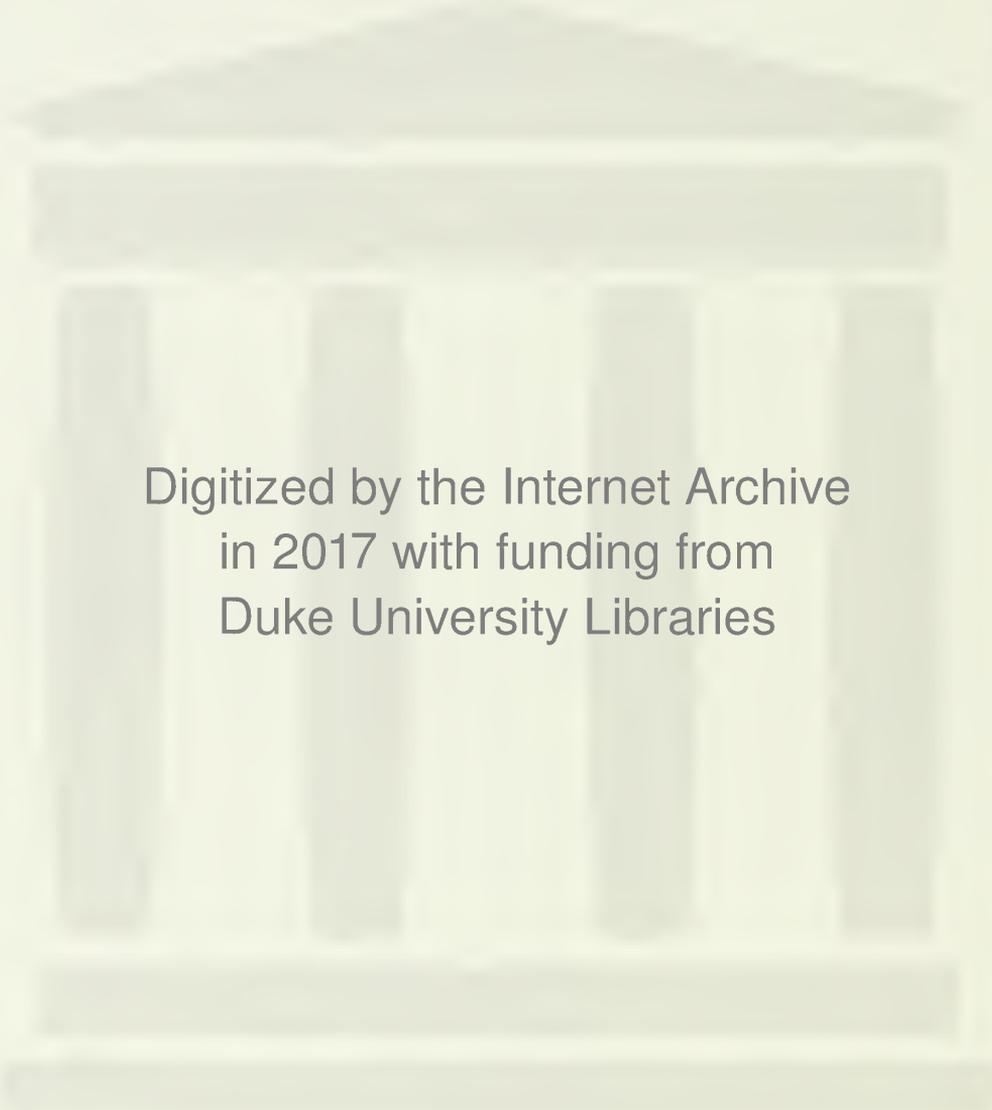


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**PHYLOGENETIC, BEHAVIORAL, AND DIETARY CONSTRAINTS
ON FELID MASTICATORY MORPHOLOGY**

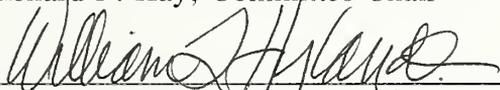
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**A thesis submitted in partial fulfillment of the requirements for
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INTRODUCTION AND SCOPE OF PAPER

A key innovation in the evolution of the mammalian masticatory apparatus was the ability to achieve medial-lateral excursion of the jaw and unilateral occlusion, leading to more precise occlusal patterns and therefore more effective comminution of food items. The masticatory apparatus and jaw movements of certain "primitive" extant mammals (e.g., *Didelphis* (Crompton & Hiiemae, 1970; Hiiemae & Crompton, 1971; Crompton et al., 1977) *Echinosorex* (Turnbull, 1970), *Tenrec* (Oron & Crompton, 1985) and *Suncus* (Dötsch & Dantuma, 1989)) have been used as models to recreate the masticatory movements of early mammals. Using these animals as a basis for the primitive mammalian condition, one can assess the relative derivation of the masticatory patterns of other mammals. As a consequence of the remodeling of the primitive mammalian condition over the course of mammalian evolution, "specialized" groups of animals such as carnivores, ungulates, and rodents can be identified based on various masticatory adaptations (Turnbull, 1970; Weijs, 1994). The adaptations in the masticatory apparatus of these specialized mammals is often linked to constraints imposed by the material properties of their diet. For example, herbivorous animals have a very coarse diet that requires extensive processing by the dentition; this has led to the association between a coarse diet and certain features of the masticatory system such as a "high" temporomandibular joint, a dominant masseter and medial pterygoid, a large mandibular angle, a high degree of lateral excursion of the mandible, and simultaneous occlusion along the length of the grinding tooth row. In contrast, carnivores, which in general process their food very little, have a "low" temporomandibular joint, a dominant temporalis, a small mandibular angle, a low degree of lateral excursion of the mandible, and back to front occlusion of the specialized carnassial teeth.

While generalizations such as these hold true for many animals, exceptions immediately come to mind, and make it apparent that divisions on the basis of diet alone are not adequate. In fact, apart from studies of the dentition, very few clear links between diet (i.e., "herbivorous" versus "carnivorous") and masticatory morphology have been demonstrated (Weijs, 1994); in many instances, numerous other aspects of animals' lives come into play, some of which may be equally, if not more important, in determining the morphology and function of the masticatory apparatus. Such factors include:

- * **Evolutionary history:** Barring extreme convergence and reorganization of the masticatory apparatus, the masticatory morphology of closely related animals, regardless of their dietary habits, will tend to be more similar than the masticatory morphology of more distantly related animals.

- * **Relative size and development of sense organs:** Due to the close proximity of the sensory and masticatory systems, the relative development of structures associated with vision, olfaction, and hearing may affect the structure of the masticatory apparatus.

- * **Relative brain size:** The size of the brain imposes certain limits on muscle attachment area; these limitations can be overcome, to some degree, by modifications in the osteological structure of the braincase, such as pneumatization and the development of bony crests.

- * **Behavior associated with food acquisition:** The mode of prey capture and the forces exerted during predatory behavior will affect the morphology of the masticatory apparatus.

- * **Non-masticatory functions:** Grooming, social display, intraspecific combat, and other aspects of animals' ecology may affect the morphology of the masticatory apparatus.

An instructive example of the effect of these numerous factors on the morphology of the masticatory apparatus is found among the members of the order Carnivora. The masticatory apparatus of carnivorans differs little from the primitive mammalian condition, in which the temporalis is the dominant jaw adductor. Their specialized dental morphology stands in stark contrast to many features of their masticatory apparatus that show only weak correlations with diet (Weijjs, 1994). For example, while herbivory is common among ursids and procyonids and is reflected in their derived dental morphology, their muscle orientation is very similar to the typical carnivoran pattern, indicating that phylogenetic influence, in this case, has a more profound effect on masticatory morphology than does diet. The influence of phylogeny is also apparent in the myrmecophagous "aardwolf" (*Proteles*), which shows clear dietary adaptation in the reduction of the cheek teeth, but which retains the muscular and cranial morphology more typical of its strong-jawed, bone-cracking relatives, such as *Crocota* and *Hyaena*. In felids, which are clearly dentally adapted to a diet of meat, cranial and masticatory morphology are also strongly influenced by the relative size of the sense organs (most notably the enlargement of the eyes and reduction of the snout), and by the demands of their predatory lifestyle.

Among carnivorans, felids are unique in possessing a relatively low degree of dietary, behavioral, and morphological diversity. While there are some exceptions, felids are in general solitary, nocturnal hunters, strict meat-eaters, and, while they are among the most variable extant carnivorans in terms of body size (Gittleman, 1985), they are extremely conservative in their overall morphology. They are easily distinguished from other carnivorans by their globular cranium, shortened rostrum, and their large, forward-facing orbits. With minor variations in detail, this gestalt appears in other carnivorans and non-carnivorans and is therefore insufficient for use in family

diagnosis, which instead relies primarily on the morphology of dental and basicranial characters.

In this paper I intend to examine the phylogenetic, behavioral, and dietary factors that influence the masticatory morphology of felids. A review of this topic is quite extensive because both the morphology and behavior of modern felids is so well studied. This great attention paid to felids has yielded a great deal of information that bears on the correlation between various aspects of their masticatory function and their ecology. Before examining this work in detail, it is necessary to place felids within a frame of reference by briefly outlining their taxonomic affinities and acknowledging the phenomenon of convergence between felids and other mammals.

CARNIVORANS AS EUTHERIANS

The late Cretaceous paleoryctid *Cimolestes* is often regarded as a "basal carnivore", although the likelihood that it is a paraphyletic assemblage of many different taxa makes precise determinations of relationships difficult (Flynn et al., 1988). The carnassial dentition of *Cimolestes* indicates that it was specialized for carnivory, but that it was clearly different from the later Carnivora and Creodonta in having its carnassial dentition spread along the length of the post-canine tooth row. In the Carnivora and Creodonta, this carnassial function is restricted to specific loci of the post-canine tooth row (M^1/M_2 or M^2/M_3 in creodonts, P^4/M_1 in carnivorans). Along with features of the tarsus and internal cranium, this restriction of carnassial function has been used to unite the Creodonta and Carnivora as sister taxa (McKenna, 1975; Flynn et al., 1988), although some workers claim that strong evidence in support of such a union is lacking (Wyss & Flynn, 1993). Other workers have proposed grouping the Carnivora with various fossil ungulates within the Ferungulata (Simpson, 1945),

with various "insectivores" (Lillegraven, 1969; Van Valen, 1969; McKenna, 1975) with the Archonta (or some subset thereof) (Goodman et al., 1985; Shoshani, 1986), or simply as somehow closely related to all eutherians other than edentates and pangolins (Novacek & Wyss, 1986). This latter claim is perhaps most revealing, as the relationship of the Carnivora to other eutherians is anything but clear-cut, and for many workers remains as one of the more persistent problems in mammalian systematics (Flynn et al, 1988; Wozencraft, 1989; Wyss & Flynn, 1993 and references therein).

Thankfully, the divisions within the confines of the Carnivora are much better understood and more widely agreed upon. Carnivorans are divided into two major clades, the Caniformia and the Feliformia (Wozencraft, 1989; Wyss & Flynn, 1993). The Caniformia consists of two subdivisions, the Ursoidea (Otariidae, Ursidae) with their more primitive bullar morphology and pattern of basicranial arterial circulation, and the more derived Canoidea (Canidae, Mustelidae, Phocidae, Procyonidae). The monophyletic Feliformia or Feloidea includes the Felidae, Herpestidae, Hyaenidae, and Viverridae and is united on the basis of various basicranial, bullar, postcranial, and dental features. Within this group, felids and hyaenids are most closely related and are distinct from the viverrids; these three families in turn are further distinguished from the more primitive herpestids (Wozencraft, 1989).

Since its inception, the Carnivora has undergone numerous changes in membership and affinities, and has acquired its own extensive vocabulary. Because this paper does not intend to serve as a review of the systematics of the Carnivora, use of these terms is limited, and a detailed explanation of them is unwarranted. However, in addition to ordinal and familial terms, the general terms "carnivoran" and "carnivore" will both be used, and may be subject to misinterpretation if not defined at the outset. "Carnivoran" will be used when referring to taxa within the order Carnivora (regardless

of dietary habits) and "carnivore" will be used to denote any meat-eater, without reference to its taxonomic position. Generic and specific names within the Felidae follow the classification by Wozencraft (1989).

FELIDS AS CARNIVORANS

The boundaries of the Felidae are unquestioned, although divisions at the generic level may be complicated by the morphological uniformity within the family (Flynn et al., 1988). Dental characters related to the reduction and simplification of the cheek teeth, and cranial characters related to high bite force and well-developed visual abilities (Radinsky, 1981a) are diagnostic for the family, and contrast markedly with the generalized nature of the postcranial skeleton. Within the Felidae, there is a clear division between the large and small cats based on a suite of cranial and dental characters (Werdelin, 1983) as well as differences in the hyoidean apparatus associated with roaring abilities (Pocock, 1916a).

