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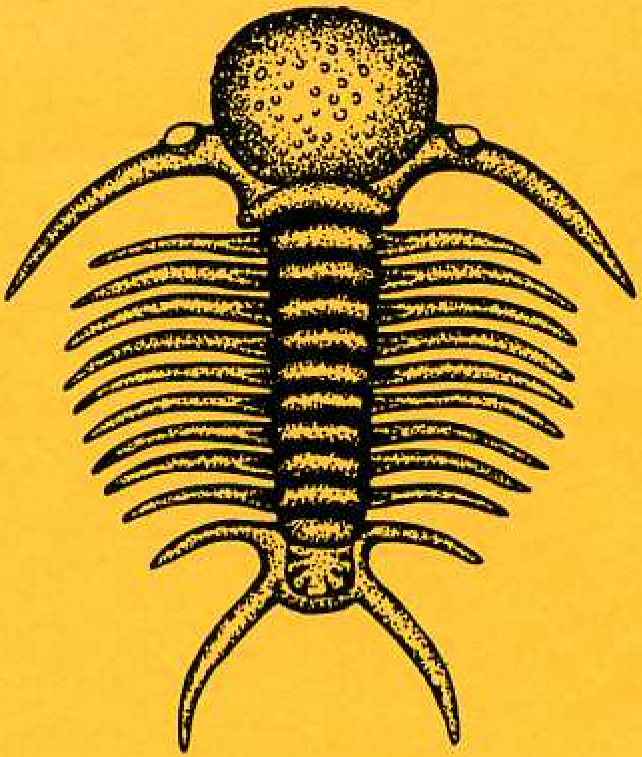

Adaptations and evolution in terrestrial carnivores

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Abstract: A review of adaptations in fossil and extant mammalian carnivores has been made. Adaptations to different locomotor behaviours can be seen in the postcranial skeleton. Typically cursorial adaptations are long distal limb segments and restrictions in the mobility of the limbs to move in other directions than forward and backward. Diggers have fore limbs constructed for large out-forces. Climbers have mobile limbs and curved, retractile claws. To what extent meat is a part of the diet can be interpreted from the dentition. Pure meat eaters have lost all the crushing area of the molars and have long anteroposterior directed cutting blades. The long canines in saber-toothed forms were probably an adaptation to kill large prey. The creodonts were the dominating carnivores during the early Tertiary but they were replaced by the Carnivora in the beginning of the Oligocene. Compared to extant carnivores, many fossil forms were heavily built and short limbed. Cursorial adaptations became common in the early Miocene when extensive grass land areas had developed. There have been a limited number of adaptive zones for carnivores through their history. **Keywords**: *Carnivora, Creodonta, locomotor adaptations, skeleton, dentition, jaws, carnassials, sabertooths, evolution.*

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The history of mammalian carnivores goes back to the early Tertiary when the radiation of mammals began. Although some fossil forms may be quite different from any living form, much information can still be gained by comparing skeletal morphology between fossil and living species. Adaptations to locomotor behaviours can be seen in the postcranial skeleton, while adaptations to different diets can be seen in the jaw apparatus.

The purpose of this paper is to explain the connection between skeletal morphology and different carnivorous ways of life in terrestrial mammals. I also consider how these different forms have evolved. To fully understand the evolution of the mammalian carnivores, the evolution of their prey and ultimately of their whole environment must be considered as well. This is, however, beyond the scope of this paper, although, of course, these matters are not totally ignored. I have restricted this investigation to terrestrial forms. The aquatic pinnipeds are ecologically and morphologically very much set apart from the terrestrial fissipeds. For similar reasons the aquatic adaptations in fissipeds (e.g. otters) are not considered.

The first part of this paper deals with the functional morphology and is based on extant carnivores. Besides deriving indicative morphological characters from these animals' ways of life (i.e. empirically), theoretical explanations are also given. The second part deals with the fossil history of carnivorous mammals. Here knowledge gained from the previous pages is applied. (The section on saber-toothed forms is however directly connected to the section on the jaws and dention of the first part.)

All the information and much of the reasoning and the conclusions have been obtained from the literature. I have allowed some personal speculations, particularly when the literature is unclear or incosistent.

Locomotor adaptations by extant carnivores

Extant carnivores exhibit a wide range of locomotor behaviours. Some are very fast runners (e.g. the cheetah) and others show a remarkable running endurance (e.g. the grey wolf). Many carnivores are good climbers (e.g. the marten, the leopard) and some are completely arboreal (e.g. the binturong). Some carnivores exhibit digging behaviours, the most specialized being the badgers.

Often terms such as cursorial, fossorial, scansorial etc. are used for more or less loosely defined categories based on the animal's locomotor behaviour. In this paper these terms will merely refer to behaviours which an animal can be more or less adapted to. Consequently a certain species can show both scansorial and cursorial adaptations. When terms like "cursorial carnivores" are used, they really mean "carnivores with cursorial adaptations". Considering this, I also believe it to be more appropriate to review the structural elements of the skeleton instead of the artificial categories.

The spine

The spine of carnivores is vertically mobile in contrast to the spine of ungulates (Gambaryan 1974). A galloping carnivore can therefore increase its stride length by extending the spine during hindlimb support. When the forelimb reaches the ground the spine is flexed (due to inertia and sometimes also to active muscle movement) which results in a forward movement of the center of mass. In many members of the Mustelidae, in fact, the running speed depends mainly on flexion and extension of the spine (Gambaryan 1974). In the Felidae the cheetah stands out as the most adapted at this maneuver. Hyenas, canids, ursids and large mustelids have a more rigid spine (Taylor 1989).

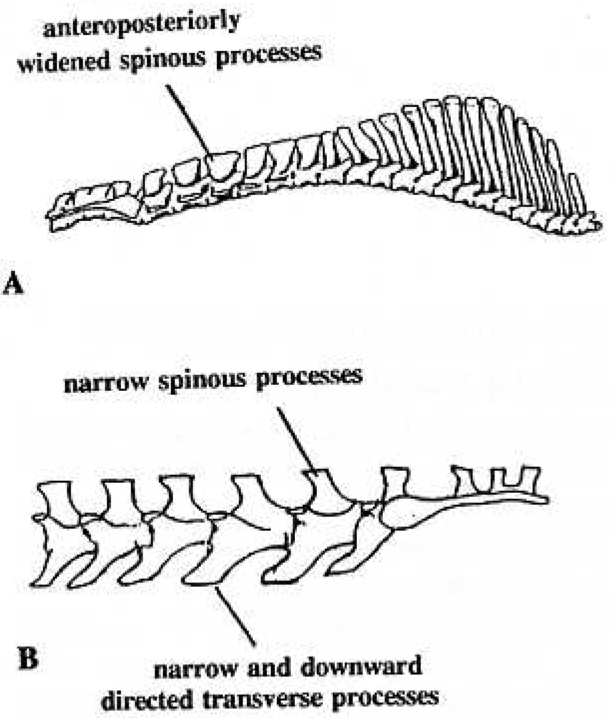


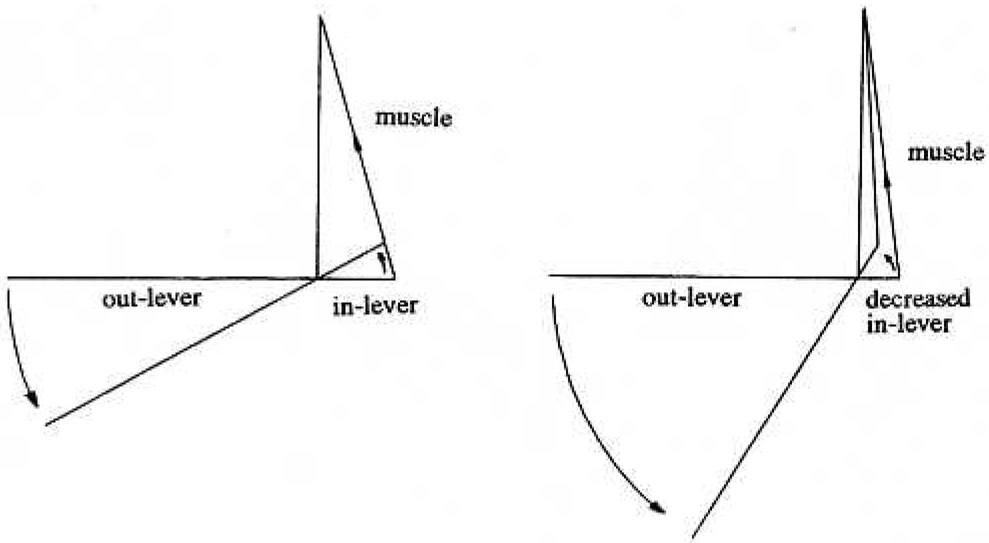
Fig. 1. The vertebral column in (A) Bison americanus and part of the vertebral column in (B) Felis pardus (from Gambaryan 1974).

In ungulates the vertebral column is maintained rigid owing to spinous processes with anteroposteriorly widened apexes (Fig. 1A) and with powerfully developed supraspinous ligaments attached to them (Gambaryan 1974). The widened apexes shorten the intervertebral parts of the supraspinous ligaments, thereby enhancing the rigidity of the spine. In carnivores the apexes of the processes are narrowed (Fig. 1B) and the supraspinous ligaments are weakly developed or absent (Gambaryan 1974). In carnivores instead a system of interspinous ligaments promotes a smooth widening and narrowing between adjacent vertebrae during flexion and extension of the spine. The particularly mobile spine in the Mustelidae is owing to a reduction of the interspinous ligaments and development of interspinal extensor muscles, which are weakly expressed in other carnivores (Gambaryan 1974).

