# Déjà vu: the evolution of feeding morphologies in the Carnivora

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**Synopsis** The fossil record of the order Carnivora extends back at least 60 million years and documents a remarkable history of adaptive radiation characterized by the repeated, independent evolution of similar feeding morphologies in distinct clades. Within the order, convergence is apparent in the iterative appearance of a variety of ecomorphs, including cat-like, hyena-like, and wolf-like hypercarnivores, as well as a variety of less carnivorous forms, such as foxes, raccoons, and ursids. The iteration of similar forms has multiple causes. First, there are a limited number of ways to ecologically partition the carnivore niche, and second, the material properties of animal tissues (muscle, skin, bone) have not changed over the Cenozoic. Consequently, similar craniodental adaptations for feeding on different proportions of animal versus plant tissues evolve repeatedly. The extent of convergence in craniodental form can be striking, affecting skull proportions and overall shape, as well as dental morphology. The tendency to evolve highly convergent ecomorphs is most apparent among feeding extremes, such as sabertooths and bone-crackers where performance requirements tend to be more acute. A survey of the fossil record indicates that large hypercarnivores evolve frequently, often in response to ecological opportunity afforded by the decline or extinction of previously dominant hypercarnivorous taxa. While the evolution of large size and carnivory may be favored at the individual level, it can lead to a macroevolutionary ratchet, wherein dietary specialization and reduced population densities result in a greater vulnerability to extinction. As a result of these opposing forces, the fossil record of Carnivora is dominated by successive clades of hypercarnivores that diversify and decline, only to be replaced by new hypercarnivorous clades. This has produced a marvelous set of natural experiments in the evolution of similar ecomorphs, each of which start from phylogenetically and morphologically unique positions.

## Introduction

The history of feeding adaptations within the mammalian order Carnivora is one of repeated, sometimes spectacular, convergences on a limited array of ecomorphologies (Martin 1989; Werdelin 1996; Van Valkenburgh 1999). Over the past 65 million years, forms as distinct as sabertooth cats, bone-cracking hypercarnivores, raccoon-like frugivores, and even arthropod specialists have evolved more than once. This tendency towards the iteration of similar forms results in numerous homoplasies that frustrate systematists but entrance functional morphologists. Convergence in form between distantly related species provides strong evidence of evolution in response to similar conditions, and is invaluable for the reconstruction of function in extinct taxa. For example, the bizarre dome-shaped skulls of extinct borophagine canids are easily understood as bone-cracking adaptations through comparison with extant hyenas. The fact that sabertooth short-faced predators evolved independently in four distinct mammalian lineages

(nimravids, felids, creodonts, marsupials) indicates the form was very successful despite their extinction and the lack of modern analogs. The fossil record of the Carnivora is rich in similar examples of natural experiments in the evolution of teeth and skulls for different diets.

In this review, I briefly summarize the history and diversity of the order, describe key elements of the carnivoran (members of the order Carnivora) feeding apparatus and compare it to that of two other groups of carnivorous mammals, extinct creodonts and extant dasyurid marsupials. I then document some of the most striking examples of convergence in feeding morphology within past and present terrestrial carnivorans, highlighting both the similarities and differences in form. The emphasis is on terrestrial species larger than about 7 kg in mass as the fossil record is much better for this size class. The dietary specialization that has evolved most often is hypercarnivory, a diet that is composed of at least 70% flesh. It tends to evolve along with an increase in body mass resulting in predators that

regularly take prey at least half their size or larger. These species tend to be keystone members of their respective ecosystems, and can alter community dynamics, including vegetation structure, through their effects on herbivores, other predators, and scavengers (Terborgh et al. 2001; Estes 2005; Wilmers and Getz 2005). Because of their ecological and evolutionary importance, I explore the causes and consequences of becoming large and hypercarnivorous, including examples from both extinct and extant species.

