

The Manus

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

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

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

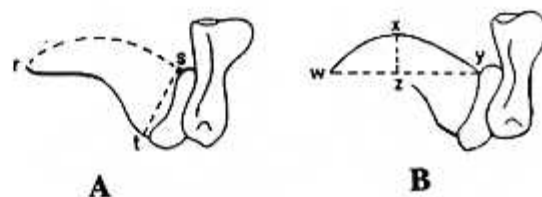


Fig. 6. Measurements of the ungual phalanx. The depth (A): Length of dorsal arc rs divided by depth at ungual base st . The curvature (B): Maximum arc height xz divided by length wy (from Van Valkenburgh 1987).

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

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

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

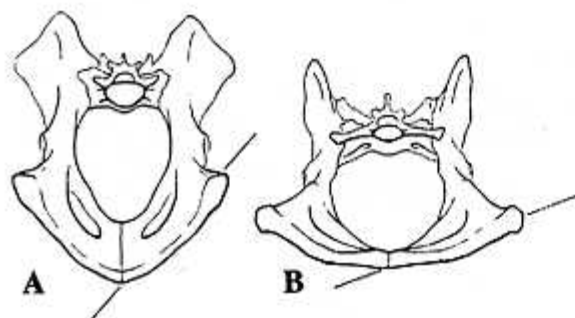


Fig. 7. Posterior view of the pelvis in (A) the raccoon and (B) the fox, showing the orientation of the ischium (from Jenkins & Camazine 1977).

The pelvis and hindlimb

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

The pelvis

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

The femur

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

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

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

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

Fibula and tibia

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

Pes

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

The tail

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

The skull

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

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

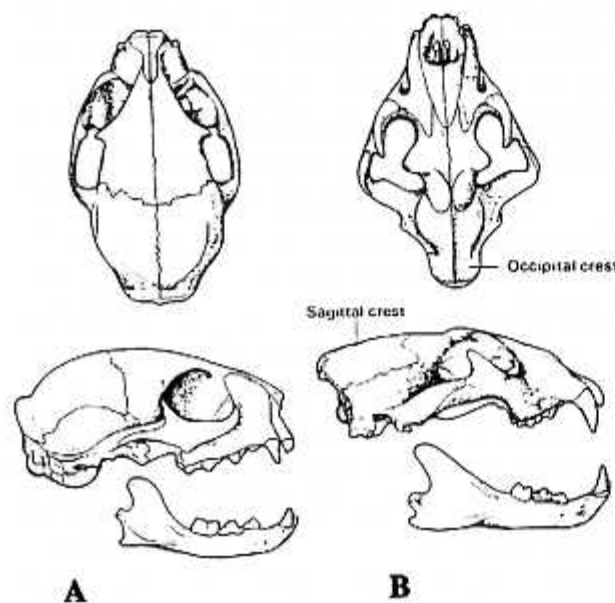


Fig. 8. The skull of (A) the small jaguarundi and (B) the big lion (from Ewer 1973).

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

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

Dentition

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

Incisors

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

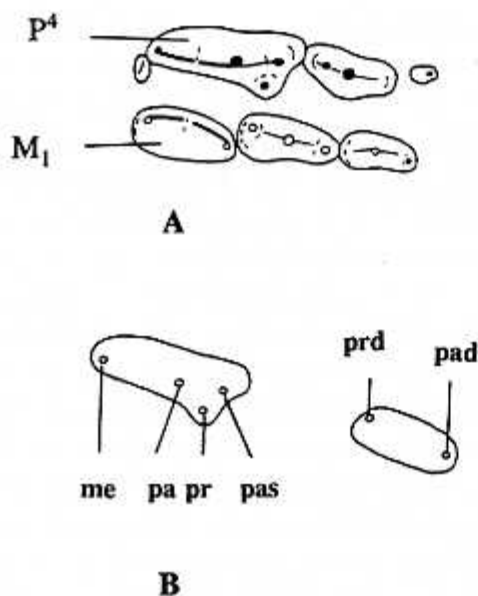


Fig. 9. (A) The carnassials (arrowed) in *Felis*. (B) The cusps of right upper carnassial: me metacone, pa paracone, pr protocone, pas parastyle. (C) The cusps of left lower carnassial: prd protoconid, pad paraconid (from Savage 1977).