Lateral mobility of the lumbar part of the spine in ungulates is limited by the transverse processes of the lumbar vertebrae. These are widened anteroposteriorly and are united with each other by intertransversal ligaments. In carnivores the transverse processes are not so wide. A downward direction of the processes and, as in mustelids, a gradually increased inclination also promote lateral mobility (Gambaryan 1974). Further, the zygapophysial articulations influence the mobility of the spine. In carnivores these allow great freedom of movment between the thoracic vertebrae (Gambaryan 1974). The zygapohysial articulations in the lumbar region are very rigid in ungulates but less so in carnivores, allowing flexion and extension to some extent (Gambaryan 1974). Rotation about the long axis of the spine though is prevented by the zygapophyses of the lumbar vertebrae and of the thoracic vertebrae posterior to the diaphragmatic vertebrae (Hildebrand 1987).

The mobility of the spine can, as explained above, be a cursorial adaptation. The burrow hunting mustelids have short legs which allow them to maintain a bigger and stronger body than their prey while remaining small enough for narrow burrows. The relatively long body then requires a very mobile spine to succesfully move in narrow burrows with sharp turns. Above ground the mobile spine then also compensates for the cursorial disadvantage of having short legs. In animals like the cheetah where the mobile spine can be considered to be a pure cursorial adaptation one must note that the extension and flexion of the spine is a very energy consuming activity. This is part of the reason why the often heavy ungulates have not developed this ability. In the cheetah the mobile spine thus can be seen as an adaptation to short-distance running. Finally, a mobile spine is advantageous for arboreal locomotion. Flexion of the back is an integral part of the vertical looping mode of progression observed to be used among others by the palm civet, *Nandinia binotata*, (Taylor 1970). This method of locomotion allows the animal to climb, in a controlled way, up and down vertical supports with the head first. The animal holds on with the fore feet and by flexing the back the hind feet are brought forward. Then the hind feet grasp the support and the fore limbs and the back are extended. The extraordinary ability of a cat to land on its feet after a fall is owing to the ability of the vertebrae to rotate about the long axis of the spine.

Fig. 2. The same shortening of the muscle moves the out-lever arm through a longer distance if the in-lever arm is decreased.



The limbs

In ungulates nearly every bone has been modified for running. Cursorial adaptations in carnivores are never as extreme as in ungulates because of other requirements than speed. The skeletal design for power is different from that constructed for speed; what is of mechanical advantage for power may in fact be of disadvantage for speed. The ability of the forelimbs to generate powerful out-forces is of special importance in digging, climbing and batteling the prey. In carnivores both the work of forelimb and the hindlimb are of importance for speed. However, specialization for running leads to an enhanced role of hindlimb work. This is not only due to the other requirements of the forelimb - the hindlimb is more advantageously placed for propulsive activity (Gambaryan 1974). The extended flight which follows hindlimb support is longer than the crossed flight which follows frontlimb support in cursors. One noteable exception is the gallopping stride of the Ursidae, where the extended flight is absent and the crossed flight strongly expresssed. The frontlimbs of bears are very strong which is probably an adaptation for food obtaining by climbing, digging and overturning stones; this strength was then used also in running. Still, the more cursorial bears, e.g. the brown bear, *Ursus arctos*, have stronger hindlimbs than less cursorial species (Gambaryan 1974).

Proportion of limbs

Many authors have tried to find correlation between the degree of cursorial adaptation and the relative length and proportion of the limbs, but probably due to the very complex nature of running, it is difficult to provide more than broad generalizations (cf. Savage 1977; Van Valkenburgh 1987).

If the in-lever arm (the distance from the joint to the insertion of the muscle) decreases relative to the out-lever arm (the distance from the joint to the distal point of the limb), the same shortening of the muscle moves the distal point through a longer distance (Fig. 2). However, the demands on the muscle and bone strength increase, especially for heavy animals during the phase of support. Cursorial carnivores often have longer limbs relative to spine length than less cursorially specialized species and markedly so compared to specialized diggers. Savage (1977) compiled a graph where the three main segments of the limbs in a number of carnivores and some ungulates are expressed. In cursorial ungulates the proximal limb segment is the shortest and the distal segment is the longest. In cursorial carnivores the manus is always the shortest segment (with the exception of some hyaenas) and the radius and ulna are of about the same length as the humerus. The hind limb segments are of more equal length, but the most distal segment, the pes, is still the shortest segment. In the less cursorial families Mustelidae, Viverridae, Ursidae and Procyonidae the humerus/femur is often the longest segment. An often used indicator of cursorial specialization is the ratio of metatarsal to femur length. Van

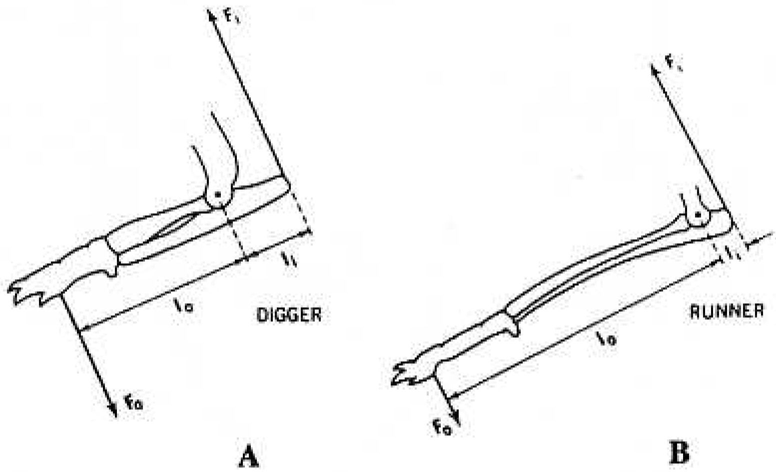


Fig. 3. The fore arm of a digger (A) compared to the fore arm of a runner (B). F_o = out-force, F_i = in-force, l_o = out-lever, l_i = in-lever (from Hildebrand 1987).

Valkenburgh (1987) found fast running carnivores to have the longest metatarsals relative to femur length, but she found the correspondence to be only rough.

A comparison between species of different families or even within the same family can be misleading. The most cursorial of the felids, the cheetah, has long limbs relative to spine length but not significantly longer than the limbs of the very good climber, the leopard (Gambaryan 1974). However, the ratios metatarsal/femur (Van Valkenburgh 1987), radius/humerus and tibia/femur (Gonyea 1976) are all higher for the cheetah. The lynx, *Felis lynx*, has the longest limbs of all felids and also the highest metatarsal/femur ratio (Van Valkenburgh 1987), but is a relatively slow runner. The long limbs of the lynx are probably an adaptation to movement in snow. A parallel is the canid *Chrysocyon brachyurus* which has the longest limbs of all canids but still is not a very good runner. In this case the long limbs are probably an adaptation to living in the long pampas grass (Savage 1977). The bears have the lowest metatarsal/femur ratio of all carnivores (Van Valkenburgh 1987) but the total limb is rather long. The most cursorial bears, the brown bear and the black bear, have the highest metatarsal/femur ratio of all ursids, but still very low compared to other carnivores. The maximum recorded speed of 48 km/hr (Van Valkenburgh) is, however, rather high. Interestingly the metatarsal/femur ratio is much higher for the american badger, *Taxidea taxus*, than for the european badger, *Meles meles*, but *Taxidea taxus* is hardly more cursorial.

Clearly, really fast running requires long limbs relative to body size. The distal segments must also be relatively long, but the length of the limb and its segments must always be considered together with the morphology as a whole. One must also remember that there are different forms of cursorial adaptations. Most canids are long distance runners specialized in pursuit hunting, while the felids rely on fast acceleration for hunting success. Excluding the cheetah, the bigger felids and the canids can achive a similar maximum speed (60-70 km/hr) but differ in endurance and acceleration ability. The requirements of the muscles and skeleton are different for these adaptations. For rapid acceleration powerful out-forces are of more importance and long distal limb segments are then not necessarily advantagous.

The digging apparatus in carnivores is restricted largely to the forelimbs, which must be able to produce large out-forces at their claws. Except for increasing the in-forces, this can be done by reducing the out-lever arm and by increasing the in-lever arm (Fig 3). Digging carnivores therefore have short distal segments. The radius and ulna are shorter than the humerus and the metacarpals of the foot are often very short (Hildebrand 1987).

As touched upon above, adaptation to climbing in felids is not very obvious in the length of the limbs. The only climbing canid, the gray fox, *Urocyon cinereoargenteus*, has a very high metatarsal/femur ratio, even compared with other canids (Van Valkenburgh 1987).

The scapula

Generally the scapula of carnivores is rather broad. Typically the scapula in cursorial carnivores is flat and more rectangular in shape than in non-cursors (Taylor 1989). In cursorial carnivores the clavicle is reduced to a vestige and the ribs form a nearly sagittal thoracic wall, so the scapula is nearly vertical (Hildebrand 1987). This means that the scapula is free to move in the same plane as the leg swings, therefore stride length is increased. In the ambulatory raccoon the weight-bearing shoulder moves at a 20 angle to the sagittal plane (Jenkins 1974). Jenkins (1974) also showed that the clavicle in mammals acts as a strut under compression during walking, preventing the shoulder from pressing in on the thoracic cage.

The abductors of the forelimb are of reduced importance in ungulates with their strong specializations toward antero-posterior limb movement. For reasons mentioned above this specialization can never be as strong in cursorial carnivores and therefore even those most specialized for running (i.e. canids) have a better developed scapular spine and acromion for the origins of the abductors of the limb. Taylor (1974) found that the more arboreal viverrids (e.g. *Nandinia binotata*) have a larger acromion than the terrestrial viverrids. The acromion provides for the origin of the m. acromiodeltoid, which abducts the humerus.

