

### The Manus

All extant carnivores are digitigrade in their forelimbs (Yalden 1970), but the proportions of the segments differ greatly. As the phalanges are in contact with the ground, they can not contribute to stride length. In fact, longer phalanges would have a negative effect on the speed of the limb during the phase of free transit, as the moment of inertia would be increased. Van Valkenburgh (1987) found the metacarpal length relative to proximal phalanx length being highest in cursorial carnivores like the canids and the hyaenas. Among the big felids, the excellent climbers the jaguar and the leopard have the shortest relative metacarpal length. Presumably, long phalanges provide a broad grasp and firm grip and are thus useful for climbing. The lynx was said above to be slow despite its long limbs. This is supported by the fact that it has the shortest relative metacarpal of all felids in the study of Van Valkenburgh (1987). Spread out their long phalanges form broad paws useful when travelling in snow. This is in a way a cursorial adaptation, but limited to snowy regions. Diggers have both short metacarpals and short proximal phalanges; the ratio being of less importance.

The metacarpals in cursorial carnivores are closely bound together. The third and fourth metacarpal are the longest and the first digit is lost or very reduced, so that the structure of the digits is symmetrical (Hildebrand 1987).

Digging carnivores are always scratch-diggers (Hildebrand 1987). They cut and loosen the soil with their claws and then shift it back. All the work is done by the forelimbs and the fore claws tend to be long, strong and very fast growing. The shape of the ungual phalanges mirrors that of the claws. While the ungual phalanges of the forelimb and the hindlimb are of equal size in other carnivores, ungual phalanges of the forelimb are typically twice the length of ungual phalanges of the hindlimb in digging carnivores (Van Valkenburgh 1987). Van Valkenburgh (1987) also measured the depth and curvature (Fig. 6) of the ungual phalanges. She found those species capable of climbing having deeper and more curved ungual phalanges than non-climbing species. Espe-

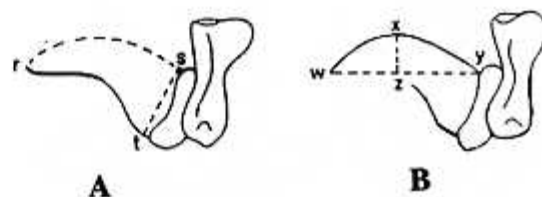


Fig. 6. Measurements of the ungual phalanx. The depth (A): Length of dorsal arc  $rs$  divided by depth at ungual base  $st$ . The curvature (B): Maximum arc height  $xz$  divided by length  $wy$  (from Van Valkenburgh 1987).

cially diggers had shallow and little curved ungual phalanges. Interestingly, the honey badger, *Mellivora capensis*, a digger also capable of climbing has ungual phalanges shaped more like those of a climber. This seems to indicate that climbing ability is more restricted to a certain claw shape than digging ability is.

The claws of felids are retractile due to the articulation surfaces between the middle phalanges and the ungual phalanges (Gonyea & Ashworth 1977). The retracted position is the normal position and protrusion requires simultaneous action of the dorsal extensor muscles and the flexors. Because of the retracted position, the claws can be kept very sharp. Sharp claws are especially favourable when seizing the prey, but also during climbing. The battling of prey with the forelimb is seen principally in felids. However, several viverrids use claw equipped forelimbs for prey seizing and they have been reported to have retractile claws (Gonyea & Ashworth 1977). The cheetah has retractile claws but they are not so well protected as those of other felids. Therefore its claws are worn down like those of canids. The claw on the pollex, however, does not touch the ground. It remains sharp and therefore constitutes a weapon of importance in prey capture (Ewer 1973). The cheetah hunting smaller prey is able to knock them over with just a blow of one paw.

In all modern carnivores the scaphoid and lunar of the carpus are fused, forming the scapholunar bone. This is thought to increase the stability of the wrist. Yalden (1970) suggests that the scapholunar developed to provide a firm base for flexion at the mid-carpal joint.