## The order Carnivora

The extant order Carnivora includes 274 species in eleven families and spans a wider range of body sizes than any other mammalian order, from the 30 g least weasel to the 1000 kg walrus (Wozencraft 1993, McKenna and Bell 1997). In addition, more than 355 fossil genera have been identified, some of which belong to extinct families (McKenna and Bell 1997). Carnivorans first appeared in the Paleocene, about 63 ma (millions of years ago) and diverged into two major branches, the Caniformia and Feliformia (Flynn 1998). The defining character of the order is the presence of carnassial teeth, a blade-like upper fourth premolar that occludes with a partially bladed lower first molar in a scissor-like action. The Caniformia includes the canids, ursids, mustelids, mephitids, procyonids, ailurids, amphicyonids (extinct bear-dogs), and aquatic carnivorans (pinnipeds), and the Feliformia includes the felids, hyaenids, herpestids, viverrids, percrocutids (extinct hyena-like forms), and nimravids (extinct cat-like forms) (Fig. 1). Recent molecular phylogenetic studies have revealed further significant subdivisions within some families such as the separation of the Malagasy species as a monophyletic sister-group to the herpestids (Flynn et al. 2005), but the primary divisions remain as described
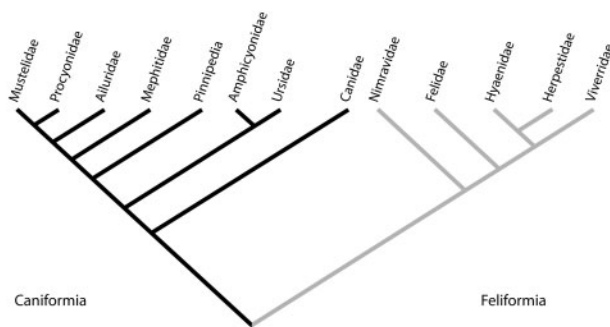
here. Excluded from further discussion in this article are the pinnipeds as they are aquatic and the mephitids as they remain small-bodied throughout their evolutionary history.

The ecological diversity expressed among carnivorans is impressive. Found on every continent and in habitats ranging from desert to rainforest, it is not surprising that the diets of carnivorans run the gamut from plants to arthropods to small and large vertebrates. This diversity of diet is paralleled by a diversity in craniodental morphology that has engendered numerous studies of functional correlates between food and craniodental form (Van Valkenburgh, 1988b; Biknevicius and Ruff, 1992; Sacco and Van Valkenburgh, 2004; Christiansen and Adolfssen, 2005; Goswami, 2006). Such studies allow the reconstruction of feeding habits of extinct species and have documented an early diversification among large (>7 kg) carnivorans into three fundamental dietary categories: hypercarnivorous (diet >70% vertebrates), mesocarnivorous (diet is 50–70% meat, with the balance made up of nonvertebrate foods), and hypocarnivorous (diet >70% nonvertebrate foods) (Van Valkenburgh 1988b; Wang et al. 1999; Wesley-Hunt 2005). These categories are not entirely discrete and grade into one another to some extent, but are useful for broad analyses. The tripartite division of diet was in place at least 40 million years ago and continued to the present, although different taxa fill the categories at various times and places. In both the Old and New Worlds, a fourth category arose about ten million years ago, hypercarnivorous bone-crackers (e.g., hyenas, borophagine canids). Appearing later were additional rare ecomorphs such as specialists on eusocial insects (e.g., sloth bear, *Melursus ursinus*, aardwolf, *Proteles cristatus*), medium to large sized molluscivores (e.g., aquatic mustelids, such as the sea otter, *Enhydra lutris*) and medium-sized herbivores that specialize on fibrous plant material (e.g., red panda, *Ailurus fulgens*, and giant panda, *Ailuropoda melanoleuca*). The early split into three dietary groupings, each recognizable on the basis of craniodental morphology and stable over the Cenozoic, likely reflects two factors. First, there are limited ways to subdivide the carnivore niche; species differ in prey size and/or how carnivorous they are (the proportion of nonvertebrate foods consumed). Second, the textural and nutritional qualities of vertebrate prey are unlikely to have changed substantially over the Cenozoic, and thus teeth that cut skin or crush bones today would have worked just as well in the past. In addition, carnivorans that consume nonvertebrate foods tend to be rather



**Fig. 1** Topological phylogeny of the Carnivora based on Flynn (1998) and Flynn et al. (2005). Caniformia are on the dark branches and Feliformia are on the gray branches. The position of the family Percrocutidae is not shown as it is uncertain, but is likely a sister group to the Hyaenidae (Werdelin and Solounias 1991).

generalized omnivores that consume arthropods as well as fruits, and these foods are also likely to have had relatively consistent material properties. This pattern of evolutionary stability of feeding morphology contrasts with secular trends seen among Cenozoic herbivorous mammals, where a cooling climate created new landscapes that favored the evolution of grazing adaptations (Janis 1993; Hunter and Jernvall 1995). An extant bison would be poorly suited for feeding in the North American early Miocene, when browse dominated grasses (Janis et al. 2004), but a wolf could have easily consumed its ungulate prey.

