not visible (HAROLD et al., 1990). HILDEBRAND (1985) showed that muscles could move the joints through wider angles and therefore contribute to the length of stride when they insert close to the joints than when they insert farther away.

For most felids the ability to accelerate to maximum speed in the shortest time seems to be essential for hunting success, giving it adequate stalking cover, which was proved to directly influence the distance traversed in the final charge (SUNQUIST, 1989). To accelerate a mass to a high velocity quickly requires providing power to the limbs and having muscle origins farther out on the lever arm. If high velocity can be achieved slowly, then muscle insertions can be located closer to the fulcra (HILDEBRAND, 1989). Since pantherine felids do not maintain sustained chases but need to accelerate rapidly, the adaptations needed are different from those of cursors such as wolves or the cheetah. Figure 5.2.10 illustrates this model on three species of the three hypothesized categories. It is shown that the quick-moving cheetah of group one has its Teres major muscle attaching very close to the inner lever arm of the humerus, while the same muscle for *Smilodon* of the third category attach much further outside. The lion in turn is shown to be intermediate in this feature together with the other pantherine cats. Surprisingly, the puma's ratios are closer to the wolf's (and thus not far behind those of *A. jubatus*) than to the extant cats of group two. It has been suggested that the puma may bear some closer relationship to the cheetah, which was recently supported by studies of biomolecular structure of the puma, which suggests a split occurring some time after 3.5 Ma ago (TURNER & ANTÓN, 1996). A resemblance with the cheetah can be seen in other comparisons as well and further elaborates this assumption. Nonetheless, muscle insertion areas on bones are sometimes hard to identify and not always a very reliable feature to predict the size of a muscle. HAROLD et al. (1990) in fact pointed out, that the full area of muscle insertion is only possible in relatively few instances.

Humerus, Cross Section:

The cross-sectional shape of a long bone shaft is modified by the mechanical stresses placed on it (ALEXANDER, 1968).

The medio-lateral compressed outline of the midshaft certainly would reduce the potential bending in the antero-posterior plane. This shape may also be related to the development of the large flexors on the humerus.

GONYEA (1976) determined the robustness of the anterior limb for the felids in a different approach, by plotting the cross-sectional area of the humerus against the length of the latter. He added a regression line for the points of the various taxa and showed that there is a strong correlation (r = 0.958) between these two measurements for the “forest felids”. The data points for the cheetah clearly fall below this regression line, whereas those of *Smilodon* fall above it.

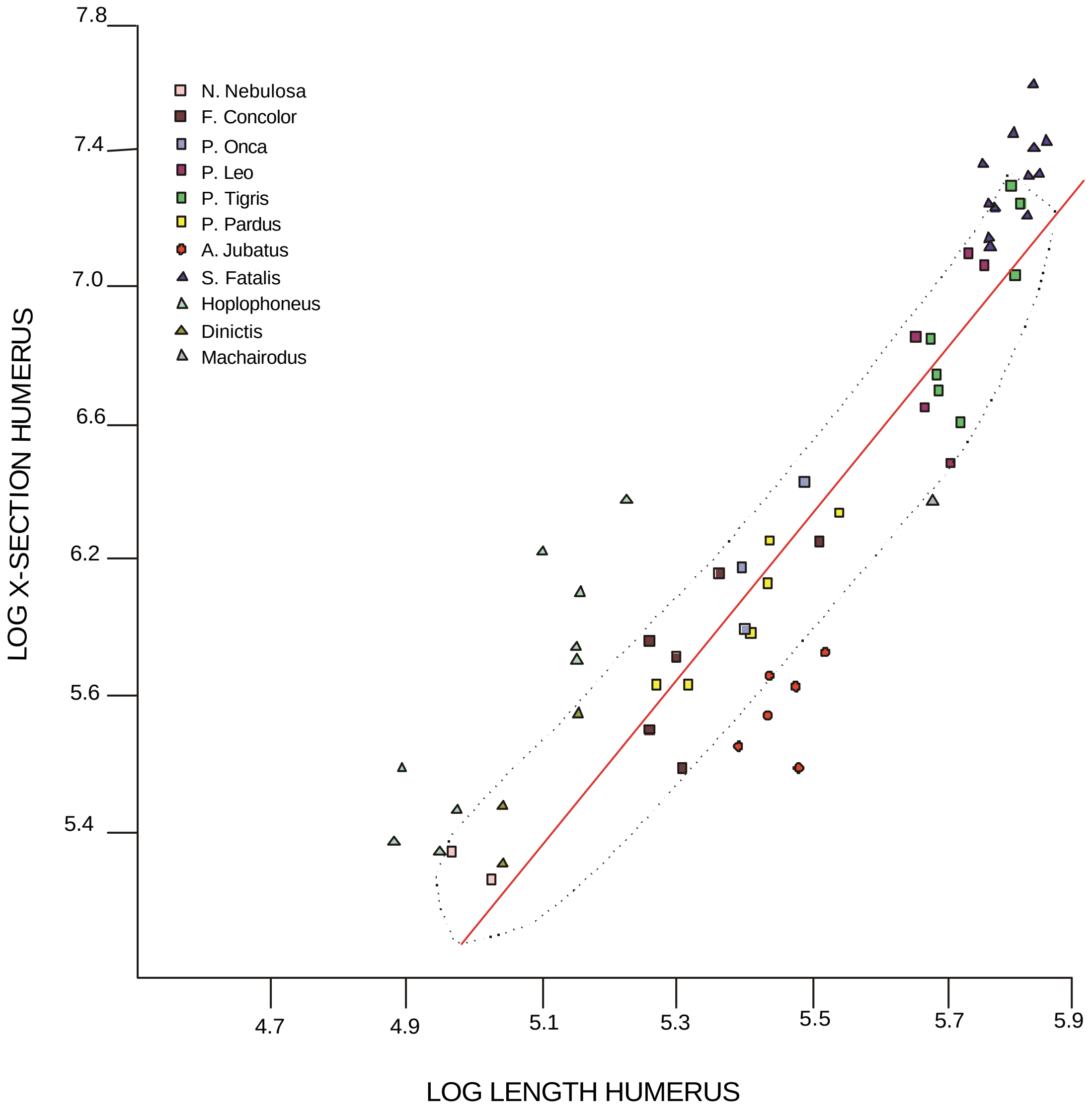

Figure 6.2.4: Relationship between cross-sectional area of the humerus and its length after GONYEA (1976) for various living and extinct cat species. The cross-sectional area is calculated by multiplying the two widths of the shaft, and the measurements are taken at the junction of the middle and distal 3rds of the shaft. In this way, the deltoid crest is not included in the measurement. The regression line is fitted to the data for the forest felids only using least squares method. The dotted line represents the range of this ratio for the pantherine cats.

Skull Proportions:

Skull proportions of Chapter 5.2 should clarify possible growth correlations within skull measurements and the front limb, which then can be further used for statistical analysis as in Chapter 5.3.

Canine Length & Skull Width:

In Figure 5.3.1 the skull width and canine height is plotted against the skull length. The expectations are, that for canids of group one the canines have the relatively smallest height, since in these animals the retention of a longer tooth row forces the skull to stay long, making the canines appear small in comparison.

The cheetah and the pantherine cats more or less are thought to have similar length ratios, though longer than those of the canids, while saber-toothed cats of course have the highest ratios with their elongated canines. This effect is enhanced through a shortening of the skull by the loss of the third upper premolar teeth. The chart in the figure proves this to be true. On the other hand, the skull width is determined by the zygomatic arches. Plotted against the length of the skull the outcome should be as following: 1. Canids with long slender skulls and relatively small masseter muscle that attach on the narrow zygomatic arches. 2. Modern cats including the cheetah with stronger masseter muscles and corresponding broader zygomatic arches and shorter skulls. 3. *Smilodon* with short and relatively narrow skull and comparatively weak masseter muscles.

Canine Distance:

The illustration below the latter discussed deals with variances between skull width and canine distance in the different postulated groups. One might think that, from an allometric point of view, these two features should stand in strong correlation to each other, but it is primarily the development of the zygomatic arches that dominates this ratio. In this regard, the relatively narrow skull in *Smilodon* apparently enhances a wider clearance for the canines in contrast to the wolf. The wolf's relative narrow skull obviously doesn't compensate for a relatively wider clearance for the canines (see Figure 5.3.2). For modern big cats the results are expected to be relatively equal, however, the cheetah falls slightly out of row with a quite close canine distance.