When both living and extinct cats are considered, a division can be made between paleofelids, an entirely extinct group with sabertooth adaptations, and the neofelids or "true cats", which includes the extant felids and their ancestors, as well as another distinct carnivoran group with sabertooth adaptations.

The paleofelids appeared during the Oligocene, and are often regarded as the earliest true felids, although some workers claim they should be relegated to a distinct family within the Carnivora, the Nimravidae, (Martin, 1980; Baskin, 1981; Hunt, 1989). Within this group is found a striking array of sabertooth adaptations, including one of the most specialized forms, *Barbourofelis* (cf. Turnbull, 1978), which survived until about 7 mya.

The neofelids trace their roots to ancestors with short canines, such as the civet-like *Proailurus* from the Miocene of France (de Beaumont, 1964; Thenius, 1967). The

civet-like features of this genus are the basis of the claim that felids arose from small, arboreal viverrid-like carnivores (Martin, 1989). The neofelids underwent a major diversification in the late Miocene, which produced the modern felids as well as several genera of sabertooths.

CONVERGENCE AND THE FELID "ECOMORPH"

Within the Carnivora, Martin (1989) recognized a series of "ecomorphs", or morphologically similar forms which have appeared over the course of carnivoran evolution and which are the result of similar selective pressures. He identifies cat-like, civet-like, mustelid-like, and dog-like forms. While some of the convergences observed within the Carnivora may be attributable to close relationship, the similarity in adaptive schemes observed between mammals of widely disparate orders suggests that the range of morphological adaptations to a carnivorous lifestyle is in fact quite narrow, resulting in a much higher probability of convergence (Martin, 1989). The cat-like ecomorph has appeared not only among felid carnivorans, but in other carnivoran families and other mammalian orders.

Perhaps the most bizarre and most widely studied incidence of convergence of cat-like forms is that of the "sabertooths" which evolved independently at least four times in three mammalian orders: in hyaenodontid creodonts (*Apataelurus*, *Machaeroides*), borhyaenid marsupials (*Thylacosmilus*), paleofelid carnivorans (*Dinictis*, *Hoplophoneus*, *Eusmilus*, *Barbourofelis*), and neofelid (*Pseudaelurus*, *Homotherium*, *Smilodon*) carnivorans. These forms converge markedly in terms of their cranial and masticatory morphology, an area studied in depth by Emerson and Radinsky (1980).

Perhaps less dramatic is the convergence seen between neofelids and the Malagasy fossa, *Cryptoprocta ferox*. The fossa is the most highly adapted of all the viverrids to a purely predaceous lifestyle (Ewer, 1973), and converges strongly on several aspects of felid morphology in its reduced dental formula ($I^{3/3}.C^{1/1}.P^{3/3}.M^{1/1}$), well-developed carnassials, and loss of postcarnassial elements. Placement of the fossa within the Felidae has been suggested on the basis of these dental characters, as well as cranial features such as a globular skull and foreshortened rostrum which result in an overall cat-like appearance (Milne-Edwards & Grandidier, 1867; Gregory & Hellman, 1939; de Beaumont, 1964; Hemmer, 1976a). However, numerous cranial, postcranial and soft tissue structures place it firmly within the Viverridae (Petter, 1974; Wozencraft, 1989), the family to which it was allocated when first described (Bennett, 1833).

In identifying a mustelid-like ecomorph, Martin (1989) grouped together animals possessing a suite of features associated with a semi-fossorial way of life. While felids and mustelids do not converge in this aspect of their lifestyles, members of one mustelid subfamily, the Mustelinae, do converge strongly on felid dental and masticatory morphology in possessing elongate, blade-like carnassials and short, powerful jaws (Ewer, 1973).

MASTICATORY ANATOMY AND FUNCTION IN THE FELIDAE

DENTAL MORPHOLOGY

While the P^4/M_1 carnassial pair is the defining dental character for the Carnivora, felids are further distinguished from other carnivorans on the basis of simplification of the dentition, particularly the carnassials, which assume the shape of two simple blades. This extreme modification of the carnassials in felids has led to the

notion that felids have the highest shearing capacity among carnivorans. This statement however, is misleading and should instead state that felids have simplified their carnassials to the point where simple two-bladed shearing is the only method of fragmenting food items. Other carnivorans, such as procyonids, for example, possess carnassials that are secondarily derived for omnivory. These teeth are-not as blade-like as those of felids, but they are likely more adapted to shearing function, for the combined length of their numerous small shearing crests is likely quite high compared to felids, which have a single shearing crest extending along the length of the tooth. Uniformity across the Felidae in development of shearing capacity to the exclusion of crushing capacity is a reflection of the low dietary diversity within the family, and is in marked contrast to many other carnivoran families, in which differences in diet result in markedly different dental morphology and specialization between taxa (Ewer, 1973). In addition to possessing a simplified dentition which emphasizes shearing over crushing capacity, felids as a group are characterized by robust canines, reduced postcarnassial elements, and a reduced dental formula through the loss of both pre- and post-carnassial elements. These dental adaptations are closely tied to the strict diet of vertebrate flesh, the high bite force, and the quick dispatch of struggling prey that characterize the feeding and predatory habits of felids.

The chisel-shaped incisors of felids usually bear three small cusps (Savage, 1977), and are unique in that they are arranged in a straight transverse row, rather than the convex arcade typical of most mammals (Flynn et al., 1988). The incisors help the canines maintain a firm hold on struggling prey during capture, and are used in feeding to remove fur or feathers from a kill and to remove bits of flesh from bones (Kitchener, 1991).

Typically, a large diastema separates the diminutive incisors from the larger, mediolaterally compressed canines, which dominate the anterior dentition, and which, along with the carnassials, are the main functional components of the felid dentition. This diastema varies greatly in size among the Felidae; it is nearly absent in the cheetah (*Acinonyx*), and largest in the clouded leopard (*Neofelis*) (Pocock, 1916b). The mediolateral compression (anteroposterior thickening) of the canines in carnivorans and many other mammals indicates that the canines are stronger in resisting bending in the parasagittal plane. This is a reflection of the fact that normal jaw adduction occurs more in the parasagittal than the transverse plane, and bending moments produced during feeding activities such as biting and ripping flesh from a kill bend the canines in the parasagittal plane (Van Valkenburgh & Ruff, 1987). However, felid canines differ from those of other carnivorans in being markedly stronger in resisting bending in the parasagittal plane (Figure 1a) (Van Valkenburgh & Ruff, 1987).

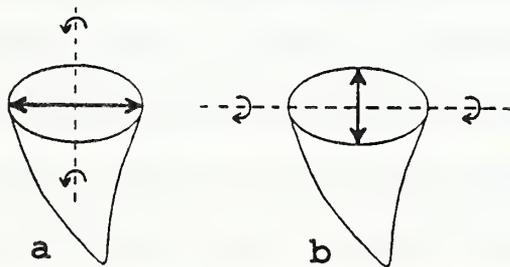


Figure 1. Schematic drawing of felid canine teeth, showing:
a) AP diameter (arrow), which reflects strength in bending in the parasagittal plane (experienced during jaw adduction and ripping flesh from a kill)
b) mediolateral diameter (arrow), which reflects strength in bending in the transverse plane (independent of orthal jaw movement; inflicted by struggling prey).
 (after Van Valkenburgh & Ruff, 1987).

This increased canine robusticity is a biomechanical necessity for felids, because their killing bites are deeper and more powerful than those of other carnivorans such as canids (Radinsky, 1981a), and therefore their canines experience greater bending moments in the parasagittal plane during jaw adduction than do those of other carnivorans. Additionally, the canines of felids are more robust mediolaterally than those of other carnivorans, and are therefore relatively stronger in resisting bending in the transverse plane (Figure 1b). This finding is not, however, attributable to jaw mechanics alone, since orthal movements of the jaws produce bending primarily in a parasagittal plane, and produce little if any bending in the transverse plane. Instead, the prey capture and killing techniques of felids have been found to account for their mediolaterally robust canines (Van Valkenburgh & Ruff, 1987).

In capturing prey, felids use one of two types of killing bites, depending on the relative size of the prey item (Leyhausen, 1979). Relatively small prey is killed instantly by a bite to the nape of the neck, which dislocates the cervical vertebrae, severs the spinal cord, and may crush the back of the skull (Kruuk & Turner, 1967; Schaller & Vasconcelos, 1978). The thick neck musculature and in certain cases the presence of horns or antlers in large prey precludes the use of the nape bite, because the canines are (usually) unable to penetrate deeply enough to reach the vertebral column, and because horns and antlers are a source of potential injury to the predator. Instead, relatively large prey are killed by a throat or snout bite, which occludes the trachea and results in eventual death by suffocation (Haglund, 1966; Kruuk & Turner, 1967; Grobler, 1981; Sunkist, 1981). In some instances (i.e. capture of medium size prey by *Acinonyx*) the throat bite may cause instantaneous death as a result of spinal cord damage, rather than by suffocation (Ewer, 1973). All these methods of prey dispatch result in large, unpredictable oblique and mediolateral stresses on the canines

due to a) the likelihood of tooth-bone contact and/or b) the struggles of prey, and require that the canines of felids be buttressed against large forces exerted both in the parasagittal and transverse planes (Van Valkenburgh & Ruff, 1987).

With the obvious exception of P⁴, felid premolars are quite simple and unspecialized, and vary in number between species. The loss of the anterior premolars in some species of felids is the source of variation in the familial dental formula (typically I^{3/3}.C^{1/1}.P^{3/2}.M^{1/1}.), which varies from a minimum of 26 to a maximum of 30; P² is regularly absent in some short-faced species of certain genera (*Lynx*, *Caracal*, *Profelis*, *Prionailurus*, *Acinonyx*, *Otocolobus*), and P₂ may also be absent as an anomaly in other species (Ewer, 1973). The upper fourth premolar is remarkably altered from the primitive carnivoran condition in its elongate shape, the reduction and anterior displacement of the protocone, and the reorientation of the cutting blade into an anteroposterior plane (Figure 2). The elongate, antero-posteriorly oriented P⁴

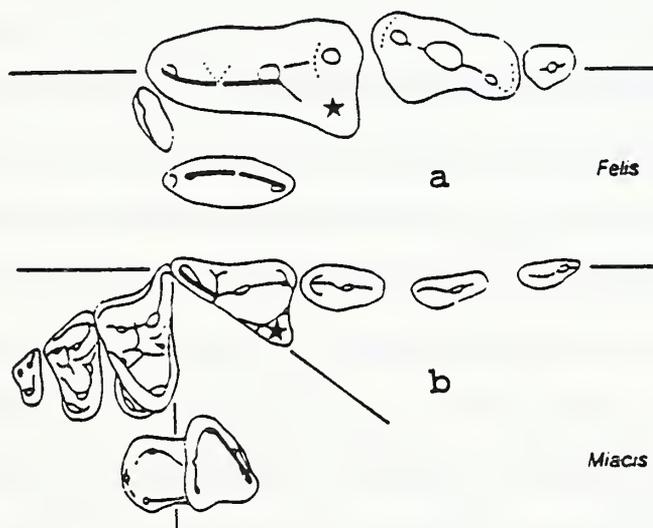


Figure 2. Occlusal view of carnassial dentition in: a) a felid (*Felis*), and b) a primitive carnivoran (*Miacis*), showing the difference in the size and placement of the protocone (★), and orientation of the shearing blades (heavy lines). (From Savage, 1977)

occludes with a similarly oriented and designed M¹. The blade of P⁴ extends from the paracone anteriorly to the metacone posteriorly, is convex lingually in occlusal view, and bears a "carnassial notch" (Matthew, 1910) at its center. The blade of M¹ extends from the paraconid anteriorly to the protoconid posteriorly, is convex labially in occlusal view, and also bears a carnassial notch. This opposing convexity of the lingual and labial surfaces of the P⁴ and the M¹, respectively, and the opposing concavity of the carnassial notches permits only limited points of contact between the blades; as the teeth occlude, the point contacts move along the blade and converge to create a lozenge shaped space, which locks food in preparation for shearing, and prevents the food item from slipping anteriorly.

The loss of crushing functions, the simplification of tooth pattern, the loss of postcarnassial elements, and the increasing efficiency of the carnassials are the main trends in the evolution of carnivore molars (Savage, 1977). Among carnivorans, felids are extreme examples of these trends. Over the course of felid evolution, all post-carnassial molars have either been lost or are reduced to mere pegs in the maxilla, leaving only one molar as a functional component of the dentition.