Canines

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

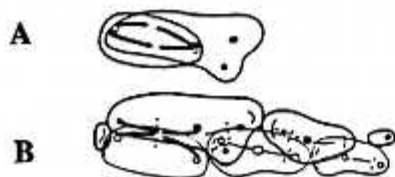


Fig. 10. The carnassials (A) at the beginning of occlusion and (B) in full occlusion (from Savage 1977).

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

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

The premolars except P^4

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

The carnassials

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

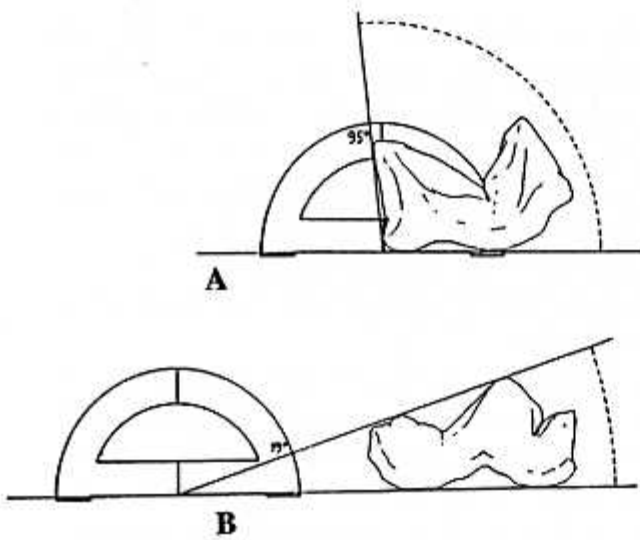


Fig. 11. Measurements of the angle *a*. The lower carnassial of (A) a highly carnivorous species and (B) a much less carnivorous species (from Crusafont-Pairo & Truyols-Santonja 1956).

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

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

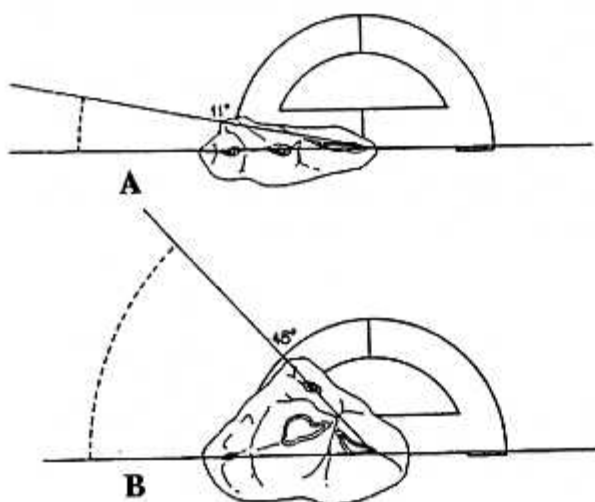


Fig. 12. Measurements of the angle *b*. The upper carnassial of (A) a highly carnivorous species and (B) a much less carnivorous species (from Crusafont-Pairo & Truyols-Santonja 1956).

crushing function. The general appearance of the P^4 of these species is therefore more like that of a molar. Crusafont-Pairo & Truyols-Santonja (1956) found two angular measurements useful for a study of the evolution of the carnassials. Angle *a* measures the relationship between the height of the protoconid and the length of the talonid on M_1 (high values = high protoconid relative to length of talonid) (Fig. 11). Angle *b* measures the development of the protocone on P^4 (high values = well developed protocone) (Fig. 12). For primitive Eocene species angle *a* is around 45° 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.

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

The molars except M_1

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

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

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

The jaws

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

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

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

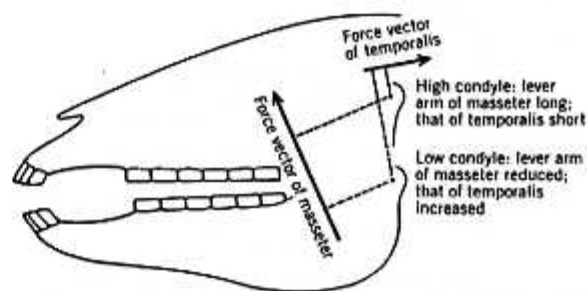


Fig. 13. Jaw mechanics in relation to the position of the mandibular condyle (from Hildebrand 1987).