Canine Shape:

Prey-killing behavior explains canine shape better than diet does, therefore the form of the canine reflects stresses incurred during biting (VAN VALKENBURGH, 1989). Felids possess rounder and more robust canines than do canids because the killing bite of felids is deeper and more forceful (EWER, 1973). VAN VALKENBURGH & RUFF (1986) studied the canine strength characteristics among living and extinct canids as well as felids. Their results indicate that felids have relatively stronger canines than canids, especially in bending about the antero-posterior (CX) rather than the medio-lateral (CY) axis. Besides, they demonstrated by an analysis of jaw muscle moment arms, that felids also have relatively stronger bites than canids. For the fossil sabertooths however, they showed that their canines are more similar in shape and strength characteristics to those of living canids than felids. Since the data is restricted on morphometric length comparisons rather than on mechanical analysis, the results illustrated in Figure 5.3.2 don't necessarily confirm with the results of VAN VALKENBURGH & RUFF. Nevertheless, the charts indeed show a likewise basic pattern, where *Smilodon* and *C. lupus* both exhibit antero-posterior flattened canines in comparison to the more conical shaped canines of modern big cats.

Dental Length:

The dental length is in any mammal strongly correlated with the retention or the loss of the premolar and molar teeth. Cats have lost an array of teeth in the upper and lower jaw. The dental bone has only one molar left, which forms the lower carnassial (M_1), in addition to two smaller premolars (P_3 & P_4), of which in *Smilodon* P_3 is reduced into a tiny cone. Thus it is not surprising to find the longest jawbone in the canids, which have kept all four premolars and three molars, while *Smilodon* has the relatively shortest dentary of all the studied carnivores. The extant big cats are all expected to fall slightly behind the ratios of *Smilodon*, which was verified in the outcome.

Skull Length & Anterior Limb:

The final comparison, illustrated in Figure 5.3.3, collates the skull lengths with the overall lengths of the anterior limb, which is comprised of the humerus, radius, and 3rd metacarpal. As pointed out in chapter five the cheetah exhibits extremely elongated front limbs. It is easy to predict that it has to have a relatively small head in comparison. The puma in turn has the relatively shortest anterior limbs as illustrated in Figure 5.2.3 thus its skull length is supposed to be longer, but not as long as in modern pantherine cats. The closer relation to the cheetah might be the reason for a comparatively small head. The pantherine cats of guild two are expected to show similar length ratios. However, the jaguar is conspicuous in having a relatively large head although its anterior limbs were shown to be quite alike the other cats of the same group. For *Smilodon* and its short limbs, the size of the skull was thought to be proportionately large in contrast, but the illustration reveals that it is rather small in size between those of *F. concolor* and modern big cats. Obviously, the changes occurring with the development of large canines preferably enlarge the skull in height rather than in length (MARINELLI, 1937). Besides, the short dental length of the saber is also evidence for a shorter skull as was mentioned before. The wolf at last was expected to broadly resemble the average cat, since both, its head and limbs are long.

Among all the species examined in this work it again should be recalled, that there is a significant added variance coefficient for the relative lengths of the anterior and posterior limb elements (see GONYEA, 1976) and that the variation for osteological characters in common usually falls between 4-6%.

7 HUNTING BEHAVIOR IN SMILODON

Based on the anatomical and proportional differences examined in *Smilodon*, its hunting behavior must have been altered in some way or the other to the one observed in modern big cats.

Before we get into this particular discussion however, one has to be confidential with the hunting behavior of *Smilodon's* closest extant relatives - the pantherine cats.

Unlike other large predators such as the wolf or the spotted hyena, which essentially kill their prey by pulling it down and eating it while still alive, cats in general tend to dispatch their chosen victims first, before they start to consume it. In cats, large claws and powerfully developed anterior limbs are ideally suited to catch prey and retaining a hold while wrestling it into a position where the canines may be employed in a bite (TURNER & ANTÓN, 1996). Canids lack retractile claws and their canines are less developed, so that sheer weight of numbers is often the most important element in bringing down prey.

The precise hunting technique, which includes the method of capture and dispatch, depends on the size of the cat, its overall morphology and the size and type of prey. Moreover, the mode of hunting also depends upon the social structures observed in various felids, meaning if they hunt in prides or rather solitary.

It is generally noticed that especially in cats, a strong interaction of innate and learned patterns of behavior is of great importance. Cats develop an early interest in chasing anything that moves, and will go through an elaborate sequence of crouching, wriggling the hind-quarters, and pouncing (TURNER & ANTÓN, 1996). However, what they seem less secure about is what to do with the object once they have seized it, although the neck region appears to be sought instinctively. Female cats have been observed of bringing live prey for their kittens to practice capture and killing. In addition, at a certain age the young offspring will join their mother in hunting, this way they get to learn what prey to take and how it is supposed to be killed.

For modern pantherine cats, smaller prey is killed by a bite at the rear of the neck, thereby the upper canines drive between the vertebrae and severe the spinal cord (LEYHAUSEN, 1965; SCHALLER, 1967 & 1972; GONYEA, 1976). Larger animals like ungulates require different approaches. They developed posteriorly directed horns along with an increase in length of the cervical spines, which possibly evolved, in part, for protection against predators. Prey animal of large size are rarely knocked over by the impact of the predators body; instead during the pounce, the hind feet of the felid usually do not leave the ground. The prey is seized and the predator pulls the prey towards itself. In this manner, as the victim is pulled down, the predator is able to maintain contact with the prey, and in doing so controls the victim’s movements (Leyhausen 1965b; Schaller, 1967 & 1972; Kleimann & Eisenberg, 1973).

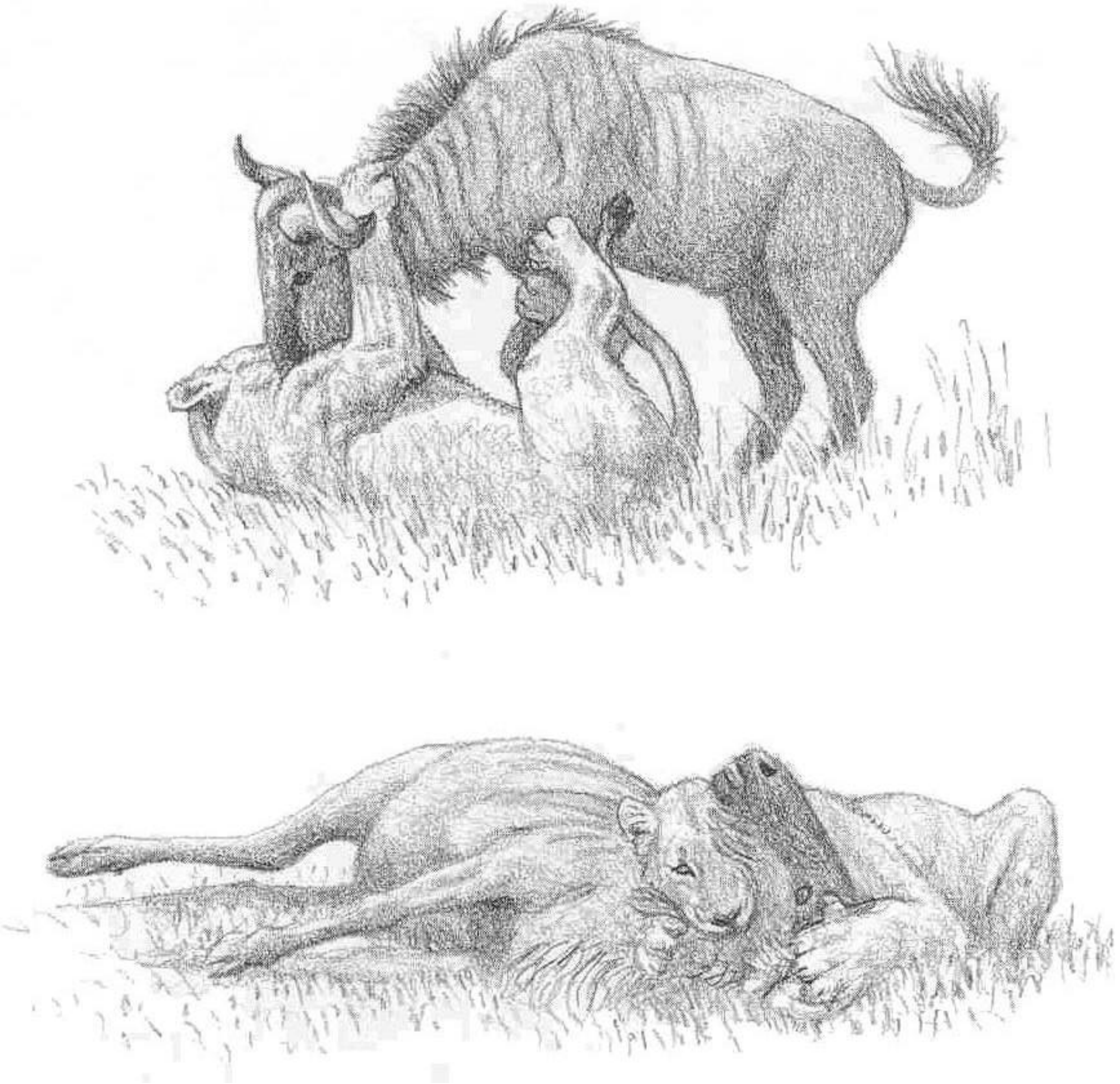

Figure 7.1: Prey capture as seen on a lioness with wildebeest (after Turner & Antón, 1996).