Both arboreal and fossorial carnivores typically have a large posterior flange for the origin of the m. teres major which flexes the shoulder (Taylor 1989). In the Ursidae the flange is developed to a regular subscapular fossa for the origin of m. subscapularis (Ewer 1973)

The humerus

The humerus of cursorial carnivores is relatively light. Taylor (1974) found that a large greater tuberosity was indicative of cursorial adaptations in viverrids. The great tuberosity provides for the insertion of the mm. supraspinatus and infraspinatus, which both extend the shoulder and therfore are the most active muscles (together with the elbow extensors) during the phase of front support. Mm. supraspinatus and infraspinatus are strengthened in the cheetah compared with other felids (Gambaryan 1974). The bicipital notch for the tendon of the m. biceps is not distinct in cursors, indicating weak flexor ability of the elbow (Taylor 1989).

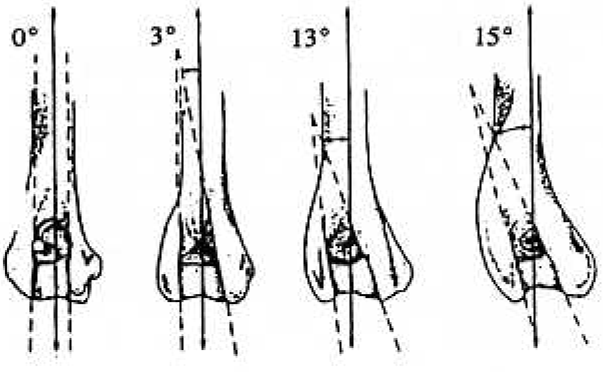


Fig. 4. The angle between the olecranon fossa and the long axis of the humerus in (A) the domestic dog, (B) the cheetah, (C) the margay and (D) the wolverine (from Gonyea 1978).

A distinct bicipital notch is characteristic for adaptation to a controlled, grasping way of climbing, where flexion of the elbow is important. This way of climbing is typical for animals, often rather large, using stealth to approach their prey (e.g. *Nandinia binotata*; binturong, *Arctictis binturong*; many of the cats) (Taylor 1989). It is generally in this group of climbers that obvious structural modifications for climbing are seen. The fast moving, jumping and leaping species have to be small sized but are otherwise not so much set apart from terrestrial species (Taylor 1989). Also typical of climbers is a large medial epicondyle, which provides for the origin of the flexors of the manus. The olecranon fossa in climbing viverrids is seldom perforated (Taylor 1974). A perforated olecranon fossa allows greater extension of the elbow and is probably a cursorial adaptation. The sharp, bony edges of the olecranon fossa guide the movements of the ulna on the trochlea of the humerus. The angle between the olecranon fossa and the long axis of the humerus indicates deviation of the fore limb from the vertical plane (Fig. 4). This angle is zero in the domestic dog and the cheetah has the smallest angle of all felids. In less cursorial species like the excellent climber the margay, *Felis wiedii*, and the good climber the wolverine the angle is 13° respectively 15° (Gonyea 1978). The elbow joint is discussed below.

The short, massive humerus of digging carnivores is rugged and rough because of the origins and insertions of their typically bulky muscles. The medial epicondyle of the humerus and the deltoid crest are particulary prominent (Hildebrand 1987). The deltoid crest provides for the insertion of m. deltoideus, which flexes the shoulder.

Radius and ulna

The olecranon process provides for the insertion of the m. triceps group which extends the elbow. The longer the olecranon process the greater the out-forces can be at the fore foot. A long olecranon process is therefore typical for digging carnivores. Cursorial carnivores have a short olecranon process as have most good climbers (Van Valkenburgh 1987). Many of the big felids (e.g. the jaguar, the lion, the tiger) have relatively long olecranon processes, which probably is useful when batteling large prey. A straight or anterior bent olecranon process maximizes the effective force of the triceps muscle when the elbow is relatively flexed (the muscle works at a right angle to the leverarm), whereas a posterior bent olecranon process maximizes the effective force when the elbow is nearly extended (Fig. 5). Cursorial carnivores have a posterior bent olecranon process (Van Valkenburgh 1987), which indicates that their need for power is greatest in the relatively extended position during the phase of support of the forelimb. The small species that can move swiftly in trees always have a straight or anterior bent olecranon process (Van Valkenburgh, 1987). By climbing with flexed limbs they keep their centers of gravity close to tree trunks or branches. The many good climbers in the Ursidae have markedly posterior bent olecranon processes (Van Valkenburgh 1987). This difference is due to the fact that the controlled grasping way of climbing, as in bears, requires strong flexion ability, rather than extension ability, of the elbow. This is also indicated by the above mentioned bicipital notch and the distal position of the bicipital tuberosity on the radius (Taylor 1989).

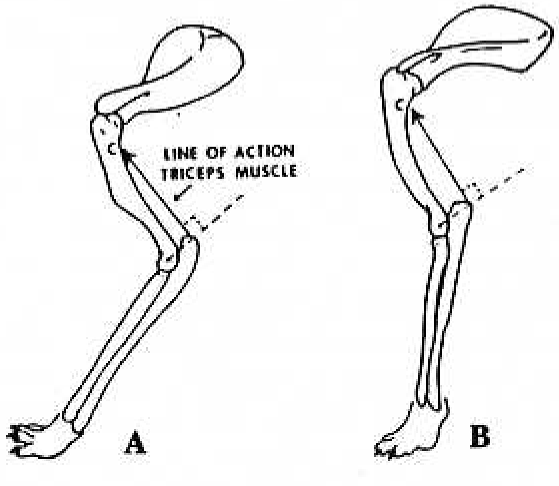


Fig. 5. The olecranon process in (A) the arboreal ring-tail possum and (B) the terrestrial tasmanian devil (from Van Valkenburgh 1987).

The elbow joint is a compilation of three joints: the hinge-like articulation between the trochlear notch of the ulna and the trochlea of the humerus; the articulation of the shallowly concave upper end of the radius with the capitulum of the humerus; the articulation of the head of the radius with the radial notch of the ulna. By losing or reducing muscles that are of little use in running the mass of the distal limb segments can be reduced. Thus the forces required of the more proximally placed muscles during the phase of free transit also are reduced. The muscles that pronate and supinate the forearm are reduced in cursorial carnivores and movement of the elbow joint is restricted to flexion and extension in the sagittal plane. Elbow stability in cursorial and digging species is maximized through the congruency of a deep trochlea with the corresponding surfaces of the radius and ulna. In *Nandinia bionata* these articulation surfaces are flatter and allow the ulna to rock on the humerus, thus aiding supination (Taylor 1974). Taylor (1974) also found that in the Viverridae the radial notch in cursorial species is deep and faces more anteriorly, while it is shallow and faces laterally in arboreal species. This is in accordance with what Gonyea (1978) found; in all the felid species studied the radial notch faced laterally but in canids and hyenids, where supination is restricted, it faced more anteriorly. In ungulates the higher cursorial specialization has led to an ulna that is distally fused to the radius, making pronation and supination impossible.

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).

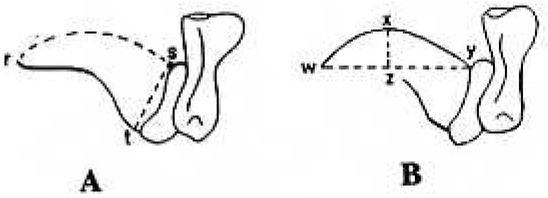


Fig. 6. Measurements of the ungual phalanx. The depth (A): Length of dorsal arc **rs** divided by depth at ungual base **st**. The curvature (B): Maximum arc height **xz** divided by length **wy** (from Van Valkenburgh 1987).

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. Especially 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 batteling 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.

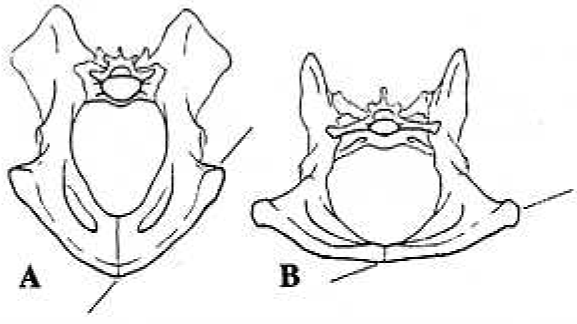


Fig. 7. Posterior view of the pelvis in (A) the raccoon and (B) the fox, showing the orientation of the ischium (from Jenkins & Camazine 1977).

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 consisiting 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 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 (Randinsky 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.

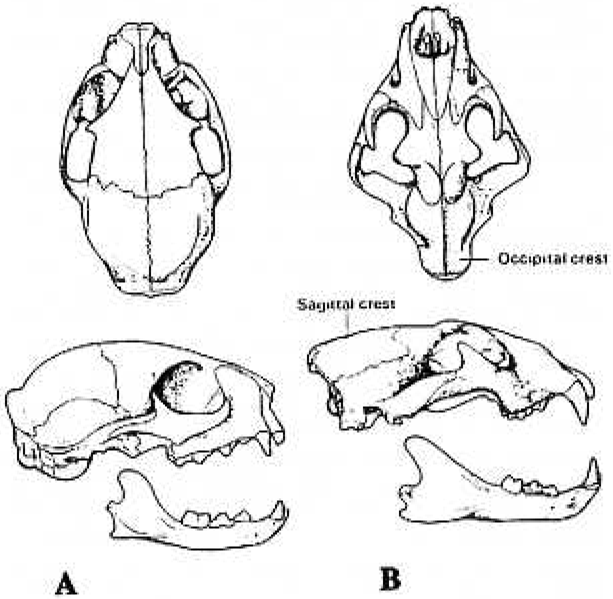


Fig. 8. The skull of (A) the small jaguarundi and (B) the big lion (from Ewer 1973).