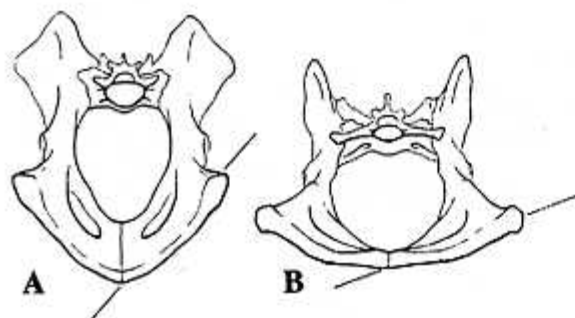


Fig. 7. Posterior view of the pelvis in (A) the raccoon and (B) the fox, showing the orientation of the ischium (from Jenkins & Camazine 1977).

### ***The pelvis and hindlimb***

In carnivores the hindlimb is used almost solely for locomotion. Structural adaptations to different ways of life is therefore not so obvious as in the forelimb.

#### ***The pelvis***

The ischiopubis and ilium in carnivores are usually of equal length. A deep acetabulum restricts abduction and rotation of the limb more than a shallow one does (Jenkins & Camazine 1977). Cursorial, non-climbing carnivores like the canids were found to have the deepest acetabulum. The ischium provides for the origin of extensor and adductor muscles of the hip joint. A ventrolateral oriented ischial surface, as seen in the climbing and ambulatory raccoon (Fig. 7A), allows the adductors to work at a less acute angle with the femur and therefore increases their effective force. The ischial surface in canids is horizontally oriented and also laterally widened (Fig. 7B). This indicates the dominance of extension movement in the hip joint.

#### ***The femur***

The extent of the articulation surface of the femoral head indicates to what degree the hindlimb can be abducted or adducted. On the femoral head is a pit, the fovea capitis femoris, in which the ligament is attached. The position of the fovea capitis femoris is accordingly related to the normal femoral posture. Felids can abduct their hindlimbs more than canids can, but normally the femur is more sagittally oriented in felids than in canids. Jenkins & Camazine (1977) think that this is due to the fact that the

hunting success of felids rely on stalking the prey. The sagittally oriented hindlimbs allow for minimal lateral displacement of the trunk, and thus minimal movement is exposed to the prey's line of vision.

In his study of African viverrids, Taylor (1976) found that a prominent and medially located lesser trochanter, as seen in *Nandinia binotata* and to a lesser extent in *Genetta*, is associated with climbing ability. The muscles that insert on a medially located lesser trochanter can rotate the femur both inwards and outwards.

A well developed patellar groove with high marginal ridges seems to be a cursorial adaptation that is required for the strong knee extensors and their tendons (Taylor 1976).

#### ***Fibula and tibia***

A mobile fibula is typical of the families other than the Canidae and Hyaenidae. The fibula articulates with the tibia at its proximal and distal ends. The distal articulation permits rotation of the fibula about its long axis, and thus some supination of the pes is possible. To hold on to a branch with the hind feet alone, the pes must be supinated. However, effective supination also requires a mobile joint between the tibia and astragalus (Taylor 1976). In canids and hyaenas the fibula is tied to the tibia distally. This gives increased stability at the expense of supination ability and is therefore considered a cursorial adaptation. The same condition is found in specialized diggers like the badger. In the cheetah both the joints are present but the fibula is bound in the middle to the tibia with fibrous tissue (Hildebrand 1987). As the function of the fibula is lost it is also typically reduced in size.

#### ***Pes***

Many of the non-cursorial carnivores have plantigrade hind feet. Whether a foot is plantigrade or not is indicated by the metatarsal length relative to phalanx length. Plantigrade carnivores have short metatarsals. In digitigrade, cursorial species the metatarsals, just like the metacarpals, are closely bound together and the first digit is lost.

## The tail

Long and powerful tails are used for balance when changing direction in high speed or when climbing (Savage 1977). The binturong, *Arctictis binturong*, and the kinkajou, *Potos flavus*, are unique among the carnivores by using the tail as a prehensile organ. In small species, a long and bushy tail coiled round the body helps to keep the animal warm.

## The skull

The skull can be divided into two functional components, the cerebral skull consisting of the braincase and sensory capsules, and a facial skull consisting of the jaw apparatus and associated muscle scaffolding. The m. temporalis and neck muscles are attached to the outer surface of the braincase. The development of bony crests adds to the area for muscle attachment that the braincase provides. A median sagittal crest (Fig. 8) gives more space for the temporalis attachment, while an occipital crest allows for larger neck muscles. Since cranial volume scales with a strong negative allometry with body size (Ewer 1973), closely related species of different size will have skulls that are superficially very different (Fig. 8).