Prey is usually grabbed by the throat or the muzzle with a strong bite, at which it is aided by its long retractile claws and powerful front legs (see Figure 7.1 and 7.2). Death results mostly from suffocation rather than a violent and bloody end (Turner & Antón, 1996). This technique may be used to avoid the pointed horns that protect the nape of the neck in many ungulate prey species (Gonyea, 1976).

The cheetah on the other hand is forced to employ a different hunting method, because its claws can’t be used as a grasping device, and its body proportions are that of a sprinter, lean and long. However, like many of the other cats it is perfectly adept at the stalk to bring itself closer to its prey. The final rush takes the form of a high speed chase, often over several

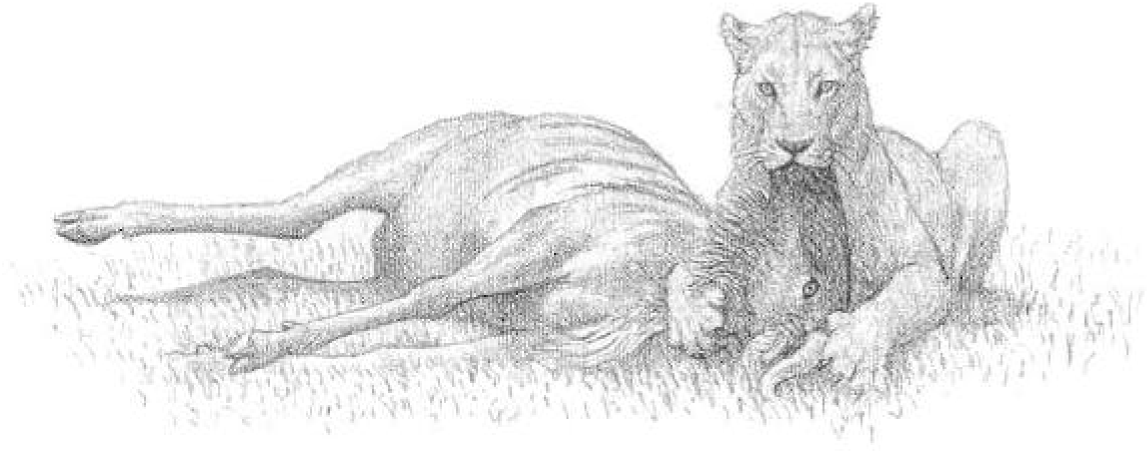

Figure 7.2: Killing scenario – a lioness suffocates its prey by applying a bite on the muzzle area (after TURNER & ANTÓN, 1996). See text for further information.

hundred meters, during which the twists and turns of the usually small prey are relentlessly followed. The capture is achieved at high speed, normally not by a leap onto the back of the animal but by clawing at one side of the rear of the prey and pulling backward in a complex and carefully coordinated maneuver. This causes the prey to lose balance and collapse, and usually results in its tumbling over. The large dewclaw on the inside of the cheetah's front paw is employed in this technique, in effect "hooking" the back leg of the unfortunate animal. Finally, it will be seized by the throat and strangled (NOWAK, 1991).

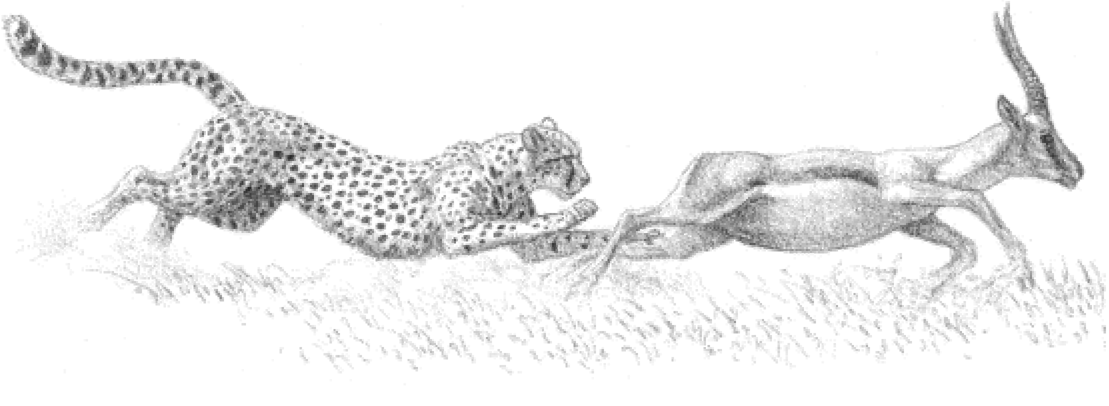

Figure 7.3: Hunting sequence of a cheetah. Contact with prey commonly occurs at very high speeds, and the cat throws its prey off balance by "hooking" a hind limb with the internal dew claw of its front paw (after TURNER & ANTÓN, 1996).

So far as the hunting behavior of fossil saber-toothed cats is concerned, we can probably assume that the same general principles would have operated as for pantherine cats.

Capture would be by stalk and a pounce, in conjunction of thicker vegetation, or perhaps by a stalk and a relatively short rush in more open terrain. The actual killing scenario however, would have clearly varied from their modern relatives.

It has generally been assumed that the large upper canines of *Smilodon* and other saber-toothed cats were adaptations for attacking large, relatively thick-skinned prey such as ground sloths or proboscideans. BAKKER (1996) argues that Tertiary sabertoothed cats and Jurassic allosaurid dinosaurs evolved convergently to prey on herbivore species that were 10 or more times heavier than themselves. The capability for taking larger prey would be advantageous for any predator within the size range of sabertooths since it would allow a potentially wider food niche for a similar sized non-sabertooth (EMERSON & RADINSKY, 1980). However, predator-prey size relationships are influenced from many factors primarily, whether food was a limiting resource or not. *Smilodon* would have certainly eaten anything that it was able to catch including carrion.

Because of the relatively fragile nature of the sabers most researchers concluded that they were not employed on bony areas of their prey (AKERSTEN, 1985; TURNER AND ANTÓN, 1996, V.VALKENBURGH, 1990;). If they were used in an attack on a bony area, such as the back of the neck or posterior skull as GONYEA (1976) suggested, one saber would almost certainly contact bone before the other, resulting in considerable lateral torque and probable breakage (BOHLIN, 1947). Repeated contact with bone would also cause wear on the tips of the canines. VAN VALKENBURGH (1989) examined dental micro wear patterns in *S. fatalis* and concluded that the sabertooth consumed very little bone, actually avoided bone in order to protect its long canines from breakage. To elude any risk of damage to the sabers the capture very likely involved bringing prey down to the ground before biting at it, unlike the living pantherine cats with their rounded canines, which often bite the standing and struggling prey animal in the throat, the muzzle, or even the rump (see Figure7.1). Such behavior would have been too risky for the long laterally compressed, blade-like canines of *Smilodon*. Furthermore, once the prey lies on the ground it will no longer try to defend itself or put up a fight, since it more or less falls in a state of shock (SCHALLER, 1972). In this stage the claws and powerful front limbs of the predator would have been easily able to control large and even struggling prey. More importantly, *Smilodon* was now able to quickly orienting itself to the abdomen or the throat and employ a fatal canine shear bite without contacting bone, causing a fatal wound in conjunction to considerable blood loss, which finally would have led to death.