## The carnivoran feeding apparatus

The earliest members of the order Carnivora were mesocarnivorous with a generalized dentition, as exemplified by the genus *Vulpavus* (Fig. 2). The cheek teeth are heterodont and their different shapes reflect distinct functions. Incisors and canines are used to apprehend food and kill prey, pointed
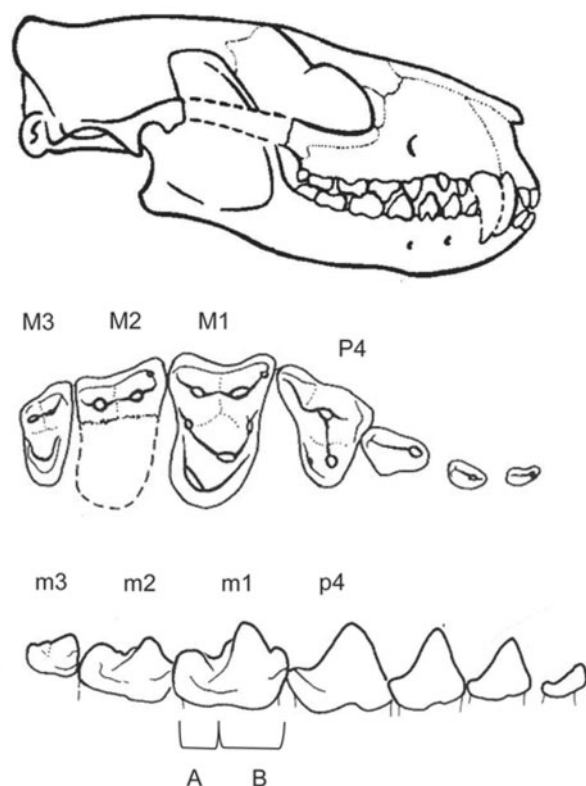


**Fig. 2** Top: Lateral view of the skull of the Eocene miacoid carnivoran, *Vulpavus profectus* (skull length approximately 10 cm). Middle: Occlusal view of the upper tooth row with the upper 4th premolar (P4) to third molar (M3) labeled. Bottom: Lateral (buccal) view of the lower tooth row with the lower 4th premolar (p4) to third molar (m3) labeled, as well as the talonid (A) and trigonid (B) of the m1. Skull from Radinsky (1982) and tooth rows after Flynn (1998).

premolars pierce and hold prey, and molars are involved in both slicing and crushing functions. As noted earlier, the slicing function of the molars is produced by occlusion between the carnassials, the lower first molar (m1), and the upper fourth premolar (P4). The m1 is usually the only tooth involved in both slicing and crushing/grinding. It is divided into an anterior blade (trigonid) and posterior basin or "heel" (talonid) (Fig. 2). Carnassial morphology can be highly informative concerning diet. A narrow blade-like P4 combined with an m1 that has an elongate trigonid is typical of hypercarnivores, such as gray wolves (*Canis lupus*). Alternatively, moderate hypocarnivores, such as black bears, tend to have a more triangular P4 and short trigonid relative to talonid on the lower carnassial. In addition, hypocarnivores tend to expand their postcarnassial molar volume, while hypercarnivores tend to do the opposite (Ewer 1973).