While the evolution of the felid dentition is characterized by the trend toward simplification of the dentition through emphasis on shearing over crushing abilities and the reduction in size, number, and complexity of teeth, this does not imply that the jaw movements effecting the function of these teeth are simple in any way. Rather, the proper functioning of the dentition requires a muscular setup sufficient in size and orientation to exert a high bite force at the canines, while also effecting fine occlusal adjustment necessary to engage the carnassials, thus ensuring their proper function and protecting their easily fractured blades from damage caused by malocclusion.

MUSCULAR ANATOMY

Turnbull's (1970) classic comparative study of mammalian masticatory musculature sets up a dichotomy between "generalized" and "specialized" masticatory arrangements. He identified "generalized" mammals (such as *Didelphis* and *Echinosorex*), which are presumed to be similar to primitive mammals, in that the temporalis is the dominant jaw adductor, and the "pterygoids" (which he grouped together) function as accessories to the temporalis. This condition is contrasted with the "specialized" masticatory morphology of mammals such as carnivores, ungulates and rodents. While carnivores rank as a specialized group relative to the generalized mammalian masticatory condition, they do so largely by virtue of their specialized dentition, as the relative size, orientation, and attachment pattern of their masticatory muscles is quite similar to that of more generalized mammals.

The masticatory musculature of the domestic cat (*Felis catus*, *Felis domesticus*) is well described in the literature and is often used as a model for all felids, or as a generalized carnivore model. While there are slight differences in the masticatory musculature among felids, these differences are for the most part a result of allometric differences seen in the large range in felid body size, and do not have marked effects on the relative size and orientation of the masticatory muscles. Some of these differences are obvious upon inspection of a large and small felid skull (Figure 3).

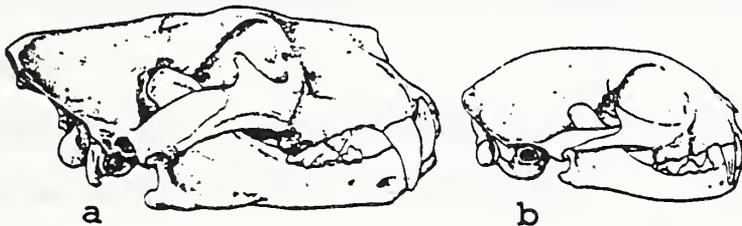


Figure 3. Comparison of skull proportions in felids of different body sizes.
a) *Panthera leo* b) *Lynx rufus* (From Vaughan, 1972)

Because brain size does not increase at the same rate as does body size, the braincase of large felids provides relatively less surface area for muscular attachment. Therefore, large and small felids differ in the degree to which crests and tuberosities provide attachment area for masticatory muscles (Ewer, 1973). With this in mind, the descriptions below are used as a rough model for all felids, although they draw largely from descriptions of the musculature of the domestic cat, particularly works by Toldt (1905) and Turnbull (1970).

Temporalis

The temporalis is the largest of the masticatory muscles in felids, accounting for roughly 50% of the total weight of the jaw musculature (Turnbull, 1970). It originates from the sides of the braincase and along the frontal and parietal bones dorsally, along the lambdoidal crest posteriorly, and along the zygomatic arch, zygomatic portion of the frontal, and ligamentous postorbital bar anteriorly (Figure 4a,c). The temporalis is divided into superficial, deep, and zygomatic portions, all of which attach either directly or indirectly to the coronoid process, and fan out to cover much of the lateral surface of the braincase. These distinct parts of the temporalis clearly have very different functions by virtue of their very different orientations. The posterior part of the temporalis has been singled out as a particularly important muscular division in carnivorans (Smith and Savage, 1959; Scapino, 1981) that functions during predation to prevent dislocation of the TMJ as a result of ventrally and anteriorly oriented forces.

Masseter

The second largest of the jaw adductors in felids is the masseter, which consists of a deep and superficial portion, and which originates from the ventral border of the zygomatic arch to insert onto the mandible (Figure 4a,d). The masseter is variously described as being divided into four lobes at both insertion and origin (Toldt, 1905) or

at its origin only (Turnbull, 1970). The deep layer of these four masseteric lobes insert into the masseteric fossa on the lateral surface of the mandibular ramus, but the superficial layers of the four lobes have no direct connection with the mandible. Instead, they insert onto a tendinous raphe which joins the masseter and medial pterygoid, and which continues posteriorly to attach to the auditory tube. Toldt (1905) described this raphe as a unique adaptation among carnivorans that allows the masseter to be well-developed without a concomitant increase in the size of the mandibular angle.

In animals with a large masseter, including most herbivores, the mandibular angle is expanded to provide a large attachment area for the masseter (Radinsky, 1985). While increasing the potential size and therefore the power of the masseter, this increase in the size of the mandibular angle may also limit gape, as extremely wide jaw opening may risk occlusion of important cervical structures (Herring, 1972). For animals in which wide gape is not an important consideration, such as herbivores, one would expect constraints on the maximum size of the mandibular angle to be minor. A notable exception to this prediction is found in certain artiodactyls in which wide gape is important in social display; in this case, wide gape is achieved despite the large size of the mandibular angles by flaring them laterally (Herring, 1975). A similar lateral shift of the angular process has also been proposed as a means of achieving the particularly large gape typical of many sabertooths (Matthew, 1916). Carnivorous mammals have the most stringent gape requirement among mammals, due to their need to engage the posteriorly situated carnassials during prey consumption (Herring & Herring, 1974). If in fact gape is constrained by the risk of occluding important cervical structures, one would expect the mandibular angle, and therefore the size of the masseter in carnivorous mammals to be highly constrained in maximum

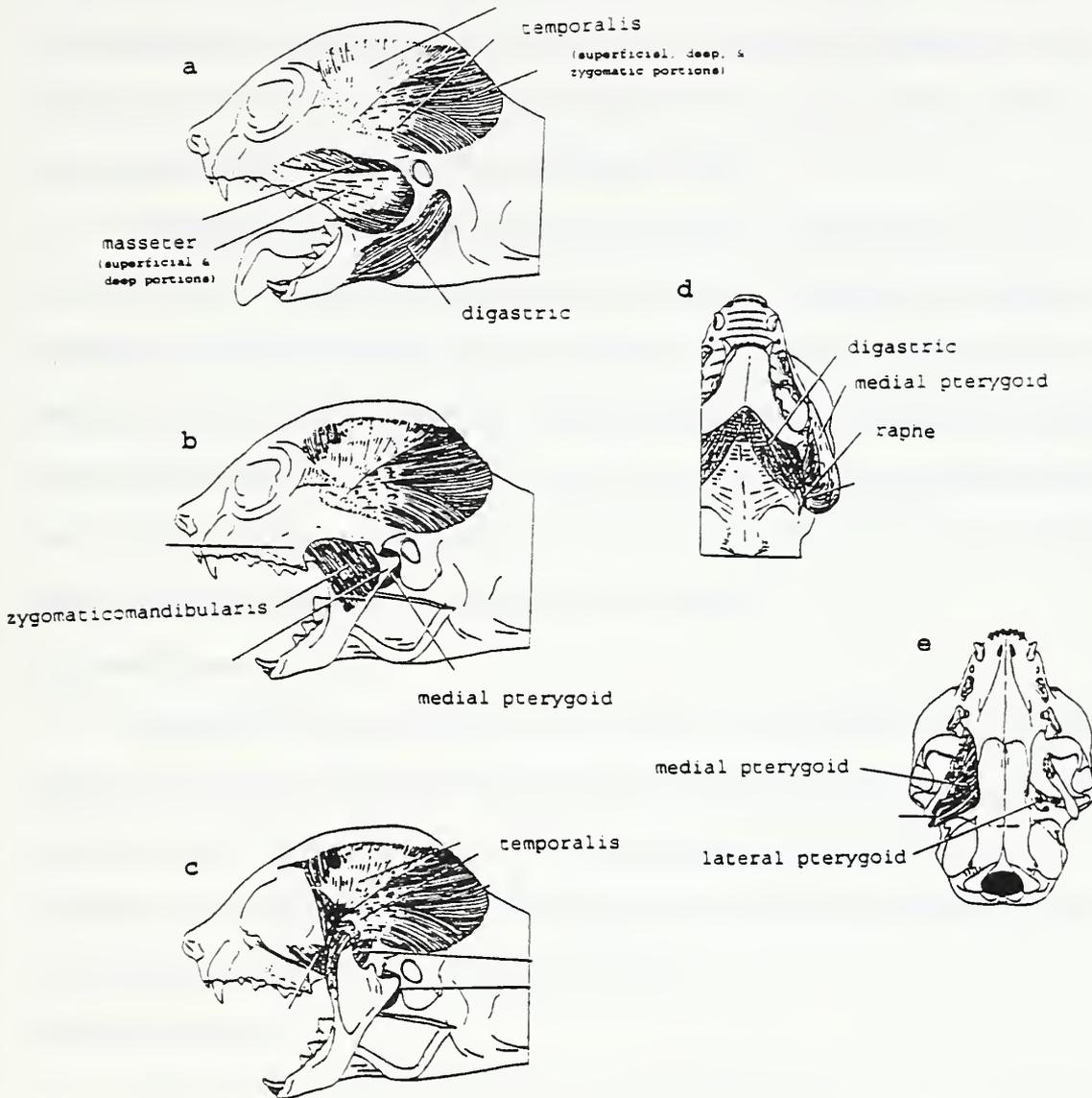


Figure 4. Masticatory musculature of *Felis*. (From Turnbull, 1970)

- a) Lateral view showing superficial aspect of temporalis, masseter and digastric.
- b) Lateral view with masseter and digastric removed, showing zygomaticomandibularis and medial pterygoid.
- c) Lateral view with zygomatic arch and zygomaticomandibularis removed, exposing the insertion of temporalis.
- d) Ventral view of superficial musculature, showing the raphe between the medial pterygoid and masseter.
- e) Ventral view of deep musculature, showing the medial and lateral pterygoids.

size. For felids, which have the largest relative masseter size among carnivorans (Buckland-Wright, 1978) this limitation might be overcome by the tendinous raphe described above, which provides a large attachment area for the masseter without a concomitant increase in the size of the mandibular angle.

An alternative view of the function of this raphe is that of Becht (1953), in which the "loop" formed by the connection of the masseter and medial pterygoid via the raphe can slide posteriorly when a particularly large food item is placed at the posterior dentition, thus increasing maximum gape. Although the superficial masseter and medial pterygoid do indeed form a loop-like structure, the fixed placement of the deep masseter within the masseteric fossa results in the anterior border of the masseter being fixed, rather than mobile, relative to the last molar.

Zygomatocmandibularis

The zygomatocmandibularis arises from the medial surface of the zygomatic arch and the temporal aponeurosis, and at points of close contact, may fuse with the masseter and the temporalis. Fibers of the zygomatocmandibularis insert on the mandible in the masseteric fossa, and converge with fibers of the temporalis to insert on the coronoid process of the mandible (Figure 4b).

Medial Pterygoid

The medial pterygoid has a deep and a superficial portion, both of which arise from the ventral border of the infratemporal fossa and portions of the pterygoid fossa. From these points of origin, its fibers extend posteriorly and laterally to insert on the medial face of the angular process, ascending ramus of the mandible, and the aforementioned tendinous raphe connected to the superficial masseter (Figure 4b,d,e).

Lateral Pterygoid

The lateral pterygoid is the smallest of the masticatory muscles in the cat, consisting only of a small bundle of fibers that arises beneath the foramen rotundum and extends posteriorly to insert just inferior and medial to the mandibular condyle (Figure 4d). The muscle consists of two similarly constructed divisions which are tendinous at one end and form a fleshy muscular belly at the opposite end. These two divisions have opposite orientations such that the fleshy end of one division lies against the tendinous end of the other division, a configuration which is functionally important, as the muscle fibers rotate through 180 degrees from origin to insertion. By having a muscle belly adjacent to a tendon, rather than another muscle belly, the muscle can contract without "wringing out its fluids" (Turnbull, 1970).

The lateral pterygoid is a feeble and, as it turns out, underutilized muscle in felids and, presumably other carnivorans (Turnbull, 1970). The lateral pterygoids on both the working and the balancing sides are silent during opening and are active only during the end of the closing phase, when they become active simultaneously with the digastrics (Gorniak & Gans, 1980). Their primary function is to aid the digastrics in jaw abduction; this is in contrast to their role in other animals in producing bilateral protrusive movements (absent in felids due to the structure of the temporomandibular joint) or lateral shifts of the mandible (accomplished in felids primarily by the medial pterygoid, deep temporalis, and zygomaticomandibularis) (Gorniak & Gans, 1980). However, the asymmetric activity of the working- and balancing-side lateral pterygoids indicates that this muscle likely plays a role in effecting close approximation of the carnassials. In felids, the lateral pterygoid has no attachment to the temporomandibular joint capsule and articular disc (Noble & Creanor, 1992), whereas most mammals show

such an attachment pattern as a reflection of the developmental history of these three structures (Harpman & Woollard, 1938).