Because of lack of time and space the braincase and sensory capsule will not be much considered in this paper. From endocranial

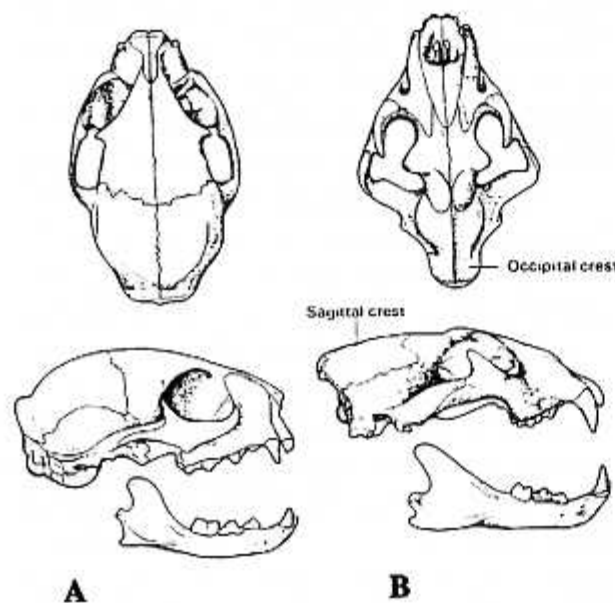


Fig. 8. The skull of (A) the small jaguarundi and (B) the big lion (from Ewer 1973).

casts of the braincase the estimated weight of the brain can be compared to the estimated weight of the body. Functional areas of the cerebral cortex and sensory specialization may be reflected in the size of various cortical areas (Radinsky 1977). The turbinal bones provide some information of the olfactory sense. In cases where the ethmoturbinals, which are innervated by the olfactory nerve, are larger than the maxilloturbinals, which are concerned with warming and filtering the air, olfaction is probably a highly important sense (Savage 1977). The size of the orbital area may to some degree reflect eyeball size and therefore visual abilities (Radinsky 1977), but more specific information, e.g. about resolution, diurnal, nocturnal, or colour vision, can not be attained (Savage 1977). However, from the orientation of the orbits the degree of stereoscopy can be reliably interpreted.

The auditory region in carnivores has been described to great detail and much taxonomic division is based on it but very little of functional significance can be deduced.

## Dentition

The feeding habits of extant carnivores range from almost pure meat eating to secondary vegetarianism. There is accordingly a large variation in the dental forms, but most species have retained a versatile dentition with different teeth adapted for cutting flesh, crushing bone, and grinding insects and fruit. The teeth are not only used for feeding but also for killing and defense.

## Incisors

The incisors are used together with the canines for gripping and tearing. They are usually packed close together and are small compared to rest of the teeth. Usually all three incisors are present but in some species the upper incisors are reduced in numbers. Due to the lost  $I_0$  in the sloth bear, *Melursus ursinus*, the tongue can be protruded through a median diastema. This is useful for licking up small insects and termites, which form an important component of the diet of this bear (Ewer 1973).



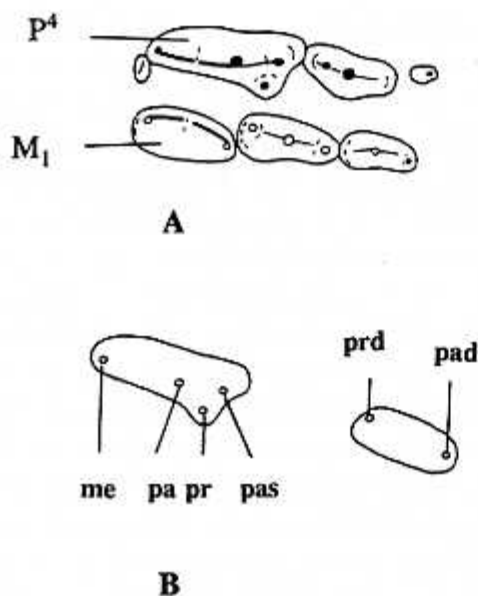


Fig. 9. (A) The carnassials (arrowed) in *Felis*. (B) The cusps of right upper carnassial: me metacone, pa paracone, pr protocone, pas parastyle. (C) The cusps of left lower carnassial: prd protoconid, pad paraconid (from Savage 1977).