The carnivoran tooth row appears to have had an evolutionary advantage over that of creodonts and marsupials (Butler 1946; Ewer 1973; Werdelin 1987a). Creodonts are an extinct order of carnivorous mammals that existed between approximately 60 and 6 million years ago but never evolved the diversity of form or taxa expressed within the Carnivora. Although creodonts exceeded carnivorans in species richness and body size in the early Eocene, their dominance was short-lived as carnivorans diversified and replaced them (Friscia 2005; Wesley-Hunt 2005) (Fig. 3). Similarly, the evolution of carnivores among borhyaenid and dasyurid marsupials has been relatively limited in South America and Australia, respectively. Although hypercarnivores (including sabertooth ecomorphs) evolved
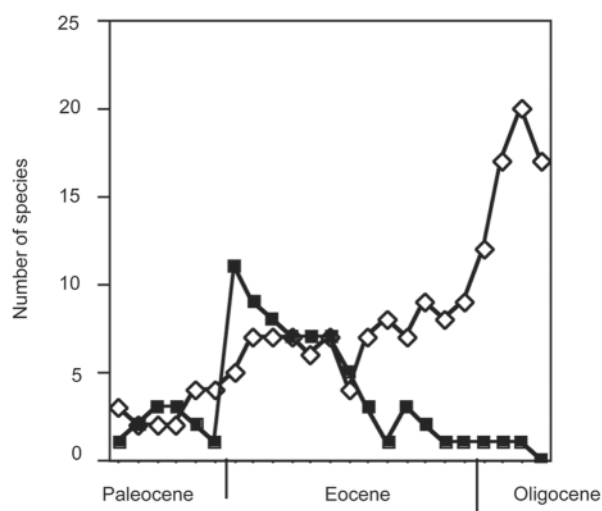


**Fig. 3** Species diversity of creodonts (solid squares) and carnivorans (open diamonds) against time. From Friscia (2005).

in both groups, the diversification of omnivorous forms has been minimal. The relative success of the Carnivora relative to both of these taxa is likely a consequence of a greater evolutionary versatility of the carnivoran tooth row. In both marsupials and creodonts, there have never been grinding post-carnassial molars. Instead, all the molars are similar and variation among species occurs in the numbers and sizes of molars, as well as in premolar shape (Fig. 4). Together, the molars and premolars of both creodonts and marsupials have less evolutionary potential than do those of carnivorans. In carnivorans, the division of the molar row into slicing teeth and grinding teeth provides a sliding window of evolutionary opportunity. By enhancing one function, such as slicing, over another, evolution can produce hypercarnivores with minimal post-carnassial grinding teeth, on the one hand, or herbivores with minimal carnassial blades, on the other (Gregory and Hellman 1939). The combination of an evolutionarily versatile dentition with a
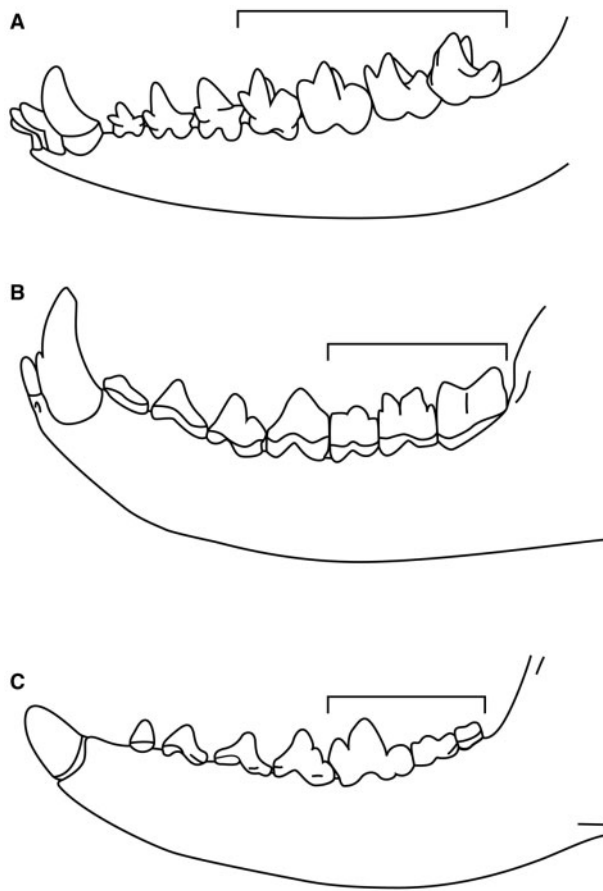


**Fig. 4** Lateral views of the lower tooth rows of the (**A**) extant dasyurid marsupial, *Sminthopsis*, (**B**) extinct creodont, *Hyaenodon crucians*, and (**C**) extinct canid *Hesperocyon gregarious*. Bracket indicates molar tooth row. (A) after Figure 19–20 from Carroll (1988), (B) and (C) from Van Valkenburgh and Jenkins (2002).

temporally stable resource (vertebrates) is largely responsible for the repeated evolution of feeding morphologies, especially hypercarnivores, among carnivorans.