Digastric

The digastric morphology of carnivorans is well-known as a result of a study (Scapino, 1976) which attempted to dispel the notion that relative to other mammals, the attachments and proportions of the digastric are highly conservative within the Carnivora. While it is true that the digastric of carnivorans is generally large and columnar and spans the distance between the cranium and mandible, some carnivorans differ markedly from the typical carnivoran pattern. In some aquatic or semi-aquatic species of several carnivoran families (otariidae, phocidae, mustelidae) the digastric is large and powerful as an adaptation for rapid abduction of the jaw immediately prior to prey capture. Felids differ from other carnivorans not in the relative size of the

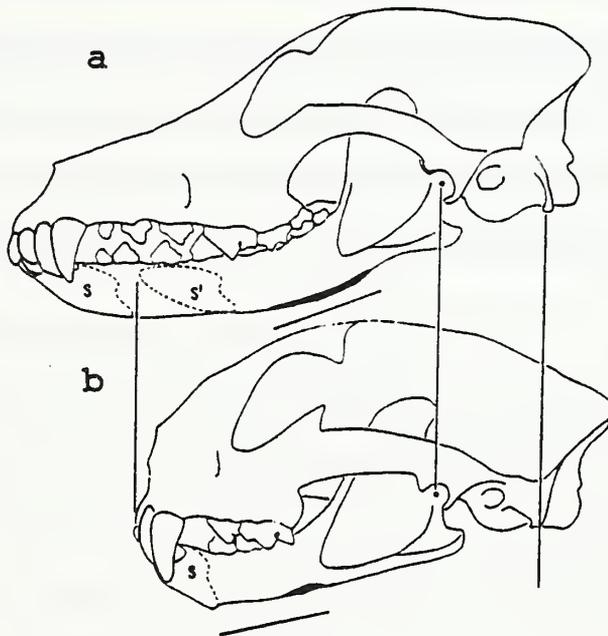


Figure 5. Lateral view of skull of *Canis familiaris* (above) and *Felis concolor* (below). (From Scapino, 1976) a) attachment areas of digastric to lateral face of mandible (shaded area), b) total length of digastric attachment (solid bar), c) position of mandibular symphysis (S), and d) position of mandibular symphysis in *Canis* if facial skeleton length is hypothetically shortened to equal that of *Felis* (S').

digastric, but in its positioning, which is altered as a result of their reduced jaw length and stringent gape requirements.

In felids, the digastric arises posterior to the tympanic bulla, and extends anteriorly medial to the masseter to insert on the mandible (Figure 4a,d,e). At roughly its midpoint, it is divided into two muscle bellies by an often indistinct tendinous intersection. As shown in Figure 5, the insertion of the digastric (solid bar below mandible) in felids differs from the typical carnivoran pattern, represented by *Canis*, in that it extends anteriorly to reach the symphyseal area; the same is not true for canids, even when the length of the facial skeleton is altered to equal that of the felids.

It has been suggested that this anterior insertion of the digastric arose in felids in conjunction with the development of a shortened facial skeleton as a means of achieving a wide gape (Scapino, 1976). Because the shorter facial skeleton of felids relative to canids requires a wider gape in order to achieve a similar degree of separation of the canines and carnassials, the insertion of the digastric is shifted anteriorly; this has the effect of lengthening the muscle and increases the distance through which the muscle can maintain tension to effect abduction.

TEMPOROMANDIBULAR JOINT (TMJ)

In determining the potential movements of the jaw it is necessary to examine not only the placement and direction of pull of the masticatory muscles, but also the gross structure of the TMJ, for its construction plays a large, perhaps even primary, role in determining the degree of mandibular movement. The temporomandibular joint of felids, as in all carnivorans, consists of an elongate, cylindrical mandibular condyle which fits into a correspondingly shaped glenoid fossa on the zygomatic process of the temporal bone. The bony structure of the glenoid fossa creates a trough for the transversely expanded mandibular condyle and therefore grossly limits motion at the

joint to the orthal movements of abduction and adduction. A well-developed postglenoid process and a small anteglenoid process form the posterior and anterior boundaries of the glenoid fossa. Interposed between the glenoid fossa and mandibular condyle is a thin articular disc that divides the joint capsule into superior and inferior compartments and is attached to the joint capsule (Fox, 1965; Gorniak & Gans, 1980).

The emphasis on the hinge-like motion of the felid mandible in descriptions of carnivoran jaw mechanics (e.g., Smith & Savage, 1959; Becht, 1954) obscures the fact that movement at the TMJ is quite complex, with rotation and translation occurring about three axes (Gorniak & Gans, 1980). While the primary jaw movement is rotation about a transverse axis passing through both mandibular condyles (as in jaw adduction), other movements, although very minor in terms of displacement, are necessary for engaging the carnassials. Most notably, this is accomplished by mediolateral translation of the condyles within the glenoid fossae. Despite the stout ante- and postglenoid processes, anterior displacement of one condyle can occur when the mandible rotates about a second axis passing vertically through the opposite condyle. A third axis of rotation is defined when the working side mandible encounters resistance in jaw closing. In this situation, the working side of the mandible is (for the most part) immobilized and rotates about its long axis as the balancing side continues to close.

In a felid skull, movement about these three axes is easy to demonstrate, and the TMJ can be disarticulated with little effort. In living felids, however, the degree to which these motions occur is restricted by the joint capsule and its ligamentous thickenings, which provide the major source of stability for the joint when gape is wide. In this situation, the capsular ligaments limit the degree of jaw rotation and translation about all three axes; they are particularly well developed in areas lacking bony support, and aid in preventing dislocation of the joint. Stout medial and lateral

capsular ligaments form the side walls of the joint capsule, and along with the posterior capsular ligament, limit transverse translation of the condyles and unilateral rotation of the mandibular rami about their long axes. The mandible is buttressed against posterior displacement by the stout postglenoid process, while anterior displacement is prevented by the posterior capsular ligament and the small anteglenoid process. The anterior wall of the joint capsule is much thinner and weaker than are the other walls which bear well-developed capsular ligaments, and it probably contributes little to limiting motion. In addition to the capsular ligaments, stability of the TMJ is achieved by the surrounding masticatory musculature, most notably the posterior parts of the temporalis and masseter (Scapino, 1981).

When considering the importance of capsular ligaments and muscles in maintaining the integrity of the joint, it is important to note that these elements limit various motions only when the jaw is opened wide (i.e., the tips of the canines are separated). As the jaw closes and the teeth near occlusion, the role of restricting motion at the TMJ is shifted from capsular to dental elements. As the tips of the canines pass one another, placement of the lower canines into the diastema between the upper canines and incisors limits translation of the condyles within the fossae, and prevents rotation of the mandibular rami about their long axes. As closing proceeds, the overlapping carnassial blades further restrict these motions while also preventing anterior displacement of the condyles.

Studies of the TMJ have attributed its position relative to the mandibular tooth row (i.e. "high", as in herbivores, or "low", as in carnivores) to improving the mechanical advantage of masticatory muscles (Smith & Savage, 1959) or effecting simultaneous occlusion of the dentition (Davis, 1964). In one of the first major studies of mammalian jaw mechanics, Smith & Savage (1959), state that the location of the

TMJ above the horizontal level of the mandibular tooth row in herbivores increases the moment arm and therefore the mechanical advantage of the masseter muscle. In contrast, the TMJ of carnivorous mammals lies in the same plane as the mandibular tooth row, resulting in a reduced moment arm and decreased mechanical advantage of the masseter, and an increased moment arm and mechanical advantage of the temporalis.

In his study of mammalian jaw joint position, Greaves (1974) presents an alternative to previous studies which focus on the relationship between the TMJ and the mandibular tooth row. He examines the rationale that movement of the TMJ results in increased mechanical advantage of certain masticatory muscles, and finds this to be an unsatisfactory explanation for TMJ position. In discussing the problems of this explanation, he focuses on ways (other than movement of the TMJ) in which increased mechanical advantage of masticatory muscles can be effected, the conservatism of the basicranial region, the importance of the relative distances between mandibular and maxillary tooth rows and the TMJ, and the TMJ position relative to discrete functional loci of the dentition, rather than relative to the tooth row as a whole.

The mechanical advantage of individual masticatory muscles can be altered in a number of ways, including changing the relative positions of the TMJ and tooth row, changing the jaw geometry and/or changing the patterns of muscle attachment. While Smith & Savage (1959) focus on the fact that elevation of the TMJ above the mandibular tooth row increases the mechanical advantage of the masseter (as in herbivores) and depression of the TMJ results in increased mechanical advantage of the temporalis (as in carnivorous mammals), Greaves points out that simply elevating the TMJ may not be the "best" method of imparting increased mechanical advantage. Remodeling of the mandible by altering its overall length, the morphology of the

coronoid and/or angular processes, and/or the orientation of the tooth row can change the moment arms and mechanical advantage of various muscles just as effectively as moving the TMJ. Furthermore, the complexity of the TMJ, its close proximity to other important basicranial structures, and the consistent relationship between the position of the TMJ relative to the maxillary tooth row in both fossil and recent mammals are cited as evidence for the conservatism of the TMJ and the low probability that sufficient selection pressure exists to warrant its movement (Greaves, 1974).

In the case of carnivorans, Greaves asserts that consideration of the position of the TMJ above, below, or on the same plane as the mandibular tooth row is a moot point. Rather, the important consideration is the difference in the position of mandibular versus maxillary tooth rows relative to the TMJ. If these distances are equal, as shown in Figure 6a, occlusion will occur simultaneously along the entire

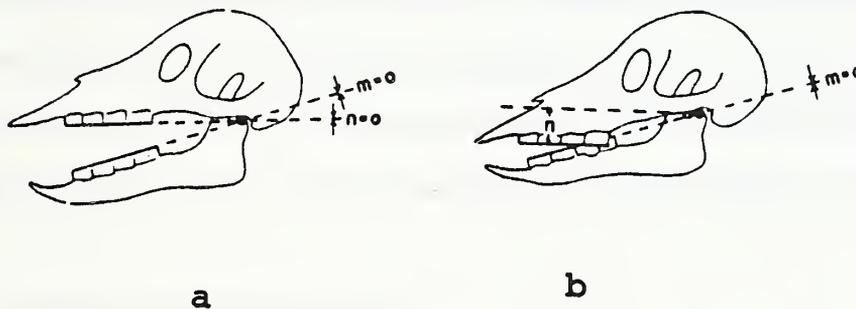


Figure 6. The effect of TMJ-tooth row distances on occlusion. (m =distance from surface of mandibular tooth row to TMJ; n =distance from surface of maxillary tooth row to TMJ.) (From Greaves, 1974)
 a) Simultaneous occlusion of the tooth rows occurs when the distance between the TMJ and both tooth rows is equal. b) Scissor-like occlusion occurs when the distance between the TMJ and both tooth rows is unequal.

length of the tooth row. If these distances are different, as shown in Figure 6b, initial occlusion occurs posteriorly and proceeds anteriorly in a scissor-like fashion. Thus, Greaves argues that whether the TMJ lies above, below or in the same horizontal plane as the mandibular tooth row is of little consequence; as long as the distances between the tooth rows and the TMJ are different, the carnassials can be correctly positioned and effect the scissor-like occlusion necessary for proper carnassial function.

Furthermore, Greaves states that in carnivorans, the positioning of the TMJ relative to the entire tooth row is not as critical as is the positioning of the TMJ relative to the carnassial blades, since this is the area where the shearing action occurs. In carnivores, he argues, the distance between the TMJ and the shearing blades of the upper and lower carnassials should be unequal (Figure 6) in order to effect scissor-like occlusion from back to front. However, this statement seems to be an unnecessary addition to Greaves' argument, because as far as the proper functioning of the carnassials is concerned, the presence of carnassial notches allows the carnassials to accomplish the task at hand regardless of the manner of occlusion. Because each carnassial possesses a carnassial notch, approximation of these teeth, whether in scissor-like or simultaneous occlusion, creates a lozenge shaped space that traps the food item between the carnassials and prevents it from slipping anteriorly.