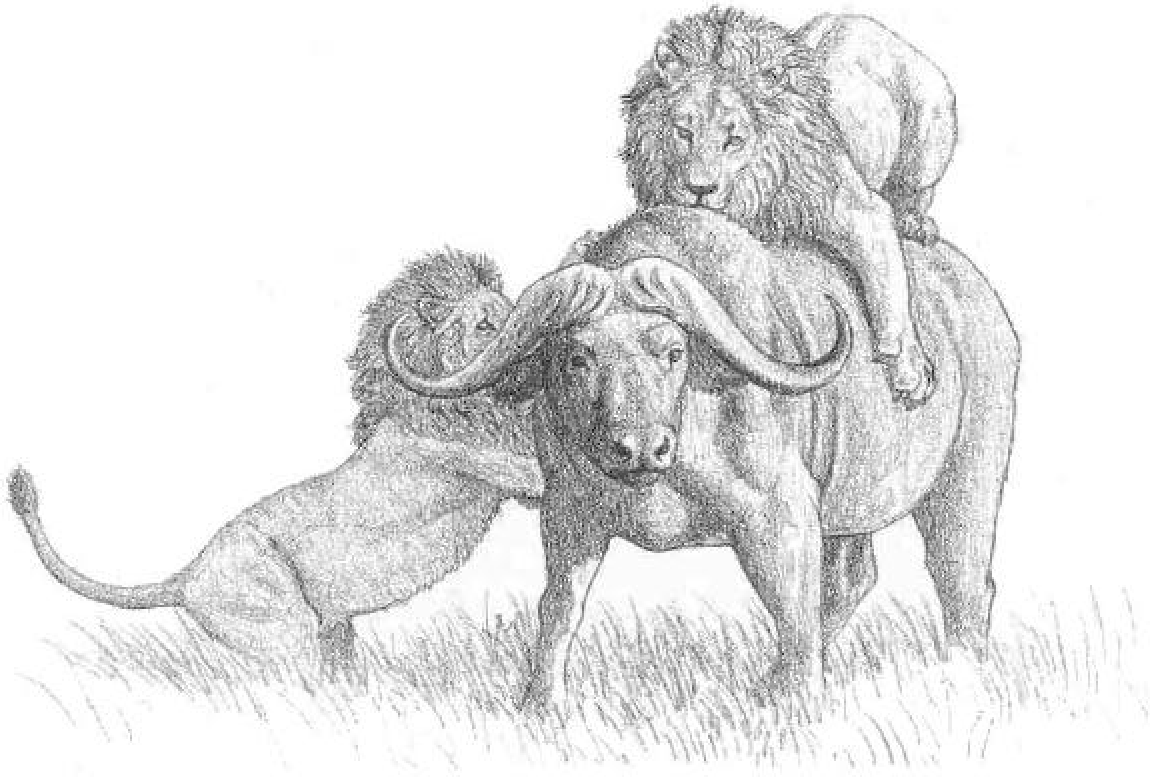

Figure 7.4: Prey capture of two male lions. The killing of larger and defensive prey, such as this buffalo requires a lot of experience, enormous power and stamina (after TURNER & ANTÓN, 1996).

Functional analysis of the gape by EMERSON & RADINSKY (1980) revealed that sabertooths had similar clearance between upper and lower canines as do modern felids, but, as KURTEN (1952) demonstrated, it is unlikely that sabertooth canines penetrated any deeper than do modern felid canines. Rather, their advantage was in creating a larger superficial wound, as would be achieved by a canine shear bite on convex body surfaces thereby severing critical blood vessels as ACKERSTEN (1985) suggested.

The morphology of the posterior cervicals, especially that of the transverse processes, indicates increased leverage for several neck muscles, including the scalenes, but also for other muscles that turn the neck up, or to one side (TURNER & ANTÓN, 1996; ANTÓN & GALOBART, 1999). This suggests that in combination with a relatively long neck in *Smilodon* (MERRIAM & STOCK, 1932) these animals had a greater range of vertical and lateral movements of the head relative to the trunk, than pantherine cats of comparable size. ANTÓN & GALOBART (1999) further argue that such a morphology would have allowed a sabertooth cat to precisely and quickly orientate its head for a bite to a specific area of the body of large prey species and that it in deed fits well with a canine shear bite killing scenario (see Figure 7.5 below).

Figure 7.5: Reconstruction of Homotherium latidens applying the canine shear-bite to the throat of a horse, while holding it down to the ground. **A**. Superior view of cat and prey, showing angle between the axis of the cat's body and head. **B**. Detail of the skull and anterior vertebral column, showing lateral flexion of the neck and trajectors of the fibers of some muscles that contribute to such lateral flexion (after ANTÓN & GALOBART, 1999).

The use of the anterior limb as a hunting weapon and its impact on forelimb anatomy should be further elucidated.

HILDEBRAND (1954) found that the radius and ulna are better adapted to a cursorial habitus in the canids than in other carnivorans. For those canids that pursue their prey over long distances, the ability to maintain a high constant speed is seemingly important. HOWELL (1944) showed that an elongation of the distal limb elements is a good indicator of cursorial specialization. Chapter 5 displays the lengthening of distal limb elements for the wolf and cheetah compared to those of pantherine- or saber-toothed cats.

As the length comparisons in Chapter 5 demonstrated, *Smilodon's* distal anterior limb segments are extremely shortened and more massive as those of modern big cats. This shortening and the presence of powerful adductor muscles improve the stability of the cat when it is wrestling with prey. Among the most important muscles involved in such an activity are the flexors and extensors of the forepaw, which form the major mass of the animal's forearm; the muscles that adduct, or pull in the arm, such as the pectoralis; and those that abduct, or pull out, the arm, such as the deltoid. Evidence from the insertion areas on the bones indicate that all these muscles were extensively developed in the smilodontine cats (TURNER & ANTÓN, 1996).

The flexion of the forearm is a further important movement and is carried out by the biceps muscle. The combined effects of the Teres major and the Latissimus dorsi aid its action.

The first arises from the posterior surface of the scapula, [29] and the second from the backbone and lumbar fascia. They join together and insert on the inside of the humerus. Since the back of the smilodontines is shorter than in pantherine cats, the contraction of the Latissimus dorsi is more effective, as is the pull of the large muscle masses of the back lying under the lumbar fascia. Moreover, as demonstrated in Figure 5.2.10, the Teres major muscle inserts farther away from the shoulder joint on the inside of the humerus as for cats of group one and two, indicating a restricted action of movements of the joint, which in turn imposes limits on the rate of stride (HILDEBRAND, 1989). Nevertheless, this anatomical feature finds its advantages for a quicker and more powerful acceleration to maximum speed, which would be typical for well-adapted stalkers. This serves as a further indication for a well-adapted stalker that ambushes its prey from concealment. Acceleration to maximum speed was probably reached in a very short time. GONYEA (1976) showed that the saber-toothed felids possessed similar morphological features in their middle- and distal phalanx than modern cats, which suggests that the claws of the former were completely retractile as well. As a rule, the larger the prey the more important are fully retractable claws (LEYHAUSEN, 1965; GONYEA & ASHWORTH, 1975), which, in conjunction to the robust forelimbs, serve as an indication that the prey taken by *S. fatalis* and *X. hodsonae* could have been substantially heavier than their own body weight. If *Smilodon* formed prides as was suggested by several authors (ACKERSTEN, 1985; TURNER & ANTÓN, 1996; et al) prey size could have been even larger and thus enhancing the assumption that it was actually hunting young proboscideans or other contemporary animals of the mega fauna, as noted above. To knock over or pull down large prey, the forepaws of the predator require some freedom in their movements (supination & pronation), because prey animals are constantly moving and trying to free themselves from the employed grip. Retractile claws aid to hold on to and immobilize prey, but to attain a perfect position of the forepaws in the first place and to maintain it on the body of the animal, a minimum prone- supine movement is of great importance for cats that deal with large prey. The orientation of the radial notch [30] of the ulna was found to face laterally with an angle of 65 º in *Smilodon*, which is about 15 º more than for modern pantherine cats, suggesting a greater freedom of a prone- supine motion in the forepaws. Moreover, a higher circular shape of the radial head in *Smilodon* provided additional advantages for such movements.

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[29] as illustrated in Figure 5.2.10