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).

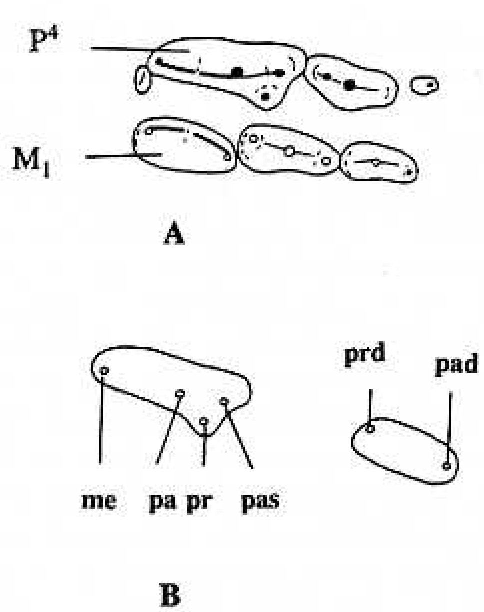


Fig. 9. (A) The carnassials (arrowed) in Felis. (B) The cusps of right upper carnassial: **me** metacone, **pa** paracone, **pr** protocone, **pas** parastyle. (C) The cusps of left lower carnassial: **prd** protoconid, **pad** paraconid (from Savage 1977).

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 cervicial 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 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).

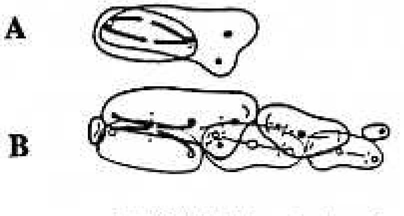


Fig. 10. The carnassials (A) at the beginning of occlusion and (B) in full occlusion (from Savage 1977).

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. Beacuse 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

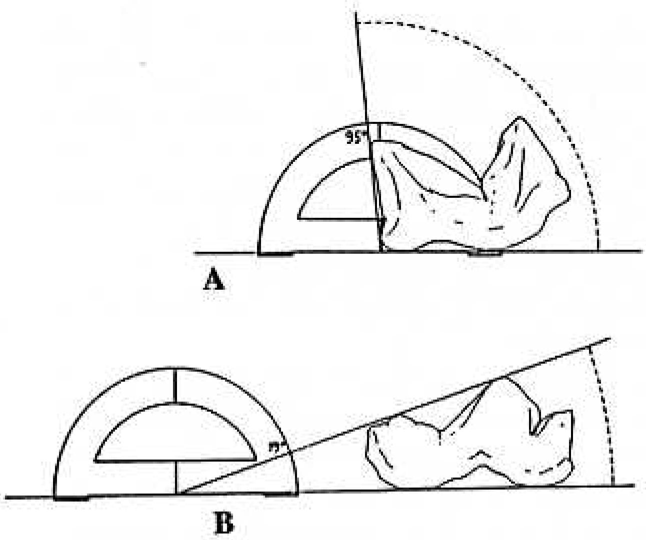


Fig. 11. Measurements of the angle **a**. The lower carnassial of (A) a highly carnivorous species and (B) a much less carnivorous species (from Crusafont-Pairo & Truyols-Santonja 1956).

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 crushing function. The general appearance of the P^4 of these species is therfore 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° and angle **b** is around 22.5°. 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° to 105° in felids and from 6.3° to 31° in ursids. Angle **b** ranges from 10° to 25° in felids and from 26° to 52° in ursids. In the fossil history the total range as seen in the order Carnivora has increased in the course of time.

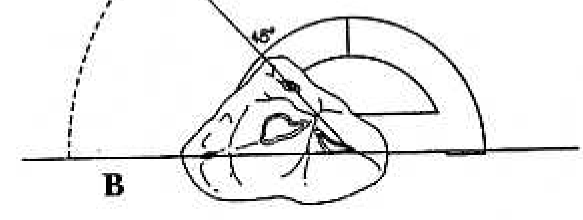


Fig. 12. Measurements of the angle **b**. The upper carnassial of (A) a highly carnivorous species and (B) a much less carnivorous species (from Crusafont-Pairo & Truyols-Santonja 1956).

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, *Lyacaon 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 subsidary 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 vestigal 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 articulation 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.

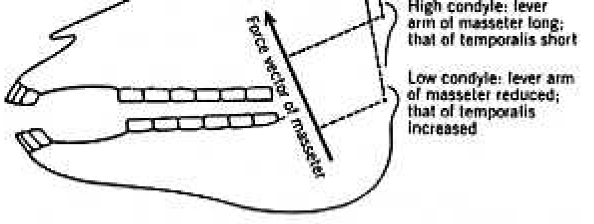


Fig. 13. Jaw mechanics in relation to the position of the mandibular condyle (from Hildebrand 1987).

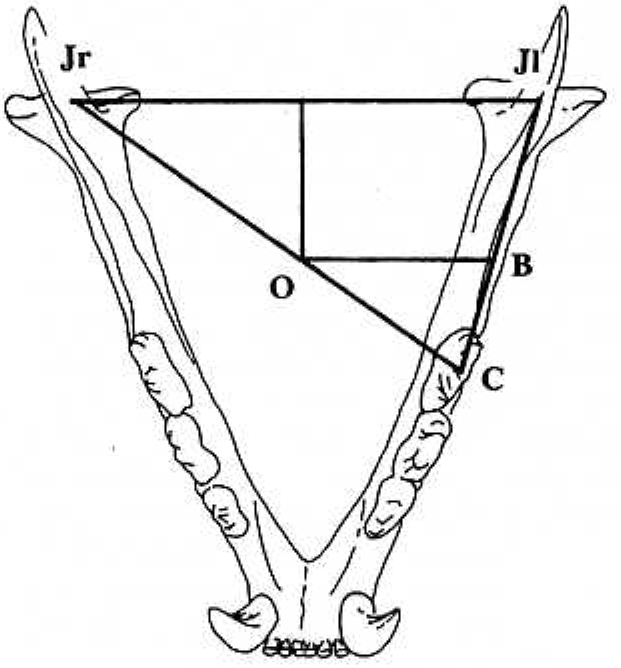


Fig. 14. Model of the lower jaw. Jr = right joint, Jl = left joint, C = carnassial tooth, O = optimal position of the resultant force, B = bite point posterior to carnassial tooth (simplified from Greaves 1983).

13). According to Ewer (1973) the m. masseter in carnivores is most effective as an adductor when the jaws are closed, while the anterior part of m. temporalis and a part of m. masseter, zygomatico-mandibularis, are most effective as adductors when the jaws are widely open. Thus a strong bite can be delivered with both the canines (widely open position) and with the carnassials (closed position). M. pterygoideus is small in carnivores and exerts a medial pull which positions the carnassials.

The traditional model of the mammalian jaw was that of a two-dimensional lever. In that model the more anterior the resultant muscle force is placed and the more posterior the position of the carnassials, the greater the out-forces at the carnassials will be. In Greaves' (1978, 1982, 1983, 1985) three-dimensional model there is a maximum anterior position for the resultant muscle force. The mandible is considered to act like a triangular plate contacting the skull at the bite point and the two jaw joints (Fig. 14). All the forces produced by the adductor muscles are resolved into a single resultant force that acts perpendicular to the plane of the triangle. The resultant muscle force is assumed not to lie anterior to the line JrC between the jaw joint and the carnassial on the opposite side otherwisee Jl the opposite jaw joint will tend to be dislocated due to rotation around the line JrC. The maximum out-force at C is then found when the resultant force acts at O, the point where the midline of the mandible intersects with the line JrC. The mechanical advantage of the in-lever remains the same if the resultant force moves laterally along the line OB but this is achieved by not maximally activating the right side muscles thus reducing the resultant force. A more anterior position of the resultant along the line OC increases the in-lever arm but the out-force at C will still be reduced as the resultant muscle force then cannot be maximized due to the simultaneous lateral movement. The anteroposterior position of the resultant force depends on the arrangement of the muscles and cannot be changed for any given jaw construction. If the muscles have been arranged to maximize out-force at C and the bite point is shifted to a more posterior position (e.g. from carnassial to molars), the resultant must move from O along line OB to still be within the plane of the triangle defined by the new bite point and the two jaw joints. This means that resultant muscle force cannot lie anterior to the posteriormost functional teeth.

In most modern carnivores the carnassials lie at the midpoint of the line from the jaw joint to the most anterior point A of the mandible (Fig. 15). If we assume that the jaw muscles are arranged to maximize the out-force at the carnassials the position of the resultant force O will divide the jaw lever JrC in the ratio of 1:2

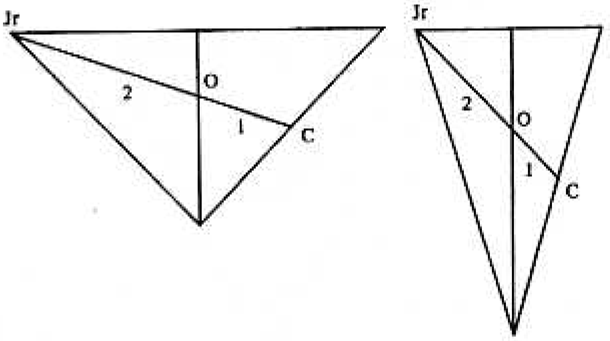


Fig. 15. Diagrams of two lower jaws of different proportions. Jr = right joint, C = carnassial tooth positioned at the midpoint of the left ramus, O = optimal position of the resultant force. Point O will divide the jaw lever JrC in the ratio of 1:2 irrespective of the proportions of the lower jaw.

irrespective of the width and length of the mandible. This would mean that the mechanical advantage of the jaw lever for the carnassial is the same in all carnivores that have the carnassials positioned at the midpoint of the ramus. In bone cracking hyenas the carnassials are positioned more posteriorly (Radinsky 1981) and this may indicate that their jaw muscles are arranged to maximize the out-force at the premolars instead. If the position of the carnassials is considered fixed to the midpoint of the ramus, then the only way to increase the out-forces at the carnassial is to increase the force of the muscle, since the position of the resultant force has been optimized. Greaves (1985) compared the skulls of felids and canids. The bobcat, *Lynx rufus*, and the domestic dog have jaws of equal width but the dog's jaws are longer. The equal width of the jaws is assumed to reflect the similar body sizes and similar masses of the jaw muscles. Therefore it is also assumed that the bobcat and the dog can exert similar bite forces. The longer jaws of the dog provides for a larger gape and a greater number of teeth. According to this hypothesis lengthening of the jaw does not produce any obviously negative effects and why felids in general have not developed the typical long jaws of canids is not clear.