MANDIBULAR MORPHOLOGY

The tight link between felid predatory behavior and the strength of dental elements was noted earlier in the discussion of the morphology of felid canines, which are able to resist the heavy mediolateral and anteroposterior loading encountered in predation and feeding. A similar adaptation is also present in felid mandibles, which possess greater strength in resisting bending in oblique, parasagittal, and transverse

planes than those of other carnivorans, a reflection of the greater loads applied to their jaws in prey capture and consumption (Radinsky, 1981a; Biknevicius & Ruff, 1992). Greater strength of the mandibular corpus in resisting bending in the parasagittal plane is a structural necessity to counter the deep, powerful, and (often) sustained killing bites of felids. The strong canine bite of felids is a consequence of the greater mechanical advantage of the felid temporalis compared to the temporalis of canids, for example (Radinsky, 1981a; Van Valkenburgh & Ruff, 1987). Because a strong canine bite results in a high degree of corpus bending (Hylander, 1986), buttressing of the felid mandible allows it to resist greater bending forces than is the case for other carnivorans.

The powerful canine killing bite of felids relative to that of other carnivorans is usually attributed to their relatively shorter jaw length (Kruuk & Turner, 1967; Eaton, 1970; Kruuk, 1972; Schaller, 1972; Ewer, 1973; Leyhausen, 1979; Van Valkenburgh & Ruff, 1987). The abbreviation of the felid skull results in a reduced moment arm of resistance, increasing the mechanical advantage of the masticatory muscles, and increasing bite force. Therefore, given a canid and a felid with similarly sized muscles, the felid will be able to produce more force at its canines (Van Valkenburgh & Ruff, 1987).

Greaves (1985) also addresses the notion of higher bite force in felids, but does so in a rather different fashion and reaches conclusions which contradict those of Van Valkenburgh & Ruff (1987). He states that the mechanical advantage of the jaw lever system in carnivores is unaffected by changes in jaw length because all carnivorans possess similar jaw geometry regardless of the length to width relationship of the jaws. Instead, the primary factor influencing bite force is the relative jaw width among carnivorans. Greaves states that in a felid and a canid of the same jaw *length* (Figure

7a,b & 7c,d), the geometry of the jaw lever system is the same, while overall body size is tremendously different. The larger body size of the felid translates into a difference

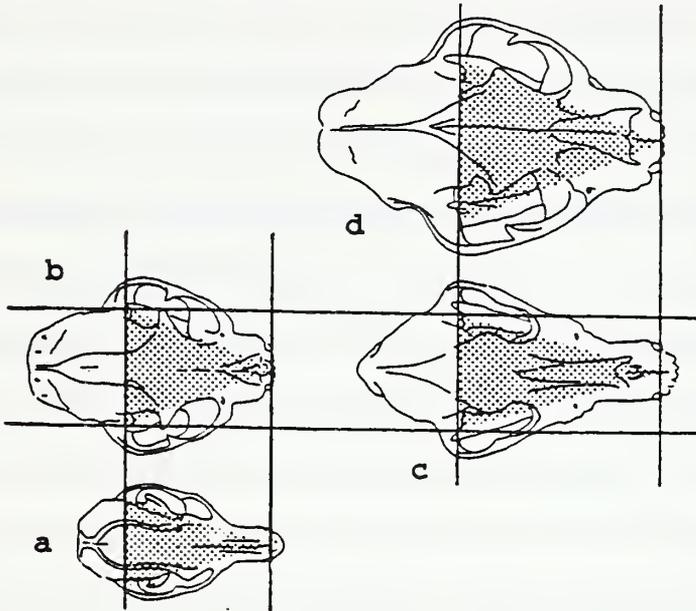


Figure 7. Dorsal views of carnivoran skulls; shaded area represents jaw length, vertical lines indicate equal jaw length, horizontal lines indicate equal jaw width. (From Greaves, 1985) a) gray fox (*Urocyon cinereoargenteus*) b) bobcat (*Lynx rufus*) c) domestic dog (*Canis familiaris*) d) mountain lion (*Felis concolor*)

in absolute muscle mass and a much greater bite force than that of the canid. In a felid and a canid of similar jaw *width* (7b,c) overall body size is similar, as is the absolute masticatory muscle mass. Thus, the similarity in jaw geometry and muscle mass translates into a similar bite force for these two animals.

The way in which the hemimandibles are joined at the midline has been investigated in depth for carnivorans (Scapino, 1981) and has been found to vary considerably depending on factors such as body size, diet, dental morphology and the demands of prey capture. The anatomy of the mandibular symphyses of carnivorans can be grouped into four classes, based on details of the hard and soft anatomy of this region, and in many carnivorans, these divisions have clear functional correlates. The

symphyseal anatomy of felids is apparently a consequence of the masticatory demands imposed upon them by virtue of their body size.

Stated in the simplest of terms, the mandibular symphysis is the site where the symphyseal plates of the hemimandibles meet in the midline and are bound together by a three-walled capsule. Ligamentous thickenings of this capsule and ligaments spanning the distance between the symphyseal plates help lend stability to the joint; the size and degree of development of these ligaments is a reflection of the various stresses imposed on the symphysis. A strong superior ligament resists the potential for separation of the joint dorsally, while the weaker inferior and posterior capsular ligaments limit the potential for separation ventrally and posteriorly. Also aiding in resisting separation forces and providing joint stability are transverse and cruciate ligaments, which span the distance between the symphyseal plates. A fibrocartilage pad is variably present anterosuperiorly between the opposing plates, and is surrounded posteriorly and inferiorly by a series of interdigitating rugosities and concavities of the symphyseal plates, which, depending on their height, provide added stability to the joint. The anatomy of these features and the degree to which they lend stability to the joint are the grounds for dividing the symphyses of carnivorans into four groups (Scapino, 1981).

Class I symphyses are characterized by symphyseal plates that are flat or which bear slight interdigitating rugosities and concavities; a conspicuous fibrocartilage pad intervenes between the symphyseal plates and fills a significant portion of the joint surface. Class II symphyses are similar to class I symphyses, but higher rugosities and deeper opposing concavities result in more interdigitation of the symphyseal plates. All symphyses of small cats are classified as class I symphyses, while class II symphyses are absent among felids. Class III symphyses have a very small or absent fibrocartilage pad and increased interdigitation of the symphyseal plates compared to class I or class

II symphyses, and are present in large cats. Class IV symphyses are totally fused, and, with the possible exception of a partially fused symphysis in *Felis marmorata*, are not present in felids.

The grouping of nearly all felids into two symphyseal classes is apparently a consequence of body size. All small cats have a class I symphysis, which allows slight flexion and mobility at the joint, while large cats (with the possible exception of *Acinonyx*) have a class III symphysis, which is much stiffer, and has little mobility compared to a class I symphysis.

Scapino (1981) attributed this difference in symphyseal anatomy to the external and internal effects of scaling encountered by large versus small cats. External effects include the fact that as animals undergo a linear size increase, the increase in the mass and load-bearing capacity of their supporting structures is positively allometric (Yamada & Evans, 1970; Anderson et al., 1979). Thus, large felids consuming large prey must exert relatively greater masticatory forces than small felids consuming small prey, because the supporting tissues of the larger prey are more resistant to fragmentation.

Intrinsic factors influencing symphyseal anatomy concern the maintenance of geometric similarity across a wide range of body sizes. If a felid were to double in size and maintain functional equivalence (i.e. the ability to exert isometric tension at optimum muscle lengths), muscle cross-sectional area would necessarily have to increase by a factor of eight, or muscle pinnation patterns would have to be drastically rearranged (Scapino, 1981). Because a marked increase in cross-sectional area does not occur, and the internal architecture of the muscle is much the same in large and small felids, the masticatory strength of large felids is expected to be relatively less than that of small felids (Davis, 1962). This, in conjunction with the aforementioned finding that

the prey of large felids is more resistant to fragmentation, leads to the conclusion that large felids are at a dual disadvantage; while the structural elements of their prey require them to generate a relatively larger masticatory force, they are less able to do so because of the limitations associated with their larger body size.

As a way of countering this dual disadvantage, Scapino (1981) states that large felids have acquired a stiff (class III) symphysis as a replacement for the primitive carnivoran condition of a flexible (class I) symphysis. Because a stiff symphysis is better able to transmit force between the balancing and working sides of the mandible (Hylander, 1977, 1979; Beecher, 1977, 1979), large felids are able to recruit more balancing side muscle force than are smaller felids which have a relatively less stiff symphysis.

JAW MECHANICS

While most recent studies of mammalian jaw mechanics assume that occlusion is unilateral, and that both jaw joint reaction forces and muscular activity are bilateral (although not equal), many early studies failed to acknowledge all of these facts, and therefore were unable to explain the forces generated during mastication (e.g. Gysi, 1921; Davis, 1955; Smith & Savage, 1959; Turnbull, 1970).

In a study of the spectacled bear (*Tremarctos ornatus*), Davis (1955), states that the typical class III lever model typically used to describe the mechanics of the vertebrate jaw is an oversimplification, particularly in the case of carnivorans, and presents a new model of the carnivoran jaw as a modified class I lever. Under a class III lever system (Figure 8a), the forces exerted by the masticatory muscles produce a dorsally oriented force at the jaw joint (the fulcrum) that exceed the physical limits of the joint and lead to failure. As an alternative, modeling the carnivoran jaw as a couple (Figure 8b) has the effect of reducing forces acting at the joint to zero,

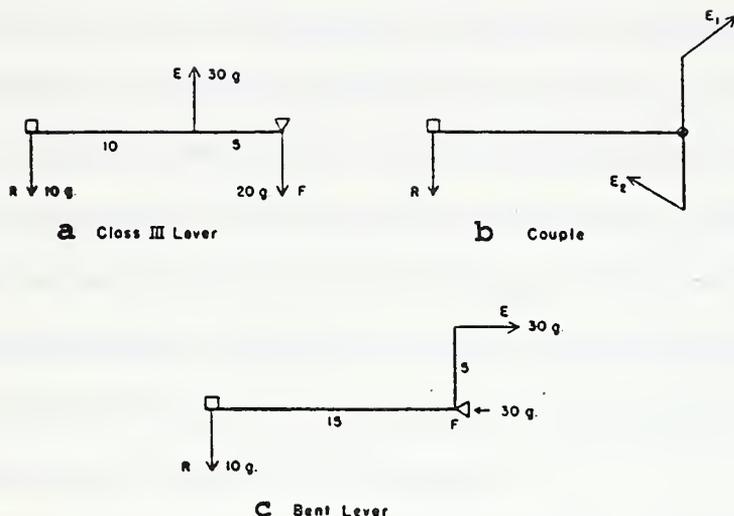


Figure 8. Three lever models of mammalian jaw mechanics. R=resistance (force exerted at dentition); E=effort exerted by masticatory muscles; F=force at temporomandibular joint. (From Davis, 1955)

assuming that the temporalis and masseter exert equal forces which act to rotate the joint around a transverse axis. However, this alternative is also not completely satisfactory given the fact that the temporalis and masseter do not in fact exert equal forces. Because the temporalis is larger and much more powerful in carnivorans than is the masseter, Davis presents a bent lever (or modified class I lever, Figure 8c), which has a better mechanical advantage than the class III lever and which is a better approximation of the true function at the joint. Because the bent lever model (Figure 8c) does not reduce the force at the fulcrum to zero, as does the couple, the large postglenoid process of carnivorans is needed to resist the large posteriorly directed force at the joint.

Turnbull (1970) slightly modified Davis' findings, by pointing out that the couple is indeed an appropriate model, especially for the Carnivora, because of the synergistic action of the masseter and medial pterygoid. He also presents the "useful

power" formula as a way of addressing jaw mechanics in a comparative light.

Combining aspects of muscle characteristics such as relative proportion (mass, weight, or volume), position, cross-sectional thickness, attachment points, shape, leverage, and direction of pull results in a single value for a given muscle, which can be used to make elementary comparisons of the mechanical efficiency of masticatory muscles between taxa. Using this formula, Turnbull finds *Felis* to be easily distinguished from other taxa on the basis of the small size and underutilization of the pterygoid musculature, a characteristic he finds is typical for carnivorans.

These and other early analyses of mammalian jaw mechanics focus on the function of the dentition, masticatory muscles, and jaw joint on only one side of the head. Such models are clearly not adequate in predicting jaw mechanics, as studies of mastication in many mammals have demonstrated that masticatory muscles are active bilaterally (Dessem, 1989; Hiiemae, 1976; Kallen and Gans, 1972; Hylander, 1979; Gorniak & Gans, 1980; Weijs & Dantuma, 1981) and that there is bilateral resistance of reaction forces at the temporomandibular joints (Hylander & Bays, 1978, 1979; Hylander, 1979). Evidence such as this led to the belief that considering the jaw in lateral perspective is not always the ideal way to address jaw function, and prompted several workers to advocate looking at jaw function in "less traditional" ways, such as from a frontal (Hylander, 1975), or occlusal perspective (Greaves, 1978), thus incorporating the bilateral function of the muscles, dentition, and TMJ.