### Canines

The canines are used for defense, killing and maintaining a grip on the prey (Van Valkenburgh & Ruff 1987). They are generally conical, long, powerful and sharp. The canines are always present and are well developed in both upper and lower jaws. In felids the mediolateral width relative to the anterioposterior length of the canine is greater than in canids (Van Valkenburgh & Ruff 1987). This is probably due to the different killing techniques. Felids sink their canines into the nape of the neck and dislocate the cervical vertebrae of the prey. Very large prey with thick and strong neck muscles and prey armed with horns may instead be killed with a throat bite (Ewer 1973). In both cases there is a risk of the canine to contact bone and be subjected to mediolateral bending. Canids usually make fairly quick and shallow wounds that are less likely to contact bone. The greater width of the canine gives it greater strength to

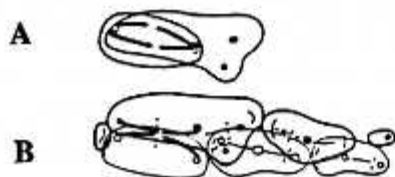


Fig. 10. The carnassials (A) at the beginning of occlusion and (B) in full occlusion (from Savage 1977).

resist mediolateral bending. Hyaenids have canines shaped like those of felids but in this case the shape probably reflects their bone crushing habits (Van Valkenburgh 1989).

The saber-like canines of extinct species will be discussed below.

### The premolars except $P^4$

The premolars are generally rather unspecialized. The anterior ones are often very small or lost. They are normally compressed mediolaterally and are in essence backward hooking blades. They often do not actually meet each other when the jaw is closed. Their function is probably to hold the prey. The subfamily Hyaeninae have no crushing molars. Instead they have very big and stout premolars which have their central cusp enlarged so the form is that of a conical hammer. Because of these powerful teeth and strong jaw muscles hyaenas can crack large bones in order to obtain the marrow inside. The reason why it is the premolars and not the molars that have become specialized to bone cracking, may be the greater gape more anteriorly in the jaws. The ursids have very reduced premolars that are often shed early. Why, is not clear.

### The carnassials

In the Carnivora the last premolar,  $P^4$ , in the upper jaw and the first molar,  $M_1$ , in the lower jaw are specially adapted to cut through flesh. The posterior two cusps of  $P^4$ , the paracone and the metacone, and the anterior two cusps of  $M_1$ , the paraconid and the protoconid, are laterally flattened forming two longitudinal blades (Fig. 9). The carnassial blades are concave in a vertical plane. Because of the concave edges, the ends of the blades meet first as the jaws close and only when almost fully closed do the centres meet. This allows the force to be exerted on a very small area at a time, thus increasing the efficiency of the blades (Savage 1977). On the outer face of the  $P^4$  and on the inner face of  $M_1$  the teeth are deeply excavated beside the blade. This creates space for the food and helps to retain it in position during cutting (Savage 1977). In the horizontal plane the blade of  $P^4$  is either slightly convex lingually or flat, while the  $M_1$  is always convex buccally. When closing the

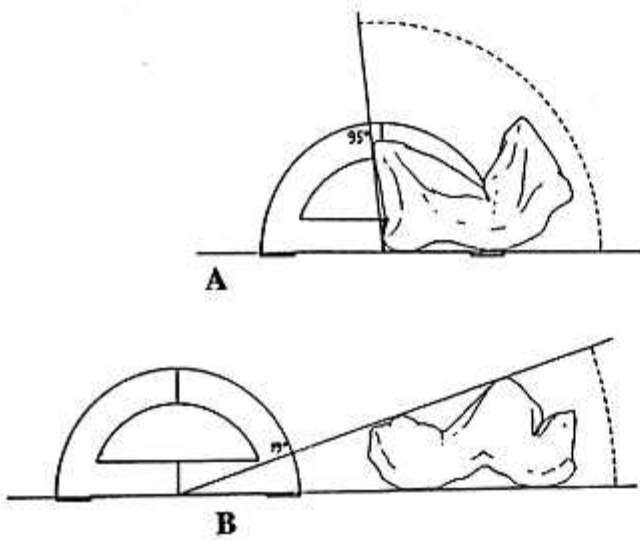


Fig. 11. Measurements of the angle *a*. The lower carnassial of (A) a highly carnivorous species and (B) a much less carnivorous species (from Crusafont-Pairo & Truyols-Santonja 1956).

jaws, contact between the two blades is made at two centrally moving points (Fig. 10). This requires a medial slide of the mandible (Savage 1977).