The consistency of the position of the most emphasized bite point has not really been explained. A more anterior position of the bite point allows for a more advantagous in-lever arm (Fig. 16). But of course, a more anterior position of the carnassial means less room for the anterior positioned teeth. Obviously for a pair of jaws of given dimensions, there is an anterior limit for the carnassials if the anterior teeth are to maintain their function. However, more room can be made by lengthening the jaws. Perhaps it is the arrangement of the muscles that is the restricting factor so that the resultant force cannot follow the bite point forward without the muscles losing in mass and thereby force. This would also suggest that the position of the resultant force cannot be optimized in longer jaws where the carnassials are maintained at the midpoint of the ramus. If so, the greater gape of the dog compared to the bobcat is bought at the expense of bite force. Also, the analysis based on the traditional two-dimensional model, where measurements of the in-lever arms of m. masseter and m. temporalis are made, still have some validity.

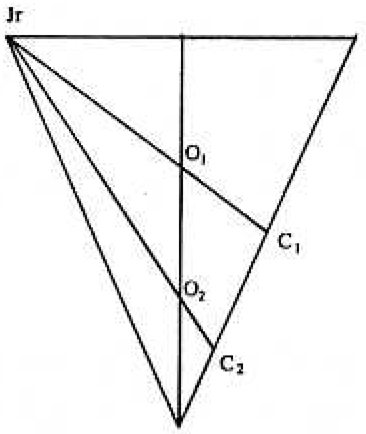


Fig. 16. Diagram of the lower jaw. The in-lever JrO_2 is more advantagous than the in-lever JrO_1.

The jaws and dentition of saber-toothed forms

Saber-like upper canines have evolved independently at least four times among mammalian carnivores: in nimravids (paleofelids), felids, creodonts and marsupial carnivores. The skulls and dentitions of all these forms show a high degree of convergence. The enlargement of the upper canines naturally demands a greater gape if the canines are still to be functionable, and most of the features of the skull seem to represent modifications for increasing the maximum gape, while retaining bite force (Emerson & Radinsky 1980). The greater gape is not attained by lengthening the jaws; on the contrary the jaws of sabertooths are typically short, just like those of modern felids. Greater gape can also be attained by lengthening the jaw muscles, as longer fibers allow a greater amount of stretch. The position of the muscle is also important. As discussed above, if the in-lever is decreased, then the same shortening/stretching of the muscle can move a certain point on the out-lever through a longer distance, but the out-force at that point is decreased. A lowered glenoid fossa and a reduced height of the coronoid process is seen in all sabertooths (Fig. 17). As m. temporalis inserts on the upper part of the coronoid process, m. temporalis was supposedly longer in sabertooths. Emerson & Radinsky (1980)

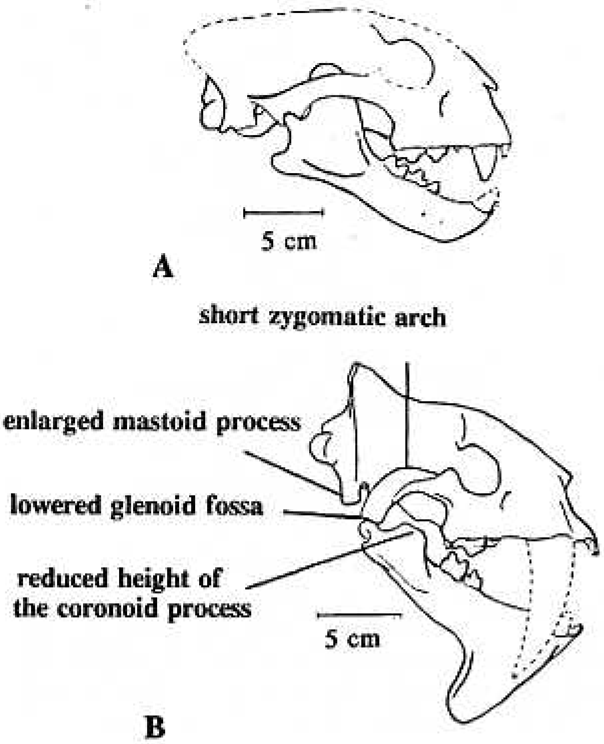


Fig. 17. The skull of (A) an early felid and (B) the sabertooth Eusmilus (from Emerson & Radinsky 1980).

showed that because of this a much wider gape was possible. They also manipulated the jaws to see at which point they disarticulated. In modern felids this occurred at about 65°, while in the two tested species of sabertooths this occurred at about 90°. The difference is due to the laterally shifted angular process and the reduced postglenoid process in sabertooths. Emerson & Radinsky (1980) also demonstrated that in spite of the reduced coronoid process, the in-lever arm of m. temporalis is not significantly shorter in sabertooths. The direction of the in-lever arm has however changed but so has the line of the muscle action, thus when biting at the carnassials, the in-lever arm is more or less perpendicular to the resultant force (Fig. 18). The carnassials in sabertooths are also placed posterior to the midpoint of the ramus and this may compensate for the somewhat decreased in-lever arm. However, the short zygomatic arch, the reduced masseteric fossa and the reduced area on the skull for origin of m. temporalis (Fig. 17) indicate that the jaw muscles were relatively small.

It has often been suggested that the typically enlarged mastoid process reflects powerful development of the muscles that depress the head and that these muscles were used when striking with the the upper canines. Emerson & Radinsky (1980) speculate that perhaps the elongation of the mastoid process was only a side-effect of the lowering of the glenoid fossa.

The saber-toothed cats can be divided into two groups depending on the shape of their upper canine. The scimitar-toothed cats have canines that are only moderately elongated and usually bear coarse crenulations. The dirk-toothed cats have canines that are much elongated and bear fine crenulations or none at all (Martin 1989). Both types of canines are flattened to give a bladelike structure, compared to the conical canines of modern felids. The lower canine is reduced, presumably to permit a wider gape, and functions like an incisor.

The shape of the upper canine must have made it vulnerable to mediolateral bending and therefore contact with bone must have been avoided. Accordingly the neck bite was very probably not employed by sabertooths. Emerson & Radinsky (1980) agreed with an earlier worker that the advantage of the long canine was in creating a large superficial wound. The most obvious target would then be the throat or ventral neck, where one slash could sever critical blood vessels and result in rapid death

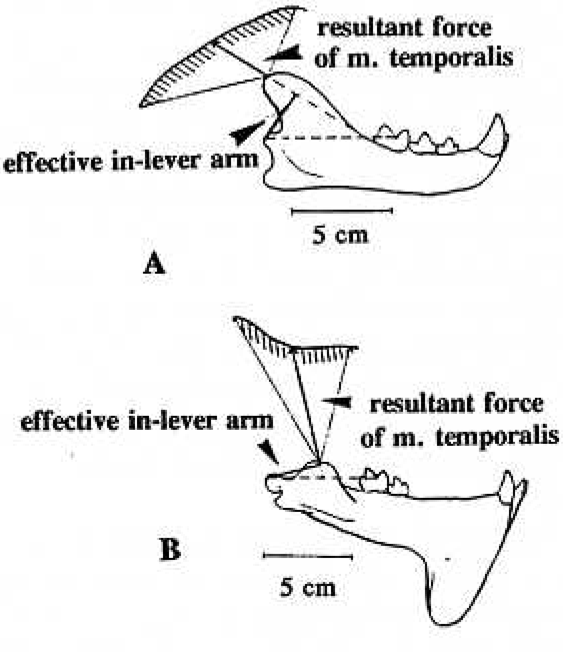


Fig. 18. The effective in-lever arm and resultant force of m. temporalis in (A) a modern felid and (B) the sabertooth Eusmilis (from Emerson & Radinsky).

Emerson & Radinsky believed that some degree of prey immobilization would probably be necessary as a misplaced bite may have resulted in bone contact. Because of the risk of bone contact, Akersten (1985) believes that the stomach rather than the throat would be chosen for the killing bite. The earliest saber-toothed cats had already developed fully retractile claws (Gonyea 1976) and the sabertooths in general had forelimbs built for power rather than speed (see below), especially when compared to modern felids. The strong forelimbs of sabertooths would probably be able to control any prey who might struggle and therefore facilitate an accurate canine strike. Presumably the sabertooths were capable of taking prey of considerably larger size than themselves, and then the slash of a pair of long canines would be the most effective killing method.

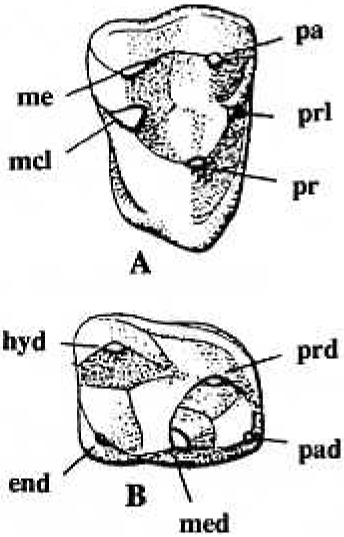


Fig. 19. The tribosphenic molar. (A) The right upper molar: **me** metacone, **pa** paracone, **mcl** metaconule, **prl** protoconule, **pr** protocone. (B) The left lower molar: **hyd** hypoconid, **prd** protoconid, **end** entoconid, **med** metaconid, **pad** paraconid (from Romer 1966).