In particular, Greaves (1983, 1985) proposed a bilateral model for studying aspects of the function of the carnivore masticatory apparatus. First developed for ungulates (Greaves, 1978), and then expanded and applied to carnivores (Greaves, 1983, 1985), this model considers the relative magnitude and position of resultant jaw muscle forces, the relative positions of masticatory muscles and teeth along the length

of the mandible, and the tradeoff between gape and bite force. Greaves' model assumes only three points of contact between the mandible and skull during mastication: one between each mandibular condyle and the corresponding glenoid fossa, and one at the vertex of the carnassial notch on the working side; these three points demarcate the "triangle of support" (Greaves, 1978). The model also assumes that the forces exerted by the jaw adductors are resolved into a resultant force acting in a plane perpendicular to that of the three contact points. Figure 9 shows a felid mandible with various points mentioned in the text indicated by the appropriate letters. Under the conditions of this

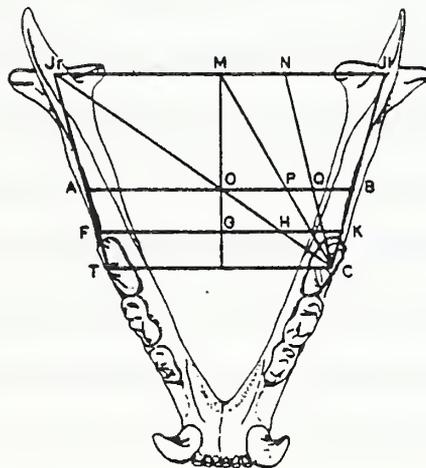


Figure 9. Dorsal view of the lower jaw of *Felis catus*. Jr, Jl=right and left jaw joints; c=carnassial tooth. (From Greaves, 1983)

model, bilaterally symmetrical action of the jaw adductors acting at points A and B produces a maximum resultant force at point O, midway between the mandibular rami near the point of muscle insertion. The jaw lever is represented by the line JrOC, which

connects the left carnassial and right mandibular condyle. The differential activity of the muscles on opposite sides of the head will determine where along the line AB (i.e. O, P, Q, B) the muscle resultant will lie and what line radiating from the carnassial notch will represent the jaw lever (i.e. JrOC, MPC, NQC), as larger forces exerted by muscles of one side will shift the resultant force toward that side. Differences in the positioning of muscles along the lines JrT and JIC will have the effect of placing the resultant force more anteriorly (along line OG) or posteriorly (along line MO).

Two models bear on the positioning of the resultant muscle force along the length of the jaw. The first (Greaves, 1982) states that placement of the muscle resultant anterior to a point one-third of the way along the length of the jaw results in large torsional forces about the long axis of the jaw, and therefore the possibility of failure of the mandibular corpus during feeding. To prevent this torsion, the resultant force of the jaw adductors is predicted to lie somewhere along the first one-third of the jaw. Greaves' model was initially developed for ungulates, the jaws of which presumably undergo torsion, which in their case would be a result of *internal* forces (their own masticatory muscles); this is in contrast to the jaws of carnivores, which are not only subject to internal torsional forces as a result of the action of masticatory muscles, but which are also subject to *external* torsional forces as a result of struggling prey. The increased robusticity of the mandibular corpus of some carnivoran jaws (Biknevicius & Ruff, 1992) may lend some resistance to torsional as well as bending forces, in which case, the anterior position of the masticatory muscles may not be as highly constrained in carnivores as Greaves states.

The second model (Greaves 1983) predicts the position of the resultant force along the length of the jaw in carnivorous mammals, in which gape and bite force are equally important. Anterior placement of the muscles (at points F and K in Figure 9)

applies a larger proportion of the muscle force at the bite point, but, in the case of carnivorans ingesting relatively large prey, has the undesired effect of limiting gape by interfering with the use of the carnassials. Maximizing gape by moving the masticatory muscles posteriorly, however, has the equally undesirable effect of severely reducing bite force. Because carnivorans need a wide gape to engage their posteriorly placed carnassials and/or to grasp relatively large prey, and because they need a high bite force to penetrate and maintain a hold on the prey, one would expect carnivorans to have a jaw geometry which maximizes both gape and bite force. By comparing bite force with the position of the jaw adductors at various points along the mandible, Greaves (1983) concluded that the widest gape is coupled with maximum bite force when the muscle resultant force is at a position 60% of the distance from jaw joint to carnassial. Movement anteriorly or posteriorly from this 60% position results in a drastic drop in either gape or bite force.

While Greaves attempts to remedy some of the inherent limitations of earlier models of mammalian jaw mechanics, his model, at least as it applies to carnivores has several limitations. When Greaves originally (1978) outlined his bilateral model of the jaw mechanics of ungulates, he assumed that maximization of bite force occurs along the length of the grinding tooth row. In extending his model to carnivores, he held this part of the model constant in assuming that bite force in carnivores is similarly maximized, but at a specific locus along the tooth row, the vertex of the carnassial notch. While for a given muscle morphology, the bite force exerted at the carnassial locus will always be higher than that exerted at the canines (due to the closer proximity of the carnassial to the TMJ), it unclear why the carnassial, rather than another tooth, such as the canine, should be site of bite force maximization.

There is indeed limited evidence that could be inferred as evidence that bite force is maximized at the carnassials; forces of 2.0-23.25 kg were recorded at the canines in *Felis domesticus* while forces up to 28 kg were recorded at the carnassials (Lucas, 1982). However, given the inherent difficulties in accurately recording bite force in often uncooperative subjects, the degree to which these numbers reflect reality is not without question. It could be argued that bite force must be higher at the carnassials than at the canines because the carnassials, by virtue of their elongate shape and therefore greater area of contact with the food item, are less able to penetrate prey than are the canines. However, the material that felid carnassials most often contact is vertebrate flesh (a soft, brittle material), whereas the canines regularly encounter bone (a hard, brittle material). As mentioned above in the discussion of felid killing behavior and dental morphology, felid canines fracture the vertebral column and occasionally the occiput of their struggling (and often relatively large) prey; this unpredictable loading regime has been used to explain the relatively robust canines of felids relative to other carnivorans (Van Valkenburgh & Ruff, 1987). In conjunction with this robusticity, it could be argued that the bite force at the canines must be higher than at the carnassials if the canines are to effectively fracture a hard, brittle material such as bone. Because prey capture and killing is a necessary precursor to the relatively less demanding task of severing flesh, it seems more logical to model the carnivore jaw under the assumption that bite force is maximized at the canine, not at the carnassial. Viewed in this manner, the bite force at the carnassials is a secondary, albeit functionally important, result of canine function, rather than the primary determinant of jaw function.

Greaves also assumes that the muscle resultant is oriented perpendicular to the long axis of the jaw. While this may be true during certain segments of feeding and predatory sequences, it is clearly an oversimplification for the activities of the felid

masticatory system as a whole, for quantification of several aspects of felid morphology (e.g., canine robusticity, mandibular robusticity, orientation and activity of masticatory and nuchal musculature), and observations of felid behavior indicate that the forces during feeding and predation are anything but predictable in terms of their magnitude and direction.

MASTICATION

Although the way in which mastication proceeds from time of food ingestion to time of swallowing is implicit in most descriptions of masticatory morphology and jaw mechanics, recent use of cineradiographic and electromyographic techniques have greatly improved the level of knowledge about the process of mastication. Along with the introduction of a great number of descriptive terms for various phases in the process of reducing food, these studies have elucidated how the patterns and degree of activity of the masticatory muscles vary within and among mammals and how these patterns are influenced by both the structural and material properties of the food items ingested.

Masticatory Sequences

A masticatory sequence can be defined as the series of events which begins with ingestion of a food item, reduction of the food item, and swallowing of the resultant bolus (Hiemae, 1978). Within this sequence, one can identify handling, transport, and masticatory cycles. Handling cycles involve the ingestion of the food item, while transport cycles can be divided into stage 1 and stage 2 transport cycles (Hiemae & Crompton, 1985), which involve moving the food item from the anterior to the posterior dentition, and moving the food posteriorly from the cheek teeth in preparation for swallowing.

Masticatory cycles intervene between handling and phase 2 transport cycles, and are concerned with the reduction of food items. Masticatory cycles are of two types: puncture-crushing cycles, in which there is tooth-food-tooth contact, and the teeth do not intercusate, and chewing cycles, in which the teeth achieve direct contact with each other. Within the masticatory cycle, three different strokes can be distinguished. The closing stroke (or fast close) occurs as the lower jaw moves upwards and the teeth converge. This is followed by the power stroke (or slow close) in which the teeth meet and muscular effort is used in breaking up the food item. The opening stroke moves the teeth apart, and is divisible into a slow open and fast open, which may be interrupted by a slight closing movement (Gorniak & Gans, 1980). More recently, opening movements of mammalian jaws have been described as consisting of three phases: O1, O2, and O3 (Hiimae & Crompton, 1985; Schwartz et al., 1989; Thexton & Crompton, 1989; Lund & Enomoto, 1988). O1 and O2 are comparable to the slow open phase identified above, while O3 corresponds to the fast open phase. While these movements may afford more precise descriptions of jaw movements, as noted by Thexton & McGarrick (1994), the fact that many of the earliest studies of cat mastication employed older terms makes comparisons between various studies cumbersome.

Jaw Movements

A widely used method of examining jaw movements in mammals has been to map the movement of the canines in vertical and horizontal planes using cineradiography (Figure 10). This method shows that felids have the lowest degree of transverse motion among the masticatory cycles among mammals. Because of this, the movements of the jaws in felids and indeed in most carnivorous mammals is usually characterized as purely hinge-like, as discussed earlier. However, concentration on this

hinge-like motion obscures the fact that lateral motion, although a small component of the masticatory cycle in felids, is crucial to the close approximation and proper function of the carnassials.

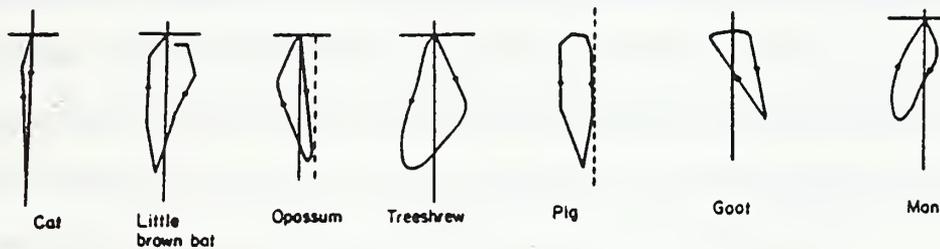


Figure 10. Lower jaw movements in various mammals, shown in frontal view with the working side on the right side of the jaws. Note small degree of lateral movement in the cat cycle, as compared to other mammals. (From Hiiemae, 1976)

Muscle Activity

The use of electromyography in studies of felids (as well as other carnivores) has led to a more detailed understanding of the activity of the masticatory muscles and has helped to dispel the widely held notion that purely vertical motion is the only direction of jaw movement in felids. As far as is known, all carnivores chew unilaterally (Scapino, 1981), and the disparity in width of upper and lower jaws necessitates that there be some asymmetrical activity of the jaw muscles to bring the carnassials into occlusion. The description that follows is based largely on the work of Gorniak & Gans (1980), unless otherwise cited.

The reduction sequence begins with bilateral activity of the digastrics effecting a slight opening of the jaws in a vertical plane. Additionally, the opening cycle may be

interrupted by "closing reversal" movements effected by low-level bilateral activity in the zygomaticomandibulares and deep masseters. This closing movement occurs as the food item is repositioned on the working side. Following this brief closing motion, the digastrics resume their bilateral activity, and continue to be active throughout the opening phase until maximum gape is achieved. As the jaw nears maximum gape, the zygomaticomandibulares become active bilaterally in order to slow jaw opening. For the most part, the jaw adductors on both sides of the head are active simultaneously during closing, with only slight differences in the relative timing of onset and end of activity. At the start of closing, the deep temporalis of the working side, the medial pterygoid of the balancing side, and the balancing- and working-side zygomaticomandibulares contract to adduct the jaw and shift it laterally toward the working side. As closing proceeds, the jaw muscles are active bilaterally. However, slight asymmetry in the activity of the working-side zygomaticomandibularis and masseter and the balancing-side medial pterygoid maintains the deviation of the jaw toward the working side throughout the reduction sequence. When the teeth contact a food item, the bilateral activity of the jaw adductors becomes increasingly asymmetric, and the speed of closure is reduced. As closure proceeds, the lower jaw rotates about its long axis due to unilateral resistance on the working side, and the adducting forces of the balancing side are transferred through the mandibular symphysis to the working side.