The shape and size of the carnassial blade reflect its efficiency as a meat cleaver and therefore indicates to what extent meat is part of the diet. In ursids the blades are replaced by broad cusps with little shearing effect. Other omnivorous species like the skunks, the procyonids and many viverrids also have blunt carnassial blades. The  $P^4$  in omnivorous species often has a well developed protocone that may occlude with the talonid of  $P_4$  thus having a

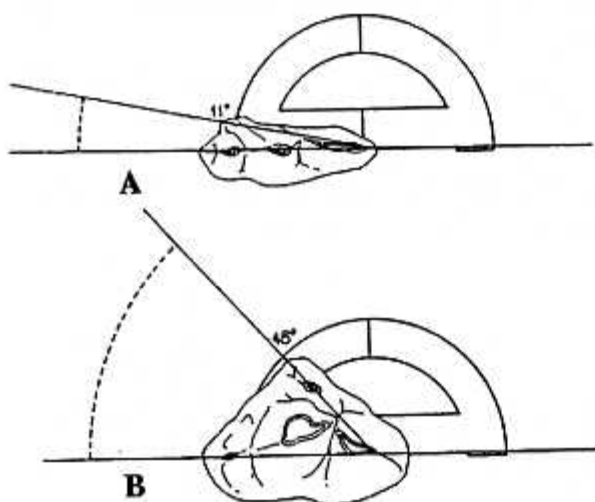


Fig. 12. Measurements of the angle *b*. The upper carnassial of (A) a highly carnivorous species and (B) a much less carnivorous species (from Crusafont-Pairo & Truyols-Santonja 1956).

crushing function. The general appearance of the  $P^4$  of these species is therefore more like that of a molar. Crusafont-Pairo & Truyols-Santonja (1956) found two angular measurements useful for a study of the evolution of the carnassials. Angle *a* measures the relationship between the height of the protoconid and the length of the talonid on  $M_1$  (high values = high protoconid relative to length of talonid) (Fig. 11). Angle *b* measures the development of the protocone on  $P^4$  (high values = well developed protocone) (Fig. 12). For primitive Eocene species angle *a* is around  $45^\circ$  and angle *b* is around  $22.5^\circ$ . The evolutionary trend is an increase in angle *a* and decrease in angle *b* for highly carnivorous species, while the opposite trend is seen in less carnivorous species. Angle *a* ranges from  $55^\circ$  to  $105^\circ$  in felids and from  $6.3^\circ$  to  $31^\circ$  in ursids. Angle *b* ranges from  $10^\circ$  to  $25^\circ$  in felids and from  $26^\circ$  to  $52^\circ$  in ursids. In the fossil history the total range as seen in the order Carnivora has increased in the course of time.

The posterior part of  $M_1$ , the talonid, remains in some species but is much reduced or absent in others. The talonid occludes with  $M^1$  and has a crushing function. Van Valkenburgh (1989) measured the length of the cutting blade relative to the length of the talonid in a number of carnivores and found the ratio to be a good indicator of the meat content of the diet. The felids are almost pure meat eaters and they have all lost the talonid. Excluding the felids, the spotted hyena has the relatively longest blade, while the ursids have the shortest. The African hunting dog, *Lycaon pictus*, and two other canids have a modified talonid known as the trenchant heel. The inner cusp is missing so that the talonid forms a subsidiary blade. Together with the wolf, these canids are considered the most specialised meat eaters in the Canidae.