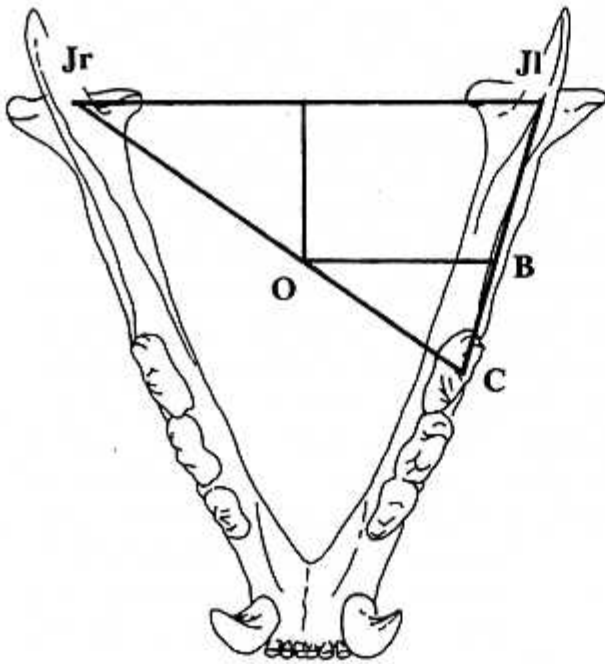


Fig. 14. Model of the lower jaw. Jr = right joint, Jl = left joint, C = carnassial tooth, O = optimal position of the resultant force, B = bite point posterior to carnassial tooth (simplified from Greaves 1983).

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 otherwise 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

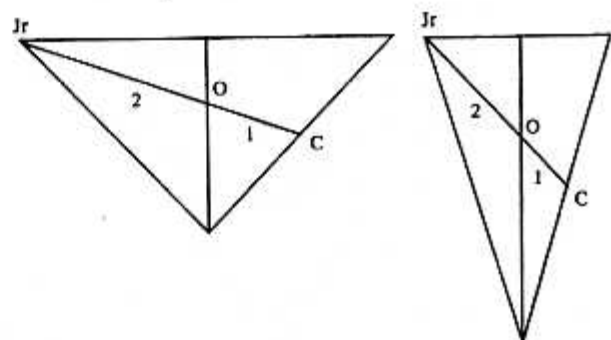


Fig. 15. Diagrams of two lower jaws of different proportions. Jr = right joint, C = carnassial tooth positioned at the midpoint of the left ramus, O = optimal position of the resultant force. Point O will divide the jaw lever JrC in the ratio of 1:2 irrespective of the proportions of the lower jaw.

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 advantageous 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

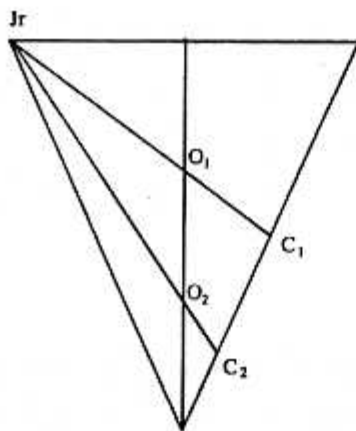


Fig. 16. Diagram of the lower jaw. The in-lever JrO_2 is more advantageous than the in-lever JrO_1 .

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.

The jaws and dentition of saber-toothed forms

Saber-like upper canines have evolved independently at least four times among mammalian carnivores: in nimravid (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 functional, 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)