The evolution and fossil history of mammalian carnivores

Mesozoicum

Throughout the Mesozoic, most mammals were small and mainly insectivorous. The only way for the mammals to compete with the dominating reptiles was to occupy niches unavailable to reptiles. Mammalian endothermy gave them an advantage over reptiles in temperate climates enabling them to feed at night. Small size allowed the mammals to hide during the day (Savage 1977). The diet of insects was probably filled up with food such as fruit, worms and eggs. Some forms may also have predated on other small vertebrates. The order Triconodonta, from the Middle Jurassic to the Late Cretaceous, had molars with three sharp conical cusps arranged in a longitudinal row, which formed a shearing device. They were also quite big for the time, *Triconodon* approached the size of a cat, and Romer (1966) interpreted them as probably true carnivores.

The therians are known from the late Cretaceous, but it was during the Paleocene, with the disappearance of the dinosaurs, that they rapidly diversified. The first marsupials were much like the modern opossum and are particulary well known from North and South America (Benton 1990). Deltatheridiidae and Leptictidae have been considered as the basal placental types (Romer 1966). Fossils of these are found in North America, South America and Mongolia.

With the therians the tribosphenic molar appeared (Fig. 19). The main shearing surface of the tribosphenic molar is transverse in the occlusal plane and between the lower molar and the upper molar or premolar anterior in position to the lower one (Fig. 20). In addition there are many smaller shearing surfaces. The talonid of the lower molar recieves the protocone of the upper molar posterior in position and a crushing effect is obtained. The early therians were probably still insectivorous to omnivorous. Lucas (1979) states that the crushing effect between the sharp cusps and the basin would result in rupture of the ectoskeleton of insects, while reduction of the insects into smaller pieces requires the action of blades. The tribosphenic molar is modifiable in two different ways. For a more carnivorous diet the shearing function is exaggerated, while a herbivorous grinding apparatus can be obtained by increasing the crushing area and rounding of the cusps. The fossil history shows that different paths have been taken in the development of carnassial teeth.

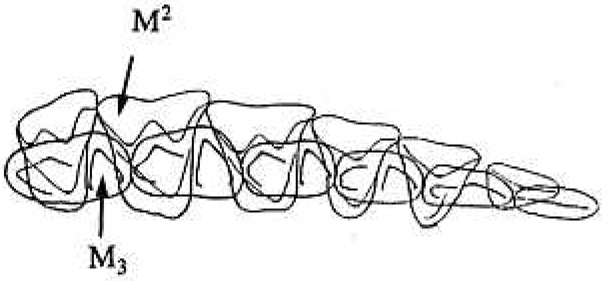


Fig. 20. Occlusal diagram showing main shearing surfaces in an early therian dentition (from Butler 1946).

Paleocene and Eocene

Marsupials spread from North America to many parts of the world. In Europe, Africa, Asia and North America they never were particularly successful because of competition with the more highly developed placentals. Only forms very similar to the modern opossum persisted there until they became extinct in the Miocene. South America was an island for most of the Cenozoic and therefore an endemic fauna of mammals evolved which was very different from those of other parts of the world. Marsupials probably spread to Australia from South America via Antarctica (Benton 1990). The earliest marsupial fossils of Australia are found in the Oligocene. In Australia the fauna was, except for bats (since the Miocene) and some rodents (since the Pliocene), solely marsupialian until the arrival of man. In South America a restricted number of placentals were present in the Paleocene, but the development of carnivorous types was only achieved among the marsupials (Romer 1966). The South American carnivorous marsupials constitute the family Borhyaenidae and the Australian forms belong to the family Dasyuridae.

In the rest of the world mammals of now extinct orders and families made up the carnivorous niches. The condylarths, from which later ungulates radiated, include forms that have been interpreted as carnivores. Szalay (1969) studied the feeding mechanism of mesonychids where some adaptations for a flesh diet can be seen. The Paleocene mesonychid *Dissacus* was plantigrade and smaller than a wolf but had a large head. Eocene wolf-sized forms like *Mesonyx* had evolved a digitigrade stance. Very large forms are known from the Eocene. From the skull, *Andrewsarchus* has been estimated to be 5-6 m long, which makes it the largest known terrestrial mammalian carnivore (Benton 1990). The shearing function of the molars were not very efficient compared with the carnassial shear of the order Carnivora and of creodonts, but the mesonychids are assumed to have had powerful jaw muscles and the carnassial notch of the lower molars is seen as an adaptation of holding the meat, thus preventing it to slip while shearing it (Szalay 1969). A scavenging mode of life probably provides the best explanation for the adaptation of the molars. Decaying flesh does not require very sharp teeth, and blunt cusps of the molars also makes bone-crushing possible. Mesonychids are found in North America, Europe and Asia and they persisted into the late Eocene of North America and Asia (Szalay 1969). The whales probably evolved from mesonychids in the Paleocene, as the early whales had mesonychid like teeth (Benton 1990).

The main flesh-eaters of the early Tertiary are the creodonts, constituting the families Oxyaenidae and Hyaenodontidae. The earliest oxyaenids appear in the late Paleocene and none survived beyond the Eocene. The oxyaenids had M^1 and M_2 developed as specialized shearing teeth. It is the posterior crest of M^1 that has been elongated from the primitive tribosphenic molar. In the more advanced forms like *Patriofelis* the posterior crest is much elongated and the protocone is greatly reduced. M_2 in *Patriofelis* has a greatly reduced talonid and no metaconid. The direction of the shear has changed from transverse to anteroposterior and both M^1 and M_2 are enlarged relative to the other teeth. The teeth posterior to M^1 and M_2 are reduced in all oxyaenids and in *Patriofelis* they are all lost (Butler 1946).

The general trend from the primitive therian dentition is a reduction in the number of shearing crests. In the primitive dentition the posterior edges of P^4 to M^2 and the anterior edges of M_1 to M_3 constituted the main shearing crest. Also important was the shear between the anterior edges of P^4 to M^2 and the posterior edges of P_4 to M_3 (Van Valen 1969). In *Patriofelis* there is only one shearing crest, the one between M^1 and M_2 , but the crest is much elongated in the anteroposterior direction. When slicing up a larger portion of meat, a long blade is obviously more effective than several smaller ones. Van Valen (1969) also states that a scissors action is most efficient when it operates perpendicular to the axis of rotation, which is the case of an anteroposterior directed blade. This general trend is seen also in Hyaenodontidae and Carnivora.

The oxyaenids were generally large sized. *Oxyaena* from the early Eocene was of wolverine size, the middle Eocene *Patriofelis* was of bearlike size and the late Eocene *Sarkasodon* was far larger still (Romer 1966). The spine of creodonts in general was less flexible than the spine of extant carnivores and *Patriofelis* in particular had zygopophyses of the lumbar vertebrae that allowed very little movement (Savage 1977). The oxyaenids had short limbs; the length of the limb relative to the length of the spine is similar to that of the ambulatory badger and there is no lengthening of the distal segments (Savage 1977). The metapodials were short and widely spread. The position of the fovea capitis femoris indicates that the femur was normally much abducted in *Patriofelis* (Jenkins & Camazine 1977). The postcranial skeleton thus shows no cursorial adaptations, not even by Paleocene and Eocene standards. All creodonts had long tails but it is hard to see a functional meaning in the long tail of the oxyaenids. Probably the long tail is a primitive character from the ancestral smaller forms. The prey capturing of oxyaenids must have been based on ambush or accidental discovery and perhaps their large size also made them successful scavengers. The scavenging mode is also supported by the fact that the premolars in all but the most primitive forms have developed a crushing function (Butler 1946). This is in contrast to the evolution in hyaenodonts where the premolars tend to diminish in size.

The hyaenodonts appeared in the early Eocene and, in contrast to the oxyaenids, survived for most of the Tertiary. The Hyaenodontidae was a much larger group with more variety of forms than the Oxyaenidae. The evolution of the shearing teeth is similar to that in the oxyaenids, but in the hyaenodonts the posterior crest of both M^1 and M^2 became elongated (Butler 1946). In an advanced form like *Hyaenodon* from the Oligocene, M^1 with M_2 and M^2 with M_3 form two anteroposterior directed shearing blades. In *Hyaenodon* M^3 has been lost and the crush of the protocone and talonid is of no importance in any teeth. In some forms, such as *Limnocyon*, M^1 and P^4 together with M_2 and M_1 have evolved in a carnassial direction.

