

### 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-

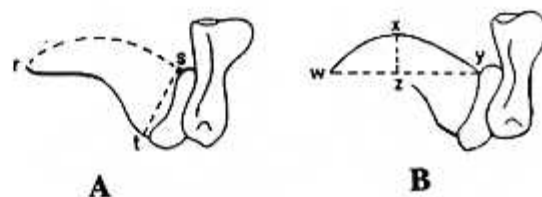


Fig. 6. Measurements of the ungual phalanx. The depth (A): Length of dorsal arc  $rs$  divided by depth at ungual base  $st$ . The curvature (B): Maximum arc height  $xz$  divided by length  $wy$  (from Van Valkenburgh 1987).

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.

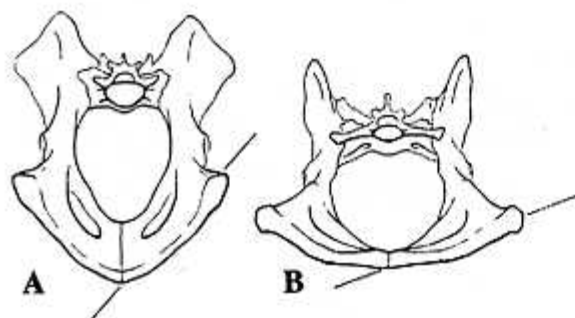


Fig. 7. Posterior view of the pelvis in (A) the raccoon and (B) the fox, showing the orientation of the ischium (from Jenkins & Camazine 1977).

### **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

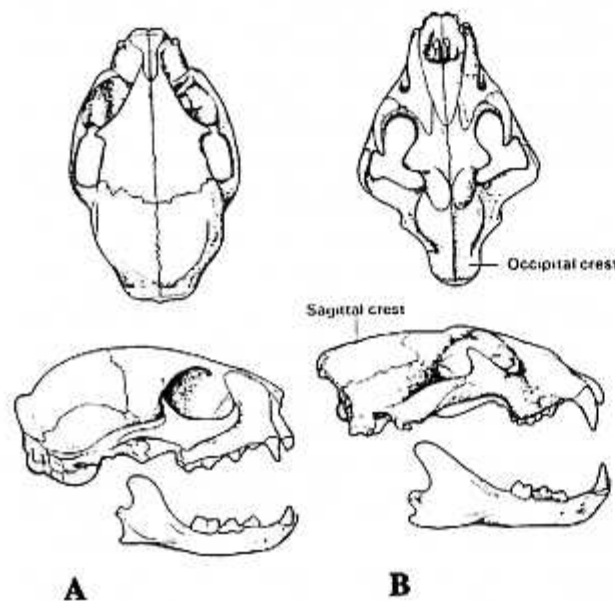


Fig. 8. The skull of (A) the small jaguarundi and (B) the big lion (from Ewer 1973).

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).