While there is indeed asymmetry in the muscle activity of felids, as described above, this asymmetry is very slight in comparison to other mammals (including some carnivorans), in which there may be significant differences in the timing and activity of muscles on either side of the head. Weijs (1994) divides the masticatory muscles of mammals into three groups based on the timing of their activity: vertically-oriented

symmetric closers (zygomaticomandibularis, temporalis), which are active symmetrically during fast close; triplet I muscles (working-side temporalis; balancing-side superficial masseter and medial pterygoid), which move the jaw toward the working side during fast close; and triplet II muscles (balancing-side temporalis; working side superficial masseter and medial pterygoid), which move the jaw to the balancing side during the power stroke. The degree of synchrony in the timing of these muscle groups is associated with the amount of transverse movement that occurs during the power stroke; variations in this synchronization led Weijs to distinguish a number of "specializations" in the masticatory patterns of mammals. One type of specialization is found among felids, mustelids, and bats, wherein synchronization of triplets I and II follows the initial activity of the symmetrical closers, and occurs as a result of the intercuspsation of the canines (bats) or of both the canines and the carnassials (felids and mustelids). Synchrony of muscle activity also occurs in rodents, but is accompanied by bilateral occlusion and protrusive/retrusive movements of the jaw. The synchrony in the jaw muscle activity of felids results in a very reduced horizontal component of the masticatory cycle.

Influences of other structures on mastication

Aside from the activity of the masticatory muscles discussed above, other structures, while not always directly exerting force to reduce food, are equally important in mastication. These accessory structures are of two types: structures which aid in positioning food for proper carnassial function (tongue, hyoid) and structures which effectively increase the force exerted by the masticatory muscles (nuchal musculature).

The tongue is vital in transferring food within the mouth. The tongue moves the food posteriorly and laterally to be chewed following ingestion, switches the food item

from side to side, and moves the resulting bolus posteriorly to be swallowed. In addition, movements of the tongue may assist the neck and masticatory musculature in disengaging food from the canines. While the bilateral activity of the digastrics produces the majority of the opening movement of the jaw, EMG observations of the activity of the semispinalis capitis musculature in cats (Gorniak & Gans, 1980) suggest that the nuchal musculature produces an upward movement of the head during opening. This effectively increases the speed of opening, which helps to disengage food from the canines so it may be transferred posteriorly to the carnassials. Similarly, closing is accompanied by a downward movement of the head that increases the speed of closing, and because of the inertia of the food item, results in it being punctured by the maxillary dentition. While these findings are the results of laboratory observations of cats feeding on prepared food items, observations of feeding and killing behavior in wild felids report downward movements of the head, suggesting that these movements may add force to the canine bite in prey capture. Studies of the attachment patterns of the head depressors in sabertooths have also suggested that head depression played an important role in their predatory behavior (Matthew, 1910; Riggs, 1934).

Influence of food size/consistency on masticatory sequences

Studies by Thexton & McGarrick (1994) and Gorniak & Gans (1980) focused on the ways in which food of varying types and sizes influence the process of mastication and the activity of masticatory musculature. With increasing hardness and size of food items, masticatory sequence length increases (due to increasing number and duration of masticatory cycles), the number of times the food changes position increases, movements of the head and tongue are more pronounced, and gape is wider. In addition, the jaw musculature is overall more active when harder foods are chewed, and the magnitude of activity in the temporalis, medial pterygoid, and masseter reflects

relative food consistency, while that in the digastric and lateral pterygoid reflects the degree of displacement of the mandible in vertical and horizontal planes.

CRANIAL MORPHOLOGY

While much of the research described thus far focuses on specific aspects of the felid masticatory apparatus such as dental elements, mandibular morphology, or anatomy of the masticatory muscles, several studies have focused on the overall structure of the skull. While some of these studies are interested in how the shape of the skull influences masticatory morphology of various taxa and vice versa (Buckland-Wright, 1978; Greaves, 1985, 1994), others focus on what functional differences exist among carnivores (Radinsky, 1981a, 1981b, 1982; Werdelin, 1986), or what differences in overall skull shape might reveal about phylogeny (Werdelin, 1983; Salles, 1992), while some consider both of these aspects (Radinsky, 1981a). The following discussion will briefly outline several of these approaches and their bearing on determining the multiplicity of factors which influence masticatory and cranial morphology.

In his work on patterns of force transmission in domestic cats, Buckland-Wright (1978) attempted to demonstrate a correspondence between the microstructure of the skull bones and the distribution of force generated by the masticatory musculature. Microradiography isolated areas within the skull that had a high concentration of force-transmitting structures and which presumably were sites of stress during mastication. *In vivo* bone strain was measured on anesthetized cats, in which electrodes stimulated activity of the masseter and temporalis musculature; this approach gave information about the magnitude and nature (compressive or tensile) of the strain occurring at various points on the skull, but did not reveal information about the direction of this strain. To make up for this limitation, the skulls were coated with colophonium resin,

threads representing the temporalis and masseter muscles were affixed to the skulls, and various loading regimes were applied. Cracks produced in the resin yielded information about the direction of the force exerted by the masticatory musculature. The skulls were then cleaned and strain gauges applied to various points, and the skull was reloaded, again bilaterally at the canines, then at the carnassials. The result of these different approaches was the identification of various helices or loops through which the forces generated during mastication pass from the facial bones to the rest of the skull. The magnitude of the force transmitted varies according to the locus of biting, but is predicted by Buckland-Wright to fall along regular, helical paths in the skull, a point later addressed by Greaves (1985, 1994).

By combining the use of stereo microradiography, strain gauges, and resin-coated skulls, Buckland-Wright attempted to remedy the inherent limitations of earlier studies, which relied on inferring force distribution from bone microstructure but said little about important matters such as the magnitude of the forces present. However, despite its use of varied and complementary approaches, the validity of Buckland-Wright's study is limited by the fact that it does not accurately reflect the ways in which the masticatory apparatus of felids functions during the unpredictable acts of feeding and predation. The most obvious of these limitations is one that is common to many experimental approaches to studies of mastication, and concerns the degree to which the experimental setup reflects the "natural" feeding behavior of the animal under investigation. More important, perhaps, is the fact that the loading regimes are not consistent with what is known about the symmetry (or, more appropriately, the asymmetry) of muscle activity and occlusal patterns in felids. Although this study did incorporate observations on living animals, the bilaterally symmetrical activity of their masticatory muscles was induced by electrodes, observed under anesthesia, and effected

a bilateral bite force. While a bilaterally symmetrical canine bite may sometimes occur during felid predation, asymmetrical, unpredictable loading of the canines occurs as a result of tooth-bone contact during the killing bite and is a more likely scenario for the loading patterns of the anterior dentition. Similarly, loading of the carnassials is not bilaterally symmetrical, as they are engaged unilaterally through asymmetry in the activity of the masticatory muscles. Unilateral rather than bilateral loading of the teeth would be likely to alter the nature and direction of force transmission in the face and cranium predicted by Buckland-Wright's model.

While the masseter and temporalis muscles comprise the bulk of the masticatory muscles, their activity is coincident with that of the less powerful, but nonetheless very important zygomaticomandibulares and medial and lateral pterygoids, all of which were ignored in Buckland-Wright's study. These muscles are oriented differently from the temporalis and masseter, and therefore would likely alter the observed patterns of force distribution were they to be included, and may act in certain cases to counteract the forces exerted by the temporalis and masseter, and thus affect the measured bone strain. A better approximation of the true patterns of force distribution might be accomplished by measuring strain in freely feeding, rather than anesthetized subjects, which would allow a closer approximation of their "true" feeding behavior by incorporating unilateral occlusion and bilaterally asymmetric and synergistic activity of the entire muscle assemblage. The data gleaned from the experiments on resin-coated skulls are similarly limited in the degree to which they accurately reflect masticatory function in felids, as they represent bilaterally applied forces from only two (temporalis and masseter) of the jaw adductors.

Studies modeling the skull as a cylinder (Greaves, 1985) or a half-cylinder (Covey & Greaves, 1994) focus on the relationship of skull form to the torsional forces

assumed to be generated by the masticatory musculature during unilateral occlusion. In the first study, Greaves developed a theoretical model to account for the presence or absence of a postorbital bar in various mammals. He hypothesized that in animals with a large masseter/pterygoid complex, such as selenodont artiodactyls, a postorbital bar acts as a strut to resist the high torsional forces generated along the outer surface of the skull; this structure is presumed to be absent in carnivores because of the different orientation of the temporalis, which exerts lower torsional forces in these animals.

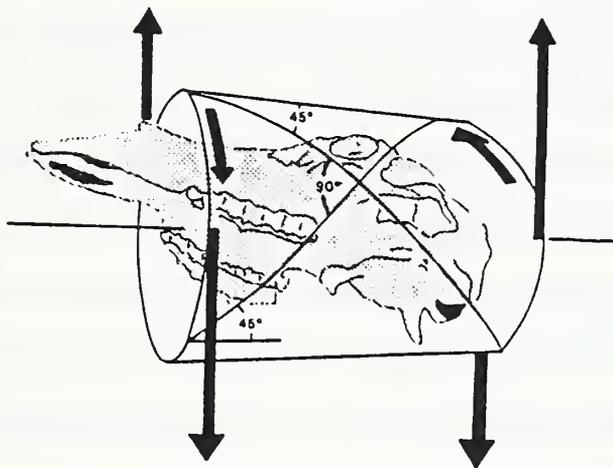


Figure 11. Drawing of a cylinder superimposed on the skull of a selenodont artiodactyl to show the direction of rotation (arrows) of the anterior and posterior ends of the skull as a result of unilateral mastication, and the torsional strains produced on the cylinder surface as a result of twisting about the long axis of the skull. (From Greaves, 1985)

Greaves hypothesizes that during unilateral chewing in selenodont artiodactyls, the masticatory musculature pulls ventrally on both sides of the skull, while the mandible of the working side pushes the skull dorsally at the bite point. The reaction force at the balancing side condyle also pushes dorsally on the skull but does so at a more posterior position. This loading regime results in the anterior and posterior parts of the skull being rotated in opposite direction at the weak orbital region (Figure 11). This in turn

results in torsion of the skull, with maximal tensile and compressive forces occurring along helices positioned at an angle of 45° to the long axis of the skull, and at an angle of 90° to each other along the surface of the skull. Greaves assumes that the tensile forces along these helices represent the weakest areas of the skull when it is loaded in torsion, and that buttressing of the skull against torsion should occur along the length of these helices. Greaves (1985) points out that the postorbital bar of selenodont artiodactyls occurs at this position, and attributes this to its role in resisting skull torsion occurring during unilateral chewing.

Greaves' model is problematic for the assumptions it makes regarding both the magnitude of the forces that produce twisting of the skull and the behavior of the skull during this twisting. In addition to these problematic assumptions, recent strain gauge data (Hylander, 1991) refutes some of the predictions of Greaves' model.

Greaves' model assumes for the sake of simplicity that the asymmetric skull loading during mastication in selenodont artiodactyls consists of three main types: ventral forces applied to either side of the skull by the masseter/pterygoid muscles, a dorsal force produced by the mandible at the bite point, and a ventral force at the balancing side condyle. Although Greaves acknowledges that balancing and working side muscle force is not always equal, he asserts that regardless of their asymmetry, they both apply "significant ventral forces to the skull". While he discounts this asymmetry in the activity of the masticatory muscles, he then emphasizes the degree of asymmetry of the condylar reaction forces to the point of disregarding the smaller reaction force at the working side condyle in favor of the greater balancing side condyle reaction forces.

Greaves' modeling of a complex biological structure such as the skull as a cylinder is problematic for a number of reasons. While he uses an example of a stick of

chalk breaking along a helix oriented at 45° to its long axis as an approximation of the behavior of the skull when loaded in torsion, it is immediately apparent that neither the material nor the structural properties of the skull are analogous to those of a stick of chalk. Bone can rarely, if ever, be modeled as a homogenous material, as it varies in its structure and therefore in its strength, depending on the location within the skull and on the nature and direction of the load applied. Secondly, even if bone could be assumed to be homogenous, the structure of the skull itself precludes one from assuming that it will act as a cylinder of homogenous material. Reasons for this include the tapering of the skull from posterior to anterior as well as the presence of vacant spaces such as the orbits, sinuses, and cranial cavity, all of which alter the patterns of force transmission in the idealized cylindrical model.