Sinopa from lower and middle Eocene is representative of a series small and lightly built genera that range in size from weasel to fox (Romer 1966). The limbs of *Sinopa* were short but somewhat longer than the limbs of oxyaenids. It has been proposed that *Sinopa* was ambulatory with some cursorial adaptations (Denison 1938). Contemporary to *Sinopa* was *Prolimnocyon*, which was thoroughly investigated by Gebo & Rose (1993). *Prolimnocyon* was small sized just like *Sinopa*. Its estimated weight was 1.5-3 kg. The forelimb shows many signs of adaptation to climbing. The biciptal notch is clearly defined. The angle between the olecranon fossa and the long axis of the humerus is about 23° indicating that the humerus was not in the sagittal plane. The olecranon process is anterior bent so that extension of the elbow was more effective in a flexed position. The radial notch faces laterally as in carnivores capable of forearm pronation and supination. There are also elements of the forelimb, like well developed muscle crests and processes, that are more characteristic for digging carnivores. These elements may also be developed to a lesser extent in climbing carnivores, but Gebo & Rose (1993) speculate that digging possibly was part of *Prolimnocyon*'s behavioral repertoire. When comparing its hindlimb to that of living carnivores, *Prolimnocyon* appears to be somewhat more cursorial than arboreal procyonids, viverrids and mustelids; the tibia is long relative to the length of the femur and rotation of the femur seems to be restricted. The articular surface of the femoral head indicates that normal femoral postures were little abducted but that abducted postures were still possible. The mobility of the ankle suggests that *Prolimnocyon* could have reversed the hind foot to some degree just like various living climbing carnivores. Finally Gebo & Rose compare *Prolimnocyon* to other Eocene creodonts. Closely related forms like *Limnocyon* and *Thinocyon* are very similar to *Prolimnocyon* but do not appear to have been as good climbers.

Oligocene hyaenodonts include much larger forms. *Hyaenodon horridus*, the largest form, was included in the study of Van Valkenburgh (1987). Its body weight was estimated to be 93 kg. Compared to other creodonts, *Hyaenodon* species had longer limbs (Savage 1977). The metatarsal/femur ratio for *Hyaenodon horridus* is rather high, similar to the ratio for the leopard, although the hindlimb of the leopard is longer. *Hyaenodon horridus* also had long metacarpals relative to phalanx length, the ratio being higher than for all the modern felids in the same study. The olecranon process is strongly posterior bent as it is in living cursorial species. The olecranon process is, however, very long and this is indictative of adaptations to either digging or batteling with large preys. The claws appear to have been shallow and only a little curved thus supporting the idea of some sort of digging behaviour. The species of *Hyaenodon* were probably among the most cursorially adopted species at the time (Van Valkenburgh 1985) and according to the dentition they were pure meat eaters. *Hyaenodon* is known from the early Oligocene in North America, Europe, Asia and Africa. The early Oligocene in North America provides the first evidence of open grass land areas (Martin 1989). With open areas cursorial adaptations became crucial for the prey and its hunter.

As mentioned above, no oxyaenids survived beyond the Eocene. The hyaenodonts did not survive beyond the Oligocene in North America but they persisted into the Miocene in Europe, Asia and Africa (Savage 1977). The hyaenodonts are the only known carnivores in Africa until the early Miocene when members of the Carnivora appear. A traditional explanation of the diminishing numbers of creodonts has been their smaller brains and inferior intelligence compared to the miacids from which the modern carnivoran families radiated. Radinsky (1977) came to the conclusion that this is not the case. According to Savage (1977) the replacement of creodonts was probably due to a combination of many factors, but see also below for a different point of view.

Miacidae is the ancestral family in the order Carnivora. They appear in the middle Paleocene and continue through the Eocene. In the late Eocene and the early Oligocene the miacids evolved into higher fissipeds and the transition is not clearly defined (Romer 1968). Miacids are known from North America, Europe and Asia. In the miacids it is P^4 and M_1 that have developed carnassial specialization. The shear between the elongated posterior crest of P^4 and the elongated anterior crest of M_1 is still more or less transversely directed in the miacids but in later, more carnivorous, forms anteroposteriorly directed blades have developed. In the Miacidae only P^4 and M_1 show carnassial specialisation. The posterior molars instead show reduced shearing crests compared to the primitive therian dentition while a crushing function was maintained by the protocones and the talonids (Butler 1946). There is thus a division of the dentition into a shearing region and a posterior crushing region. In the creodonts the shearing function is emphasized at the expense of crushing function in all the cheek teeth (Butler 1946), although one tooth is usually more specialized than the others and may become the only remaining shearing tooth in more advanced forms. The dentition of the miacids is therefore not as specialized as the dentition of the creodonts and according to some authors this explains the replacement of the creodonts (Ewer 1973). From the Miacidae forms evolved that either emphasized the shearing function (e.g. felids, hyaenas) or emphasized the crushing function (e.g. procyonids, ursids).

The miacids were of small size and are generally believed to have been arboreal. In their study of the hyaenodont *Prolimnocyon*, Gebo & Rose (1993) also examined some miacids. Early Eocene forms like *Vulpavus* and *Miacis* resemble *Prolimnocyon* in most of the characters, differing in ways that reflect greater arboreal specialization. Contemporary *Didymictis*, however, seems to be more terrestrial in habit. Its ungual phalanges are shallow and little curved. The muscle crests and processes of the humerus are reduced but the greater trochanter of the femur, on which hip extensors inserts, are large.

The radiation of the Carnivora

Representatives of most of the modern families had appeared by the middle Oligocene, but Hyaenidae and Procyonidae did not appear until the Miocene. Catlike forms are known from the beginning of the Oligocene but some authors place these early forms in the now extinct family Nimravidae (Martin 1989). According a classification like that, the Felidae Felidae is first known from the early Miocene. A now extinct family that is generally accepted is the Amphicyonidae, with forms formerly placed in the Canidae.

Canidae

Hesperocyon is considered to be the first canid. It is known from the early Oligocene and is restricted to North America, as are all canids until the late Miocene. *Hesperocyon* had short limbs, spreading feet and generally did not show many advancements from the miacids (Romer 1966). A species of *Hesperocyon* was included in the study of hip strucyure in carnivores of Jenkins and Camazine (1977). The position of the fovea indicates a sagittally oriented femur in *Hesperocyon*, but not more sagittally oriented than the femur in species of *Miacis* and *Vulpavus*. However, the limited articular surface of the femoral head and the deep acetabulum indicates that abduction was not possible to the same extent in *Hesperocyon*. The hip structure in *Hesperocyon* thus shows a high degree of cursorial specialization, although the limbs are short. During the late Oligocene there was a radiation of canids, which may be grouped together as the Hesperocyoninae. This group included small frugivorous forms, larger forms with large, round premolars suitable for bone-cracking, and the coyote-sized *Mesocyon* (Martin 1989). The relative length of the carnassial blade and the relative size of the grinding area in early species of *Mesocyon* are similar to those measured in the red fox, but later forms had smaller grinding areas and some had developed a trenchant heel, indicating a diet largely cosisting of meat (Van Valkenburgh 1991).

At the beginning of the Miocene the Hesperocyoninae became extinct, except for one branch that gave rise to new radiations (Martin 1989). Among these were frugivouros and more or less omnivorous forms, but later also large bone-cracking forms evolved. *Osteoborus* and *Borophagus* were such hyaena-sized, bone-cracking forms that existed from the late Miocene to the early Pleistocene. While P^3 and P_3 are the major bone-cracking teeth in hyaenas, P^4 and P_4 are the major bone-cracking teeth in *Osteoborus* and *Borophagus*. This means that the upper carnassial, P^4, in the bone-cracking canids is quickly worn down, and this is also true for the lower carnassial, as it is so close in position. *Osteoborus* and *Borophagus* must have been less capable of handling fresh meat than the hyaenas and therefore were probably more specialized scavengers (Werdelin 1989).

The radiation of modern canids occurred probably in Asia and began in the late Miocene. *Canis davisi* was an early form that probably was similar to the canid that crossed Beringa and entered Asia (Martin 1989). *Canis davisi* was about the size of a small coyote, and according to the size of the grinding area, fruit and insects were a substantial part of the diet (Van Valkenburgh 1991). Modern canids appear in North America first at the beginning of the Pleistocene.

Amphicyonidae

In the early Oligocene a tremendous variety of the Amphicyonidae evolved in Euroasia, while only three genera are known from North America (Martin 1989). Amphicyonids vary from fairly light-built forms to very large bear-like forms. In general the amphicyonids have rather short limbs, but unlike the bears they had digitigrade hindlimbs. The molars were well developed and the shearing function of the carnassials was reduced (Romer 1966). One species of the american genus *Dapheonus* was included in a study of Van Valkenburgh (1987). She came to the conclusion that *Dapheonus* was a capable climber like many of the felids today. The deep and curved ungual phalanges, the metacarpal/

phalanx ratio and the moderately posterior bent olecranon process are all features which are shared by modern felids. *Dapheonus* had short limbs, shorter than those of contemporary *Hyaenodon* and much shorter than those of similar sized (40 kg), living felids (Savage 1977), and was probably not a fast runner. The relative size of the grinding area is similar to that of more omnivorous species today (Van Valkenburgh 1985).

During the late Oligocene the American genera became extinct and Asian forms are known from this time in North America (Martin 1989). One of these, *Daphoenodon* from the early Miocene, was bear sized and dug large subterranaen dens that have been excavated along with skeletons of *Daphoenodon* itself (Martin 1989). *Amphicyon* which replaced *Daphoenodon*, had a reduced grinding area (Van Valkenburgh 1991) and was probably highly carnivorous. At the end of the middle Miocene the amphicyonids became extinct.

Mustelidae

During the late Oligocene the expansion of open spaces within the savannas reached a point where there was a large radiation of burrowing mammals, especially rodents. From this time many mustelid-like forms appear but these probably belong to other families and are not ancestral to the Mustelidae (Martin 1989). The earliest true mustelids were weasel-like and are known from the early Miocene in North America and Eurasia. During the Miocene marten-like forms, early wolverines, badgers and skunks appear. Gambaryan (1974) has presented his idea of the evolution in the Mustelidae. He envisaged that the burrow hunting mustelids evolved adaptations to digging to widen narrow parts of the burrows. While digging they came upon root swellings and insect larvae. Some eventually went over to such a diet and became further specialized for digging, like the European badger. In forests, where rodents do not have complicated burrows, development to hunt in trees and on the ground took place, whereby martens evolved. On the ground, an increase in body size for hunting large animals led to the evolution of wolverines. If his idea that all forms evolved from a weasel-like ancestor is correct, the development of martens must be considered as a reversion of the evolutionary trend.