[30] the proximal radio-ulnar joint

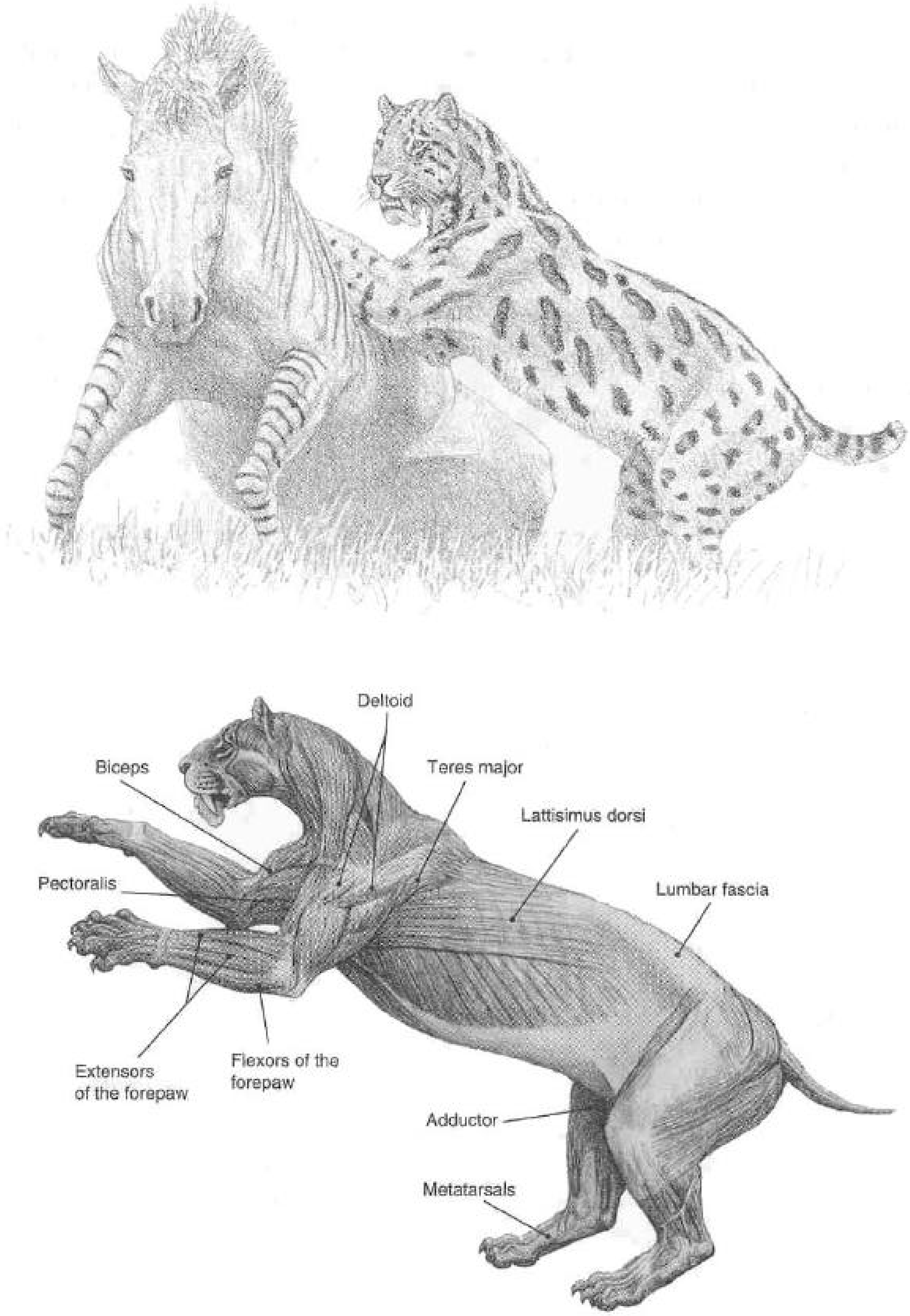

Figure 7.5: Postulated prey seizing in sabertoothed cats and the different muscles involved in such an action. Note the strong forepaws, the Latissimus and Teres major muscles (after TURNER & ANTÓN, 1996).

In the posterior limb, well developed and powerfully build adductor muscles in conjunction to the shortened metatarsals, must have improved the stability of the cat when it was wrestling with its prey. Furthermore, *Smilodon's* relatively thicker transversal breadth of the tibia (LT) provided it with extra strength and stability in the articular knee joint. The calcaneus was also shown to be relatively longer than for pantherine cats and must have improved its ability to jump and leap onto the back of a prey animal. Additionally, since *Smilodon* couldn't sustain long chases, it relied on stalking its prey from concealment thereby trying to get as close as possible. A long leaping ability would have been definitely beneficial in the first phase of the pursuit to gain on distance to its prey.

8 CONCLUSIONS

The anterior- and posterior limbs, the short back, and the overall skull peculiarities of *Smilodon fatalis* all possess morphological traits related to deal with large prey. Particularly the front limbs exhibit proportions that are unparalleled in modern pantherine cats. Radius, ulna, and metacarpals are shown to be extremely shortened, suggesting functional advantages to seize and struggle with bigger prey. Discrete large muscle attachment areas on the humerus for the Teres major and Latissimus dorsi indicate that these muscles insert farther away from the articular shoulder joint than for extant cat members, decreasing the amplitude of arc of movement while increasing its force. Together with a shorter back, a large cross-sectional area of the humerus and huge pectoralis muscles attaching on the humeral crest, strong flexors and extensors of the front paws, etc, these formidable cats were equipped to pull down and immobilize prey of their contemporary megafauna.

The radial head, which articulates with the ulna on the radial notch and the capitulum on the distal end of the humerus is found to be more circular than in any other examined cat species. The radial notch in turn displays an angle that exceeds those of modern pantherine cats of about 15 ° and is clearly faced laterally. The wide angle of the olecranon fossa on the distal humerus, which articulates with the olecranon of the ulna, provides more clearance and play in the forearm than in any other living feline.

The hind limbs are shown to be similarly arranged in morphology to the front limbs in order to stabilize the body of the predator, which would have to withstand great forces during a fight. Tibia and metatarsals are shorter than for any modern representative. However, in comparison to the anterior extremity they were much more gracile and restricted in movement. Moreover, the knee joints appear to be stronger and the long length of the calcaneus indicates good jumping abilities, although the posterior limbs reveal to be relatively long against the anterior limbs.

Smilodon's elongated canines, its long muscular neck, and shortened, sturdy limb proportions and peculiarities make it to one of the most terrifying predators of prehistoric times, that was perfectly equipped to deal with large prey.

Factorial analysis proved a strong correlation between the development of sabertooth canines and a strengthening in the anterior limbs. Statistical analysis revealed three different guilds for the studied cat species:

1. Cursors, with slender and elongated limb proportions, a short calcaneus, muscle insertions that attach closer to the relatively weak articular joints, which in turn show restrictions in their maneuverability, non-retractile claws, etc. The cheetah and wolf belong to this category.
2. Pantherine cats as the tiger, lion, jaguar, leopard, and cougar, of which all more or less show the same morphology and proportions. The exception is the puma, which seems to

share a common ancestry with the cheetah. However, they all possess retractile claws, relatively short and powerful limb proportions compared to those of guild one; muscle attachments that insert closer to the joints, etc. In general they were shown to be intermediate in their morphology between guild one and three.

3. Saber-toothed cats with elongated canines, narrow skull, even shorter and more powerfully build extremities, etc (see above).

The above observations do not support GONYEA'S previous idea about the relationship between body proportions and habitat preferences, but they fit well with the relations between movements in the elbow joint and the shape and size of the canines.

9 LITERATURE

✍✍ABEL, O. (1914). Die vorzeitlichen Säugetiere. – G. Fischer. Jena.

✍✍AKERSTEN, W. A. (1985). Canine function in *Smilodon* (Mammalia; Felidae; Machairodontinae). – Contribution in Science, Number 356, pp. 1-22; Natural History Museum of Los Angeles County.

✍✍ANTÓN, M. & GALOBART, À. (1999). Neck Function and Predatory Behavior in the Scimitar Toothed Cat *Homotherium latidens* (OWEN). – Journal of Vertebrate Paleontology, Vol. 19(4), pp. 771-784.

✍✍BABIARZ, J. P., HEARST, J., MARTIN, L. D.& NAPLES, V. L. (1999). Three Ways to be a Saber-Toothed Cat – Naturwissenschaften 87, pp. 41-44.

✍✍BAKKER, R.T. (1983). The deer flees, the wolf pursues: incongruencies in predator-prey coevolution; pp.350-383 in Futuyma, D. and Slatkin, M. (eds.), Coevolution. Sinauer Press, Massachusetts.

✍✍BOHLIN, B. (1940). Food habit of the machaerodonts, with special regard to *Smilodon*. Bulletin of the Geological Institute of Upsala 28: 156-174.

✍✍BRYANT, H. N. (1991). Phylogenetic Relationships and Systematics of the Nimravidae (Carnivora). – Journal of Mammalogy, Vol. 72, pp. 56-78.

✍✍BRYANT, H.N. (1996). Force generation by the jaw adductor musculature at different gapes in the Pleistocene saber-toothed felid *Smilodon*; pp.283-299 in K.M. STEWARD and K.L. SEYMOUR (eds.), Paleoecology and Paleoenvironments of Late Cenozoic Mammals. University of Toronto Press, Toronto.

✍✍COPE, E: D. (1880). On the extinct cats of America. – The American Naturalist, Vol. 14, December, 1880, No. 12.

✍✍DE BONIS, L. (1976). Un Félidé a longues canines de la colline de Perrier (Puy-de-Dome): ses rapports avec les félines machairodontes. – Annales de Paléontologie (Vertébrés). 1976, t. 62, fasc. 2, pp. 159-198.

✍✍DIAMOND, J. M. (1986). How great white sharks, saber-toothed cats and soldiers kill. – Nature, Vol.332, 28 August 1986, pp. 773-774.

✍✍DUCKLER, G.L. (1997). Parietal depressions in skulls of the extinct saber-toothed felid *Smilodon fatalis*: evidence of mechanical strain. – Journal of Vertebrate Paleontology, Vol. 17, pp. 600-609.

✍✍EMERSON, S. B. and RADINSKY, L. (1980). Functional Analysis of Sabertooth Cranial Morphology. – Paleobiology, 6 (3), pp. 295-312.

✍✍EISENBERG, J. F. & LOCKHART, M. (1972). An Ecological Renaissance of Wilpattu National Park. – Smithsonian Contrib. Zool. Vol. 101, pp. 1-118.

✍✍EWER, R.F. (1973). The Carnivores. Ithaca, N.Y.: Cornell University Press.

✍✍GEIST, V. (1974). On the Relationship of Social Evolution and Ecology in Ungulates. – American Zoologist, Vol. 14, pp. 205-220.

✍✍GITTLEMAN, J. L. (1989). Carnivore Behavior, Ecology, and Evolution. – Comstock/Cornell Paperbacks; Cornell University Press; Ithaca, New York.

✍✍GONYEA, W. J. & ASHWORTH R. (1975). The Form and Function of Retractile Claws in the Felidae and other Representative Carnivorans. – Journal of Morphology, 145, pp. 229-238.