In addition to the theoretical difficulties imposed by the complexity of the skull, and therefore the limited applicability of a cylindrical model for the behavior of the skull during mastication, recent experimental evidence refutes Greaves' predictions about the types of forces generated in the skull during mastication. In addition to the role of the postorbital bar in resisting torsional forces during mastication, Greaves asserts that the supraorbital ridges found in primates also play a significant role in resisting torsion of the skull. The postorbital bar of the working side is predicted to resist compressive forces, while the supraorbital ridge of the same side, lying at an angle of approximately 90° to the postorbital bar, is predicted to resist tensile forces. Recent measurements of *in vivo* bone strain of the working-side primate supraorbital region indicate that tensile forces do not in fact occur in this region. Instead, this region experiences bending in the frontal plane, and the strain produced in this area is in fact low compared to other regions of the face due to increased buttressing of this area (Hylander, 1991).

Despite these problems, the cylindrical model is used by Covey & Greaves (1994) to explore the behavior of the carnivore skull under torsion. Unlike artiodactyls, which presumably experience great torsional forces as a result of unilateral biting along the cheek teeth (Greaves, 1985), the authors assert that carnivores experience high torsional forces generated during unilateral canine, rather than carnassial, biting.

With this in mind, the authors hypothesize that, as in ungulates, asymmetrical loading of the jaw during canine biting should result in tensile and compressive forces that are along helices oriented at 45° angles to the long axis of the skull, and that emanate from the two structures encountering the most resistance during unilateral canine biting: the working side canine and the balancing side condyle (Figure 12). Additionally, the length to width ratio of the skull determines its strength in resisting these forces, since variation in skull length and width presumably result in different positioning of these helices relative to one another and to the ends of the skull. In short, the authors state that for skulls of the same width, longer skulls will experience greater torsion than will shorter skulls.

Because of the relations between skull length and width and the relative positions of the canine and TMJ, the helices in the dog-like skull (Figure 12a) are equivalent and lie along a line connecting the anterior and posterior aspects of the skull, any additional skull strength would be accomplished by buttressing in the area along this helical path. In contrast, the helices in a more elongate skull (Figure 12b) are separated and do not extend to both anterior and posterior aspects of the skull. In this situation, torsional strains will occur along each helix and the space between them must be bridged with bone, a "metabolically expensive" building material (Covey & Greaves, 1994), in order to form a single helix which connects the anterior and posterior ends of the skull, and which

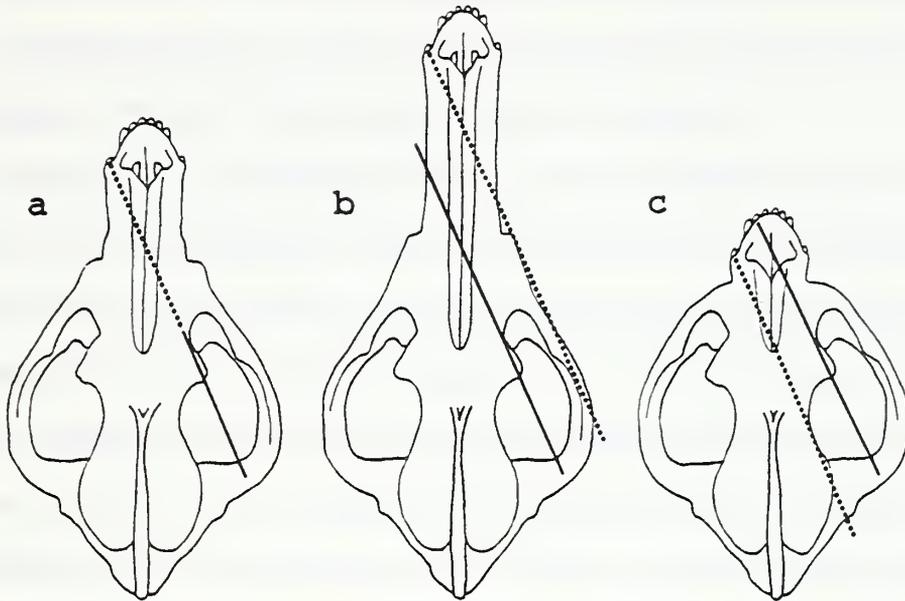


Figure 12. Three skulls with different length to width ratios, which influence the placement of the helices emanating from the jaw joint (solid line) and from the working canine (dotted line). (from Greaves, 1994)

resists failure under tension along this helix. In the cat-like skull (Figure 12c), two helices extending from the anterior to the posterior end of the skull are presumed to impart these skulls with added strength in resisting torsion, without needing extra bone to do so.

The authors describe skulls of this type (found in felids and some mustelids) as "overbuilt", for they are shorter than they need to be to effectively resist torsion. Additionally, they assert that such an overbuilt skull is important for animals in which large forces are exerted during unilateral canine biting, and/or in which the canine teeth

are subjected to large unilateral loading, as is the case in felids. By extension, the "underbuilt" skulls, with a high length to width ratio (Figure 12b), are less equipped to resist torsion; in order to do so, they require buttressing along helical paths on the skull. In apparent justification of this model, the authors state that carnivorans with a high length to width ratio "are not expected and are not found".

Unfortunately, the extension of Greaves' original model to carnivores is not without its own set of problems. It suffers from the same limitations regarding the legitimacy of the analogy between a complex structure such as the skull and a cylinder of homogeneous material. More importantly, perhaps is the fact that torsion in a cylinder is independent of that cylinder's length. Therefore, each of the skulls in Figure 12 should experience the same degree of torsion despite differences in length.

Additionally, the helices superimposed on the skulls in Figure 12 are not oriented at 45 degrees to the long axis of the skull, but are actually closer to 25 or 30 degrees; this invalidates the assumption that helices oriented at 45 degrees to the long axis of the skull will connect the canine and the balancing side condyle, which are presumably experiencing the most resistance. In light of the various problems mentioned above for both of these models, Greaves' acknowledgment that torsional forces are not the only important influence on carnivoran skull shape seems particularly fitting, and leads one to look at other factors, many of them discussed above, and others discussed below, which may be more important in determining cranial and masticatory morphology.

In a series of papers, Radinsky (1980, 1981a, 1981b, 1982, 1984) measured variables pertaining to aspects of jaw geometry, overall skull shape (length, width, height), relative brain size, relative development of sensory organs, and size and strength of the masticatory muscles and linked his findings to aspects of the killing behavior of some carnivorans. He inferred that among carnivorans, felids have a high

bite force (indicated by a large temporalis moment arm), and powerful neck musculature (indicated by high occipital width), presumably as a reflection of their killing behavior.

Werdelin (1986) used a subset of Radinsky's original variables to assess the primary functional differences between placental carnivorans and the dasyurid marsupials. In possessing canid-like, viverrid-like, and hyaenid-like forms, the ecological diversity of the marsupial family Dasyuridae is, in many respects comparable to that of the Carnivora. However, Werdelin found dasyurid cranial morphology to be no more variable than that of a single family within the Carnivora, an observation that he attributed to the posterior placement of the marsupial carnassials within the tooth row. Werdelin argues that in contrast to carnivorans, this posterior placement reduces the evolutionary plasticity of the dasyurid dentition. This is in contrast to carnivorans, in which postcarnassial teeth are present and modified in many families to yield markedly different adaptations (Butler, 1946). Therefore, based on Werdelin's findings, the phylogenetic history of dasyurids and the constraints it imposes on their masticatory morphology seems to have a much stronger influence on the morphology of the skull and the masticatory apparatus than do aspects of their diet and ecology. This argument is weakened, however, when it is noted that the species included in Werdelin's study represent only those dasyurids that have a diet composed primarily of vertebrates. By excluding those species that include a large portion of non-vertebrate food items in their diet, Werdelin has in fact excluded the majority of the species within this family of marsupials. Perhaps if the rest of these species were to be included in his analysis, the diversity in dasyurid cranial and dental morphology would approach that of the Carnivora.

While many studies are focused primarily on determining functionally important aspects of cranial morphology in carnivorans, they may also have some implications for systematics. Based on his initial results from canids, felids, mustelids, and viverrids, Radinsky (1981a) suggested that certain features of skull morphology might afford a means (in addition to using middle ear and basicranial anatomy) by which family-level diagnoses among carnivorans could be made. Subsequent analyses revealed a great deal of overlap in the skull morphology of these carnivorans with additional taxa (hyaenids, procyonids, and ursids), which precludes their use in family-level diagnoses, but which may not preclude their use in making distinctions within carnivoran families (Radinsky, 1982).

Another approach that concentrated on the potential systematic implications of cranial morphology is a study by Werdelin (1983), in which dental characters were used along with a small set of cranial characters to make systematic distinctions among felids. He found that species of the genus *Lynx*, while only weakly linked as a group on the basis of dental characters, are strongly linked on the basis of cranial characters such as postorbital constriction and postorbital width. His results show a fairly clear division between large and small cats, although two species intermediate to these two groups reveal interesting aspects of the constraints of size on cranial morphology.

The first species, the clouded leopard (*Neofelis nebulosa*), is intermediate in size between large and small cats, and is most notable for its large canines, which, relative to skull size, mirror the proportions of some sabertooths. *Neofelis* seems to have cranial proportions similar to those of the large cats (pantherines), without having reached pantherine cranial size. *Felis concolor*, on the other hand, has cranial proportions more typical of small cats (such as *Lynx*), but in overall size is more similar to the large cats. These results show that there are in fact quite distinct differences in skull morphology

in at least a few felid species, and that these differences may be largely the result of size change within lineages.

Another area examined in Radinsky's (1981a) research on the differences in carnivoran skulls is that of relative orbit size, which is highest in felids, suggesting a larger eyeball size and greater visual abilities. In addition to the implications that sheer size has for visual abilities, orbital convergence (the degree to which the orbits are directed forward) and frontation (the degree to which the orbits are directed toward the end of the snout) are also important considerations for a visually-directed predator. Other than primates, felids have the highest degree of convergence coupled with relatively high frontation and rostral regression (Cartmill, 1970). These features are presumed to be the result of shifting the duties of prey detection and capture away from the snout to the eyes and forelimbs, respectively. The result is a rostrum which in felids is "reduced to a visually-guided killing instrument" (Cartmill, 1970 p. 374).

CONCLUSIONS AND AREAS FOR FUTURE RESEARCH

As the preceding overview indicates, felid masticatory morphology has been the subject of many studies, some of which have managed to outline clear links between the demands of a predatory lifestyle and the form and function of the masticatory apparatus. Despite the depth of inquiry and the extent of the data that has been gleaned from such studies, however, much work remains to be done. Potential areas for future research fall into two general categories: refining what is already known about felid mastication and expanding this field of inquiry to other carnivorous mammals.

As stated above, a common criticism of studies of mastication concerns the degree to which data gathered reflect the true masticatory activities of freely feeding animals. This criticism is particularly valid for felids, given the very different demands

placed on their masticatory apparatus depending on whether they are engaged in feeding or predatory behavior. Most of the work done thus far has emphasized the first of these two behaviors by focusing on the muscular activity necessary to bring the carnassials into occlusion and break up food items of varying size, shape, and consistency. While carnassial function is certainly important in breaking food up into pieces small enough to be swallowed, I believe that for felids the importance of carnassial function is secondary to that of the canines, in that the use of the canines precedes that of the carnassials, and proper canine function is therefore a necessary precursor to carnassial use. In this respect, I believe it is important that future studies of felid mastication also concentrate on the canines and the activity patterns of the masticatory muscles when these teeth are engaged during predation. Doing so would allow a comparison of the patterns of muscular activity during these two types of jaw adduction that presumably place very different demands on the masticatory system.

In addition to gathering further data on the masticatory apparatus of felids, investigation of other mammals that have been said to converge on felids in cranial and masticatory morphology, diet, and behavior will shed light on the degree to which this perceived convergence is valid. The most notable candidates for such a study include the Malagasy "fossa", *Cryptoprocta ferox* (Carnivora, Viverridae), and mustelids of the subfamily Mustelinae. Both the fossa and the mustelines converge on felids in their reduced dental formula, well-developed carnassials, loss of postcarnassial elements, shortened rostrum, convergent orbits, and predatory behavior. Using the data that is presently known for felids, a comprehensive study of the predatory behavior, masticatory morphology and masticatory function of these convergent carnivorans would identify those aspects of their morphology which are dictated by the demands of a predatory lifestyle.

Through further study of felid behavior as well as masticatory morphology and function, much can be learned about the demands of a lifestyle which is characterized by a strict diet of vertebrate flesh, solitary hunting, and predation on (often) relatively large prey. Additionally, by studying other animals that converge on this way of life, we can not only better understand how and in what instances this lifestyle dictates cranial and masticatory morphology, but we can also begin to address how other important, non-masticatory features of animals also dictate their cranial and masticatory morphology.

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