Ursidae

The raccoon-sized *Cephalogale* from the late Oligocene of Europe is an early ursid with a dentition very similar to typical canids (Ewer 1973). In the early Miocene there was a radiation of larger forms. *Hemicyon* was sized like a small brown bear but the grinding areas of the molars were yet not considerably enlarged (Van Valkenburgh 1991). It seems that the radiation of ursids occurred in Asia from where they immigrated to other regions. Ursids are known from the middle Miocene in North America and one genus reached Africa, where they persisted into the late Pliocene. The genus *Ursus* is known from the late Pliocene of Europe (Martin 1989).

Procyonidae

Fossils of procyonids are rare, probably because of their arboreal habits. The dentition of procyonids seems to represent a reversion from the more carnivorous diet of primitive canids back towards a more omnivorous diet (Romer 1966). The radiation of procyonids took place in the early Miocene and was restricted to North America. One genus is known from the late Miocene of South America, when some sort of connection between North and South America existed (Martin 1989).

Nimravidae

The earliest nimravids are known from the late Eocene of Asia, where they probably radiated before entering North America, where they are known from the early Oligocene. The early forms had already developed retractile claws, reduced molars and saber-toothed upper canines (Martin 1989). The North American forms were already divided into scimitar-toothed forms of the genus *Dinictis* and dirk-toothed forms of the genera *Hoplophoneus* and *Eusmilis*.

Two species of *Hoplophoneus* and one species of *Dinictis* were included in the study of locomotor behaviour by Van Valkenburgh

(1987). The largest *Hoplophoneus* species was about the size of a jaguar. Compared to modern felids the metacarpal/phalanx ratio and the metatarsal/femur ratio were very low and the olecranon process very long. *Hoplophoneus* appears to have been been less cursorially specialized than contemporary amphicyonids and hyaenodonts. These features instead suggest adaptations to kill prey of relative large size. The shape of the claws does not indicate any digging behaviour and climbing adaptations alone can not explain the differences to the similar sized climbing felids of today, i.e. the jaguar and the leopard.

The *Dinictis* species were of smaller size and the features seen in *Dinictis* are not so extreme as those seen in *Hoplophenus*, although similar. Other measurements in the hindlimb and forelimb of *Dinictis* show some similarites with modern cats and Gonyea (1976) believes that *Dinictis* was more cursorial than *Hoplophenus*.

The differences between *Hoplophenus* and *Dinictis* also generally hold between scimitar-toothed and dirk-toothed forms (Martin 1989). As the dirk-toothed cats had the longest upper canines, this supports the idea that long canines were primarily an adaptation to kill larger prey (see the section on the jaws and dentition of saber-toothed forms above).

Hoplophoneus and *Dinictis* are restricted to North America but *Eusmilis* and a close relative to *Dinictis* are known form the late Oligocene of Eurasia. In North America the nimravids became extinct during the early Miocene but they persisted in Eurasia, where the highly specialized Barbourofelini developed. The Barbourofelini entered Africa during the Miocene and North America during the late Miocene but they did not survive into the Pliocene (Martin 1989).

The Felidae

Martin (1989) believes that the common ancestor of the nimravids and felids were more miacid-like than cat-like. The earliest true felid seems to be the middle Miocene genus *Pseudaelurus*, which probably is descendend from an advanced viverrid. *Pseudaelurus* diversified into a series of conical-toothed and scimitar-toothed forms ranging in size from that of a domestic cat to that of a small jaguar. The larger forms are often scimitar-toothed (Martin 1989). Some very long-limbed forms evolved but when the Barbourofelini became extinct it was replaced by a dirk-toothed and short-limbed felid lineage, the Smilodentini. At that time, the early Pliocene, species of modern genera became established. The felidae is almost from the start known in Eurasia, North America and Africa (Martin 1989). *Smilodon* was the last saber-toothed cat when it became extinct at the end of the Pleistocene.

Ewer (1973) speculated on the replacement of sabertooths by modern felids. The modern felids were better adapted to hunt the modern swift ungulate fauna, and also the slower sabertooths, regarded as a competitor and as a personal danger, perhaps were more easily killed by early human hunters.

The Viverridae

The viverrids are very primitive in their morphology and it is hard to draw a boundary between them and the miacids (Ewer 1973). It is possible that the viverrids are descended from an early Tertiary stock that does not include any known miacids (Martin 1989). The diversification in the Viverridae has involved emphasis on either the carnassial shear or the crushing molars. Also, some forms developed terrestrial adaptations like the mongooses, which are known from the early Oligocene. The viverrids never reached North America, which suggests that their center of radiation was at relatively low latitudes, thus making it difficult to traverse northern Asia and the Bering land bridge (Martin 1989).

The Hyaenidae

The hyaenids probably arose from an advanced viverrid just like the felids. *Ictitherium* from the middle Miocene still has two upper molars but they are are slightly reduced and the premolars show some enlargement of the central cusps (Ewer 1973). *Ictitherium* was about the size of a small canid. Later forms established the trend toward reduction of the molars and lengthening of the carnassial blade. Among these forms, larger species and cursorial adaptations evolved (Werdelin & Solounias 1991). In the Pliocene there was a split into two major clades. One included forms that developed highly cursorial adaptations and the shearing function was increased at the expense of the bone-cracking premolars. The second group, to which the extant genera except *Proteles* belong, has developed the bone-cracking premolars at the expense of the shearing blades. There is also a clear trend towards size increase in the latter group (Werdelin & Solounias 1991). The hyaenids were abundant in Eurasia and Africa but did not reach North America until the Pliocene. The reson for this is probably that the scavenging niches were occupied by the bone-cracking canids, and the first hyaenids in North America belonged to the group that had a reduced bone-cracking dentition (Werdelin & Solounias 1991).

Discussion and conclusions

There has been an overall increase in world carnivore diversity since the early Tertiary (Savage 1977; Martin 1989). One factor that may be responsible for this increase is faunal interchange. The Carnivora entered Africa in the early Miocene and South America in the late Miocene (Martin 1989). Before the entry of the Carnivora, the hyaenodonts were occupying the carnivore niche in Africa, while borhyaenids and large phororhachid birds were the carnivores of South America. The appearance of new adaptive zones is probably responsible for much of the increase in diversity. The earliest cursorial adaptations are seen in *Hyaenodon* species in the early Oligocene. But it was not until the early Miocene, when there was a change from tropical forests to tropical savannas, that cursorial adaptations (e.g. in canids) became common. It was also during this time that digging adaptations appeared.

However, these new adaptive zones were induced by climatic changes, and it is apparent from the fossil record that there are only a limited number of solutions to a carnivorous way of life in terrestrial mammals. There are few, if any, really odd fossil forms that are without parallels today. The saber-toothed forms are of course conspicuous, but many authors believe that they were only adapted to take considerably large prey. Anyway, it is worth considering that there are many large herbivores today that are free from predation due to their size. Also, hunting sucsess of extant carnivores is nearly always dependent on whether they are able to catch up with their prey; the hunters must also be able to kill their prey, but that is usually the secondary demand. The fact is that there are few carnivores today that rely on ambush to catch prey of larger size. Forest felids like the tiger and jaguar are the closest to ambush predators today, although the attack is commonly initiated by a short dash. Also, the bears may rely on their strength if they accidentally come upon a large animal like an elk. Probably active hunting is a strategy preferred by predators with endothermy. If then cursorial adaptations are considered, it is obvious that the cursors of the Oligocene were quite different from their modern counterparts. But they can hardly be assigned to different adaptive zones as the difference is due to coevolution with their prey. The evolution of cursorial adaptations appear to be a relatively slow process (e.g. compared to the evolution of large size). Probably this is due to the complex nature of cursorial adaptations. There must be simultaneous modifications in different parts of the skeleton and of the muscles if the effect is to be positive (e.g. a shorter in-lever arm requires a stronger muscle; the proportions of the limb segments seem to be more important than the total length of the limb). It is easy to believe that the cheetah has reached perfection in short sprint ability, but it is not an old form, it appeared in the late Pleistocene. Earlier cheetah-like forms have been considered less cursorial. Admittedly, it would be very interesting to know the future evolution of the cheetah.

That there are few adaptive types of carnivores is also supported by the cycle of extiction and reevolution of adaptive types (Martin 1989). These cycles created chronologically separated but very similar, although often distantly related, carnivores. For instance, coyote-like carnivores evolved in the Amphicyonidae. The nimravids are not closely related to the Felidae according to Martin (1989). Sabertooths evolved several times in different families and also separately in the same family. Bone-crackers have evolved in hyaenids and canids.

Hypercarnivorous dentition with no chrushing teeth has evolved several times and seems to be a rather fast process. Early nimravids had already lost the crushing teeth. When the postcarnassial teeth have been lost, it is highly unlikely that they will reappear. There have neither been any nimravids nor any felids with crushing teeth during their history. Unlike felids, canids have evolved a diversity of dietary types, including some hypercarnivorous species. The early specialization in felids has probably made them a less versatile group than canids. Van Valkenburgh (1991) quotes as an example the rapid diversification of canids as compared to felids in the South American Pleistocene.

Finally, all the modern terrestrial carnivores belong to the order Carnivora, and this has not always been the case. One may speculate whether new carnivorous forms can evolve in other orders at the present time of mammalian evolution. Some primates add meat to their diet and I find it quite easy to imagine active predators at least in arboreal monkeys. Their prey could include other monkeys and even species of the Carnivora. The arboreal locomotion of monkeys differs very much from that of arboreal species of the Carnivora so carnivorous monkeys would represent a truly new adaptive type. A necessary modification for successful hunting in monkeys would be a wider gape for effective killing and wounding bites.

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