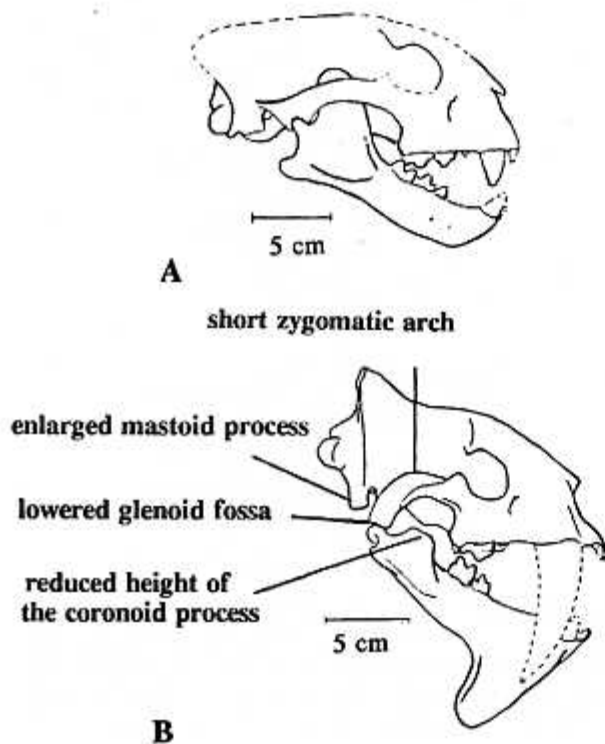


Fig. 17. The skull of (A) an early felid and (B) the sabertooth *Eusmilus* (from Emerson & Radinsky 1980).

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

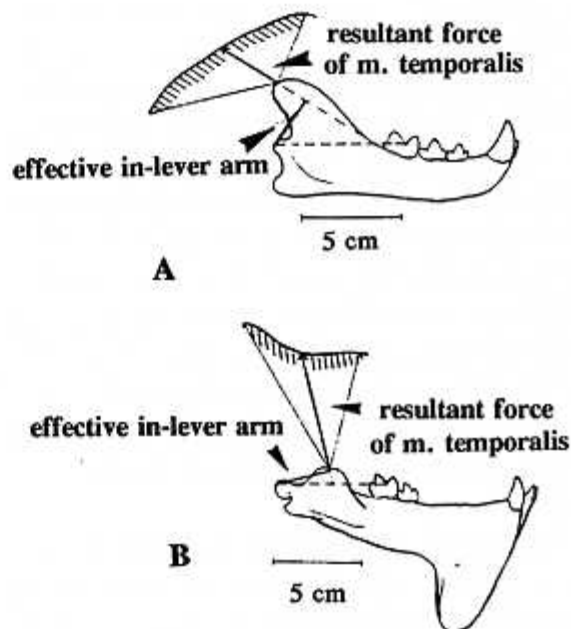


Fig. 18. The effective in-lever arm and resultant force of *m. temporalis* in (A) a modern felid and (B) the sabertooth *Eusmilus* (from Emerson & Radinsky).

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.

The evolution and fossil history of mammalian carnivores

Mesozoic

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 preyed 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 particularly well known from North and South America

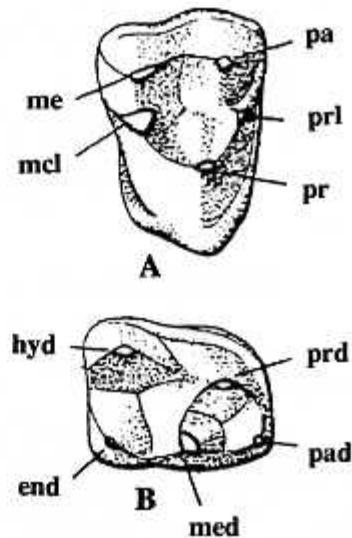


Fig. 19. The tribosphenic molar. (A) The right upper molar: **me** metacone, **pa** paracone, **mcl** metaconule, **prl** protoconule, **pr** protocone. (B) The left lower molar: **hyd** hypoconid, **prd** protoconid, **end** entoconid, **med** metaconid, **pad** paraconid (from Romer 1966).

(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 receives 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.

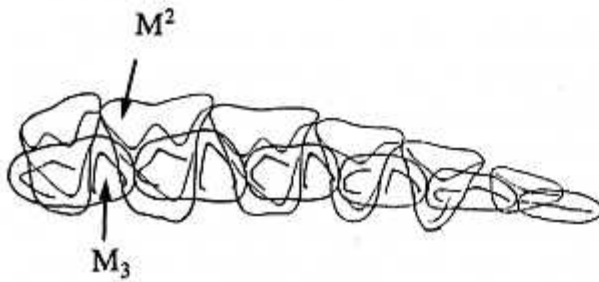


Fig. 20. Occlusal diagram showing main shearing surfaces in an early therian dentition (from Butler 1946).

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 zygapophyses 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 bicipital 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