✍✍GONYEA, W. J. (1976). Adaptive differences in the body proportions of large felids. – Acta Anatomica, Vol. 96, pp. 81-96.

✍✍GONYEA, W. J. (1976). Behavioral implications of saber-toothed felid morphology. - Paleobiology, vol.2, pp. 332-342.

✍✍GONYEA, W. J. (1978). Functional implications of felid forelimb anatomy. – Acta Anatomica, Vol. 102, pp. 111-121.

✍✍GREGORY, W.K. (1912). Notes on the principals of quadrupedal locomotion and on the mechanism of the limbs in hoofed animals. Annals, New York Academy of Sciences, Vol. 22, pp. 267-294.

✍✍HARVEY POUGH, F., HEISER, J.B & W.N. MCFARLAND (1996). Vertebrate Life. – 4th Edition, Prentice Hall, New Jersey.

✍✍HILDEBRAND, M. (1959). Motions of the running Cheetah and Horse. – Journal of Mammalogy, Vol. 40, No. 4, pp. 481-495.

✍✍HILDEBRAND, M. (1961). Further Studies on the Locomotion of the Cheetah. – Journal of Mammalogy, Vol. 42, No. 1, pp. 84-91.

✍✍HILDEBRAND, M. (1988). Analysis of Vertebrate Structure. – 3d ed. New York: Dover.

✍✍HILDEBRAND, M & HURLEY, J.P (1985). Energy of the oscillating legs of a fast-moving cheetah, jackrabbit and elephant. Journal of Morphology Vol.184, pp. 23-31.

✍✍HOWELL, A. B. (1944). Speed in animals. – University of Chicago Press, Chicago, 270 pp.

✍✍HUNT, R. M. (1989).

✍✍JENKINS, S. A. (1971). Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. J. Zool. Lond. Vol. 165, pp. 303-315.

✍✍JENKINS, F. A. (1973). The Functional Anatomy and Evolution of the Mammalian Humero-Ulnar Articulation. – American Jouranl of Anatomy, Vol. 137, pp. 281-298.

✍✍JENKINS, F. A. (1974). The Movement of the Shoulder in Claviculate and Aclaviculate Mammals. – Journal of Morphology, Vol. 144, pp. 71-84.

✍✍KLEIMAN, D.& EISENBERG, J. (1973). Comparisons of Canid and Felid Social Systems from an Evolutionary Perspective. – Animal Behavior, Vol. 21, pp. 637-659.

✍✍KURTÉN, B. (1952). The Chinese Hipparion fauna. – Comment. Biol. (Soc. Sci. Fennica). Vol. 13, pp. 1-82.

✍✍LEYHAUSEN, P. (1965b). Über die Funktion der relativen ?Stenamungshierarchie?. – Z. Tierpsychologie, Vol. 22., pp. 412-494.

✍✍MACFADDEN, B. (19??). Equids

✍✍MARINELLI, W. (1937). Der Schädel von Smilodon der Funktion des Kieferapparates analysiert.

✍✍MARTIN, L. D. (1989). Fossil History of the Terrestrial Carnivora. Carnivore Behavior, Ecology, and Evolution: pp. 536-568. Gittleman, J.L. (Ed.). Ithaca, N.Y.: Cornell University Press.

✍✍MARTIN, L. D. & SCHULTZ, L. D. (1975). Scimitar-toothed Cats, Machairodus and Nimravides, from the Pliocene of Kansas and Nebraska. – Bulletin of The University of Nebraska State Museum, Vol. 10, Number 1, Part 5, February, 1975.

✍✍MATTHEW, W. D. (1901). Fossil Mammals of the Tertiary of Northwestern Colorado. – American Museum of Natural History. Mem. Vol. 1, pp. 353-447.

✍✍MATTHEW, W. D. (1910). The Phylogeny of the Felidae. - Bull. Am. Mus. Nat. Hist., Vol. 28, pp. 289-316.

✍✍MERRIAM, J. C & STOCK, C. (1932). The Felidae of Rancho La Brea. – Carnegie Institution of Washington, December,1932.

✍✍MILLER, G. J. (1969). A new hypothesis to explain the method of food ingestion used by Smilodon californicus Bovard. – TEBIWA. Vol. 12, pp. 9-19. (Published by Idaho State University).

✍✍MILLER, G. (1984). On the jaw mechanism of *Smilodon californicus* bovard and some other carnivores. - Occasional Paper No.7; IVC Museum Society, El Centro, California.

✍✍NICKEL, R., SCHUMMER, A. & E. SEIFERLE (1977). Lehrbuch der Anatomie der Haustiere. - Band 1, Verlag Paul Parey, Berlin und Hamburg.

✍✍NOWAK, R.M. (1991). Walker's Mammals of the World. - 5th Edition, Vol. 2; The John Hopkins University Press; Baltimore and London, 1991.

✍✍OSBORN, H.F. (1929). The titanotheres of ancient Wyoming, Dakota and Nebraska. 2 vols. United States Geological Survey Monograph 55. Departement of the Interior, Washington, D.C.

✍✍PIENAAR, U. de V. (1969). Predatory-prey relationships amongst the larger mammals of the Kruger National Park. Koedoe Vol. 12, pp. 108-176.

✍✍RAWN-SCHATZINGER, V. (1992). The scimitar cat *Homotherium serum* cope. Illinos State Museum Reports of Investigations 47, pp. 1-80.

✍✍RIGGS, E. S. (1934). A new Marsupial Saber-Tooth from the Pliocene of Argentina and its Relationship to other South American Predacious Marsupials.

✍✍SCHALLER, G. B. (1967). The Deer and the Tiger. Chicago: University of Chicago Press.

✍✍SCHAUB, S. (1925). Über die Osteologie von Machaerodus cultridens Cuvier. – Versammlung in Luzern 1924, pp. 255-266

✍✍SCHULTZ, C. B., SCHULTZ, M. R. & MARTIN, L. D. (1970). A New Tribe of Saber-toothed Cats (Barbourofelini) from the Pliocene of North America. – Bulletin of The University of Nebraska State Museum, Vol. 9, Number 1, October, 1970.

✍✍SCHULTZ, C. B. & MARTIN, L. D. (1970). Machairodont Cats from the Early Pleistocene. – Bulletin of the University of Nebraska State Museum, Vol. 9, Number 2, November 1970.

✍✍SIMPSON, G. G. (1941). The function of saber-like canines in carnivorous mammals. – The American Museum of Natural History, New York City, Number 1130, August 4, 1941.

✍✍STOCK, C. (1968). Rancho La Brea, A record of Pleistocene life in California. – Los Angeles County Museum of Natural History. Science Series No. 20. Paleontology No. 11: 1-81.

✍✍SUNQUIST, M. E. & SUNQUIST, F. C. (1989). Ecological Constraints on Predation by Large Felids. Carnivore Behavior, Ecology, and Evolution: pp. 283-301. Gittleman, J.L. (Ed.). Ithaca, N.Y.: Cornell University Press.

✍✍TAYLOR, M. A. (1974). The functional anatomy of the forelimb of some African Viverridae (Carnivora). J. Morphology, Vol. 143, pp.307-336.

✍✍TAYLOR, M. A. (1989). Locomotor Adaptations by Carnivores. Carnivore Behavior, Ecology, and Evolution: pp. 382-409. Gittleman, J.L. (Ed.). Ithaca, N.Y.: Cornell University Press.

✍✍TURNER, A. & ANTÓN, M.(1997). The Big Cats and their Fossil Relatives. – Columbia University Press, New York.

✍✍VAN VALKENBURGH, B. & RUFF, C. B. (1986). Canine tooth strength and killing behavior in large carnivores. – *J. Zool., Lond.* (1987) 212**,** 379-397.

✍✍VAN VALKENBURGH, B. (1985). Locomotor diversity within past and present guilds of large predatory mammals. – Paleobiology, 11(4), pp. 406-428.

✍✍VAN VALKENBURGH, B. (1987). Skeletal indicators of locomotor behavior in living and extinct carnivores. – Journal of Vertebrate Paleontology, 7: 162-182.

✍✍VAN VALKENBURGH, B. (1989). Carnivore Dental Adaptations and Diet: A Study of Trophic Diversity within Guilds. Carnivore Behavior, Ecology, and Evolution; pp. 410-436. Gittleman, J. L. (Ed.). Ithaca, N.Y.: Cornell University Press.

✍✍VAN VALKENBURGH, B. (1990). Molar Microwear and Diet in large carnivores: Inferences concerning Diet in the Sabertooth cat, *Smilodon fatalis*. – Journal of Zoology (Lond.), 222, pp. 319-340.

✍✍VON DEN DRIESCH, A. (1976). The Measurement of Animal Bones from Archaeological Sites. – Peabody Museum Bulletin 1.

✍✍WARREN, J. C. (1853). Remarks on *Felis smylodon*. – Proc. Boston Soc. Nat. Hist., Vol. 4, pp. 256-258.