#### *The molars except $M_1$*

The carnivoran molars posterior to the carnassials are used for crushing and grinding food other than meat. The felids have lost all the post-carnassial teeth except  $M^1$ , which is reduced to a vestige. This is also true for the hyaenids, although both the striped hyena, *Hyaena hyaena*, and the brown hyena, *Hyaena brunnea*, are

known to eat fruits and insects with some regularity (Van Valkenburgh 1989). In carnivores where vegetable food and insects are a considerable part of the diet the molars increase in importance. In some species like the raccoon dog, *Nyctereutes procyonoides*, there are three upper molars, but usually the molars increase in size and not in number for the less carnivorous species. Van Valkenburgh (1989) measured the area of the lower post-carnassial molars plus the area of the talonid and related it to the length of the lower carnassial blade. She found that the species with the most fruit or nonvertebrates in their diet generally have the largest relative crushing area. The largest area was found in the ursids. The polar bear feeds mostly on seals and fish and its crushing area is the smallest among the ursids. Due to the very close relationship with the omnivorous brown bear, its molars are still larger than in less carnivorous species of other families. The insectivorous bat-eared fox, *Otocyon megalotis*, has three to four upper molars and four to five lower molars. The molars are small and high cusped similar to the molars in the Insectivora. High and narrow cusps are well suited for puncturing the hard exoskeleton of many insects (Lucas 1979).

Finally, the extremely reduced dentition of the aardwolf, *Proteles cristatus*, should be mentioned. The premolars and molars are much reduced in numbers; there may be as few as 24 teeth in all. The few remaining cheek teeth are almost vestigial and placed far apart from each other. The diet of the aardwolf consists mainly of termites and other insects that do not have to be masticated (Ewer 1973).

### The jaws

The mandibular dentition is narrower than the maxillary dentition in carnivores and therefore chewing occurs on one side at a time (Savage 1977). The mandible articulates with the cranium through the mandibular condyle and the glenoid fossa of the squamosal. As tough, fibrous foods such as grass are not included in the diet of carnivores, a grinding, lateral movement of the jaw is not needed. The mandibular condyle in carnivores is transverse and the glenoid fossa is hingelike. The structure of the articula-

tion therefore restricts movements other than closing and opening of the jaw and a precise shear of the carnassial can be maintained (Smith 1993). The tight articulation joint also allows for a short and loose mandibular symphysis, which allows for some lateral bending when the carnassials are brought into occlusion. The symphysis is not mobile neither in felids nor in ursids (Ewer 1973).

Closure of the jaws is brought about by the action of three sets of muscles. *M. temporalis* originates from the lateral surface of the braincase and inserts on the anterior border and upper part of the coronoid process. *M. masseter* originates from the lower border of the zygomatic arch and inserts on the masseteric fossa and the outside of angular process of the mandible. *M. pterygoideus* originates on the on the side of the skull beside the palate and behind of the orbit, and inserts on the inside of the ramus and the angular process. In carnivores the *m. temporalis* comprises more than half the total mass of the jaw muscles while in ungulates *m. masseter* comprimises about two-thirds of the total mass (Hildebrand 1987). The difference can in part be explained by that *m. masseter* produces lateral grinding motions that are important for ungulates. In carnivores the lateral movements of *m. masseter* merely serves to stabilise the articulation of the jaw (Hildebrand 1987). This is also indicated by position of the mandibular condyles and the height of the coronoid process. In carnivores the mandibular condyles are in line with the occlusal plane and the coronoid process is prominent (Hildebrand 1987). Compared to the higher jaw joint and smaller coronoid process in ungulates this increases the lever arm of the temporalis and decreases the lever arm of the masseter (Fig.

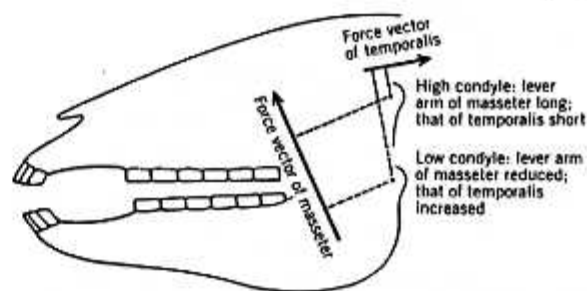


Fig. 13. Jaw mechanics in relation to the position of the mandibular condyle (from Hildebrand 1987).