✍✍YALDEN, D. W. (1970). The functional Morphology of the Carpal Bones in Carnivores. – Acta Anatomica, Vol. 77, pp. 481-500.

✍✍ZIEMEN, E. (1980). Der Wolf – Mythos und Verhalten. – Fischer Taschenbuch Verlag GmbH, Frankfurt am Main.

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APPENDIX

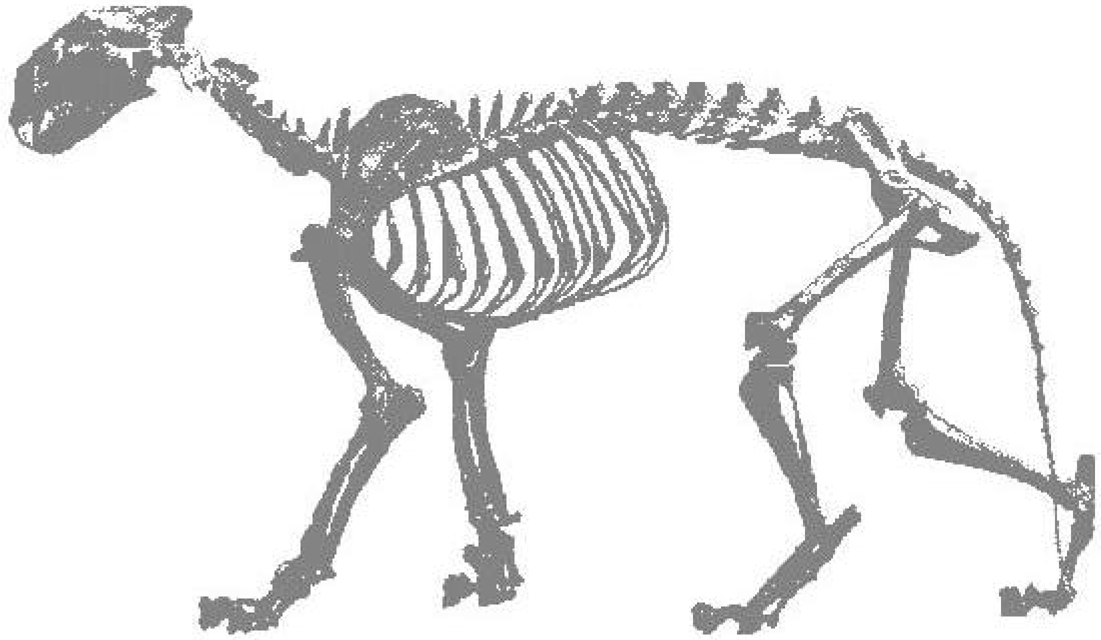
	A. jubatus	A. jubatus	P. tigris	P. tigris (f)	P. pardus (m)	P. pardus (f)	P. pardus (m)	P. leo (f)	P. leo (m)
	SZ 3797	(m) M. 202	SZ 3769	SZ 3728	SZ 4227	M. 203	SZ 7301	SZ 3280	SZ 7497
Skull:									
SL	17,5	16,4	32,6	31,1	23,6	20,5	23,6	30,7	35,3
DL	11,78	10,55	22,6	20,3	15,0	12,9	16,2	21,2	23,65
SW	12,56	12,3	23,25	20,8	15,1	13,9	16,1	21,7	24,6
CD	4,5	4,04	9,36	8,8	5,85	5,0	6,23	8,16	9,83
CH	2,83	1,65	5,06	4,85	3,55	-	3,65	3,96	4,9
CX	1,0	0,85	2,6	2,31	1,5	-	1,77	1,90	2,31
CY	0,8	0,68	2,0	1,75	1,2	-	1,38	1,43	1,77
Humerus									
GL	24,05	19,4	31,15	32,6	22,8	20,7	23,9	31,55	34,5
Li	6,0	4,83	11,02	12,8	7,69	6,53	8,3	11,2	12,7
Bd	4,99	3,22	7,98	7,8	5,87	4,91	6,1	8,08	9,99
Bt	2,98	2,39	5,28	5,5	4,0	3,25	4,16	5,56	6,35
T. major	3,25	2,96	5,1	4,6	3,92	2,7	4,05	4,46	6,82
Radius									
GL	24,0	19,5	25,15	27,4	18,4	17,5	20,1	28,3	30,8
BP	2,05	1,7	3,67	3,8	2,56	2,12	2,65	3,65	4,18
Qr	1,48	1,36	2,68	2,82	1,85	1,97	1,96	2,76	3,13
Ulna									
GL	27,8	22,7	31,3	33,2	23,0	21,35	25,0	33,6	36,3
LO	2,98	2,3	5,41	4,8	3,82	3,05	3,9	5,5	7,1
Mtc									
GL	8,2	7,55	10,6	11,1	8,02	7,21	8,25	10,89	12,2
Femur									
GL	26,6	21,6	35,1	36,4	24,85	23,75	26,0	35,0	37,3
GLC	26,45	21,1	34,8	36,2	24,6	23,4	25,7	34,3	36,8
BP	5,14	4,4	7,66	8,3	5,64	4,38	5,67	8,4	9,28
Bd	4,56	3,98	7,14	7,31	4,96	4,32	5,38	7,04	8,12
Tibia									
GL	26,85	22,2	29,4	32,1	23,8	21,7	24,2	29,85	32,6
LT	5,56	4,7	7,72	7,36	5,66	4,38	5,71	8,0	9,0
Astragalus									
GL	3,0	-	5,32	5,64	4,14	3,8	4,0	5,25	5,0
Calcaneus									
GL	7,1	6,34	9,34	10,65	6,56	6,3	7,5	10,24	10,5
Scapula									
GLP	3,43	2,83	6,16	5,75	3,9	3,47	4,26	5,89	6,51
HS	17,7	14,6	23,5	24,7	18,1	16,0	18,5	25,7	26,85
T. major	7,0	5,64	8,0	9,05	5,29	4,88	5,71	8,1	10,51
Mtt.									
GL	10,7	9,65	12,2	12,8	9,69	8,76	9,3	12,59	13,2

	P. leo (m) 6805 *	P. onca (f) Mam. 199	F. concolor (f) Mam. 198	S. fatalis	C. lupus Mam. 190
Skull:					
SL	36,35	24,5	17,2	29,3	23,0
DL	25,1	16,05	11,6	18,9	17,5
SW	27,0	16,5	12,1	18,0	12,3
CD	9,79	6,53	4,63	8,45	4,47
CH	5,03	3,36	2,31	14,6 *	2,8
CX	2,45	1,71	1,3	4,0	1,6
CY	1,82	1,39	1,0	1,95	0,8
Humerus					
GL	-	22,1	18,5	32,7	19,6
Li	-	8,25	5,58	~13,5	5,85
Bd	-	6,14	4,4	10,54	4,7
Bt	-	3,91	2,77	6,8	3,1
T. major	-	3,0	2,84	~6,3	2,87
Radius					
GL	-	18,1	15,3	25,8	19,95
BP	-	2,6	1,86	5,1	2,45
Qr	-	1,9	1,44	4,0	1,69
Ulna					
GL	-	22,25	18,8	31,6	23,5
LO	-	4,2	3,5	5,29	3,15
Mtc					
GL	-	7,25	6,76	8,3	8,85
Femur					
GL	-	24,4	22,35	35,6	21,35
GLC	-	24,35	21,7	35,8	21,7
BP	-	5,74	4,57	9,41	5,08
Bd	-	5,41	4,2	7,53	4,57
Tibia					
GL	-	21,2	19,7	27,0	21,9
LT	-	5,73	4,72	7,97	4,78
Astragalus					
GL	-	3,45	2,61	5,25	3,95
Calcaneus					
GL	-	6,7	6,0	9,74	6,1
Scapula					
GLP	-	4,25	3,32	8,34	4,91
HS	-	17,1	13,4	33,6	14,2
T. major	-	4,68	5,5	9,39	4,0
Mtt.					
GL	-	8,77	8,47	9,45	9,41

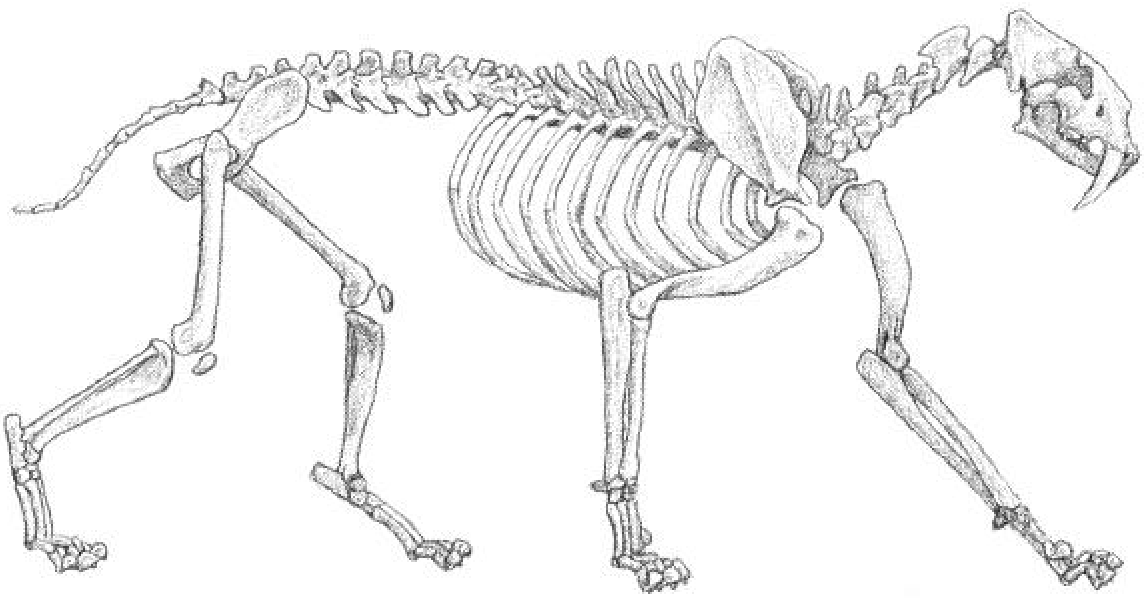
Table 5.1: Measurements taken from skeletal material after Van den Driesch.

Explanations: SL=skull length; DL= dental length; SW=skull width; CD= canine distance; CH= crown height; CX=crown, antero-posterior diameter; CY=crown, medio-lateral diameter; GL= greatest length; Li=inner lever of T.major; Bp=proximal greatest breadth; Bd=distal greatest breadth; Bt=greatest breadth of trochlea; Qr=antero-posterior breadth of radial head; GLC= greatest length of caput femoris; LT=max. transversal depth of distal end of tibia; HS=height spina scapulae; GLP= greatest length of processus articularis.

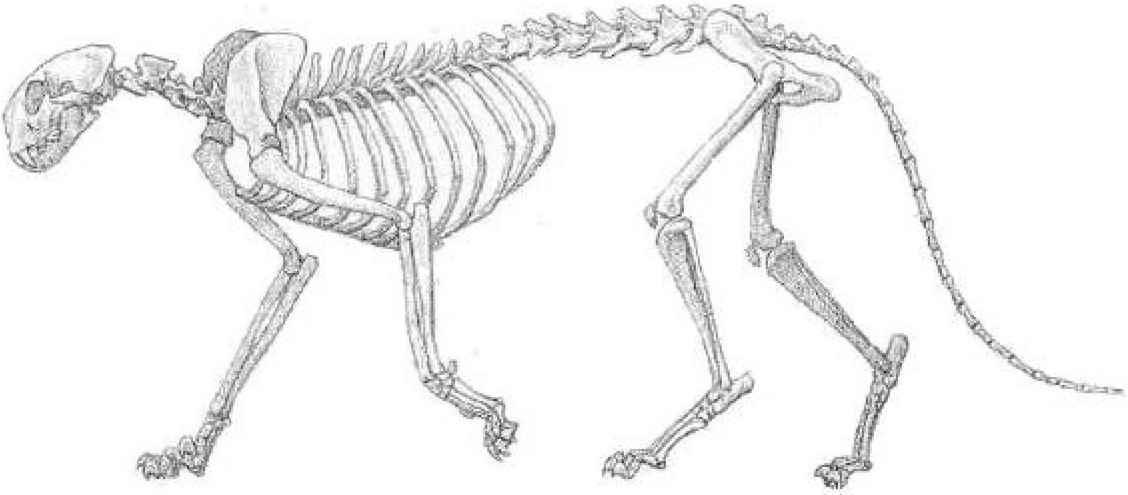
Illustrations of complete skeletons of the three various cat guilds.



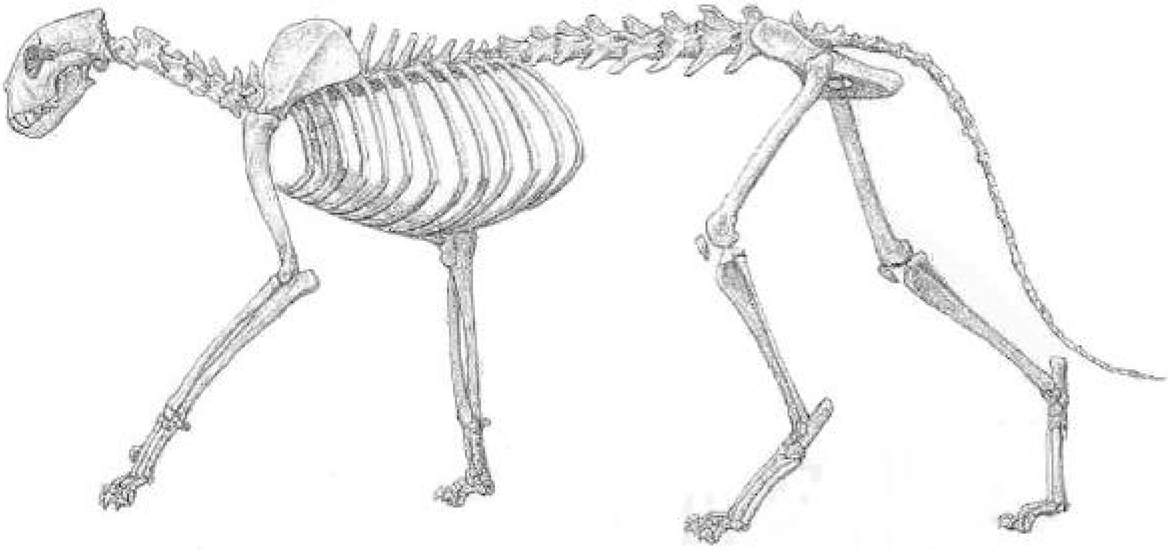
Panthera leo (atrox) – lion of the Rancho La Brea tar pits – represents the basic felid phenotype (guild two).



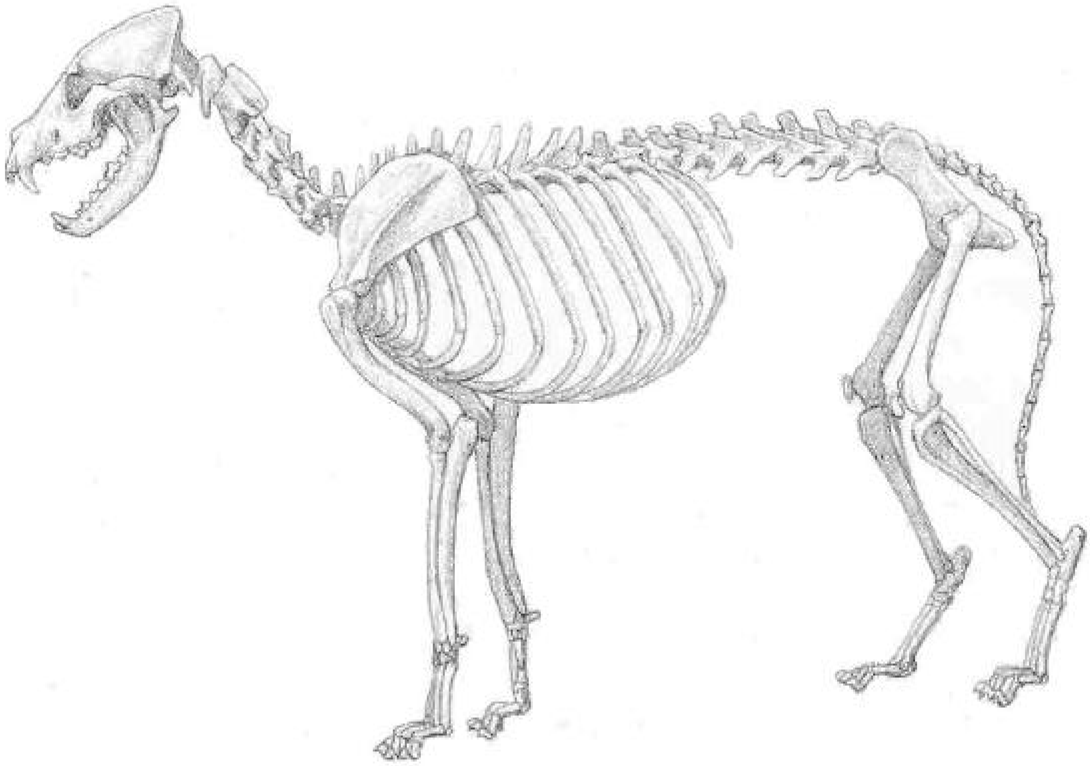
S. fatalis – Rancho La Brea (guild three)



Felis concolor – puma or mountain lion (possesses traits of both guild one and two).



Acinonyx pardinensis – cheetah (guild one).



Canis lupus – the wolf.