## *Déjà Vu*: examples of convergence

The generalized mesocarnivorous morphology of *Vulpavus* is typical of the early members of most of the carnivoran families, except for felids and nimravids (Radinsky 1982), and is seen today among canids (e.g., foxes), viverrids (e.g., civets), mustelids (e.g., martens, tayra), procyonids (e.g., ring-tailed cat), mephitids (e.g., skunks), and herpestids (e.g., some mongooses). For example, the basal canid *Prohesperocyon wilsoni* (36–35 ma, about 4 kg, subfamily Hesperocyoninae) exemplifies a mesocarnivorous species with a dentition capable of some slicing as well as grinding (Fig. 5A and B). It had three incisors, one canine tooth, four premolars above and below, as well as three molars below, and two molars above, on each side (total teeth = 42). The lower carnassial has a blade-like trigonid that exceeds the talonid in length, suggesting a slightly greater tendency towards vertebrate than non-vertebrate foods, but the postcarnassial grinding molars are largely retained, consistent with ominivory. Note that the upper first molar is triangular in occlusal view, retaining the primitive condition. The skull is long relative to its breadth with a smooth dorsal profile that slopes upward posteriorly and the dentaries are shallow dorsoventrally relative to their length. As demonstrated in the fossil record, this generalized morphology had the potential to evolve either towards or away from a greater reliance on vertebrate foods and is still present among extant carnivorans as noted above (Fig. 5D). Below I describe some remarkable examples of convergence of similar dietary ecomorphs. Much of the following relies on illustrations and description, but previous relevant quantitative work on carnivoran function and form is cited.

### Hypocarnivores

The extant raccoon, *Procyon lotor*, is a medium-sized species (5–8 kg) that consumes a wide variety of nonvertebrate foods. Its upper carnassial is nearly square in outline with little evidence of a scissor-like blade, and the postcarnassial molars are also quadrate and expanded to produce an effective grinding area (Fig. 6D). The lower carnassial (m1) displays a low trigonid that is only half the length of the entire tooth, and the m2 is almost as a large as the carnassial. The largest living viverrid,
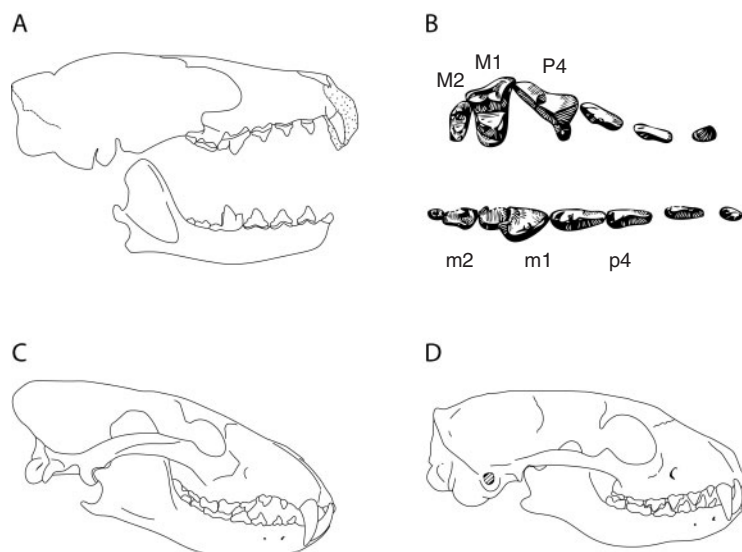
Fig. 5 Mesocarnivores. Lateral view of the (**A**) skull and (**B**) upper and lower cheek teeth of the earliest canid *Prohesperocyon wilsoni*. Teeth labeled as in Fig. 2. Lateral view of the skulls of (**C**) *Daphoenus vetus*, an amphicyonid, and (**D**) the white-tailed mongoose, *Ichneumia albicauda*, a viverrid. (A) and (B) from Gustafson (1986); C from Radinsky (1982); and D from Radinsky (1981).
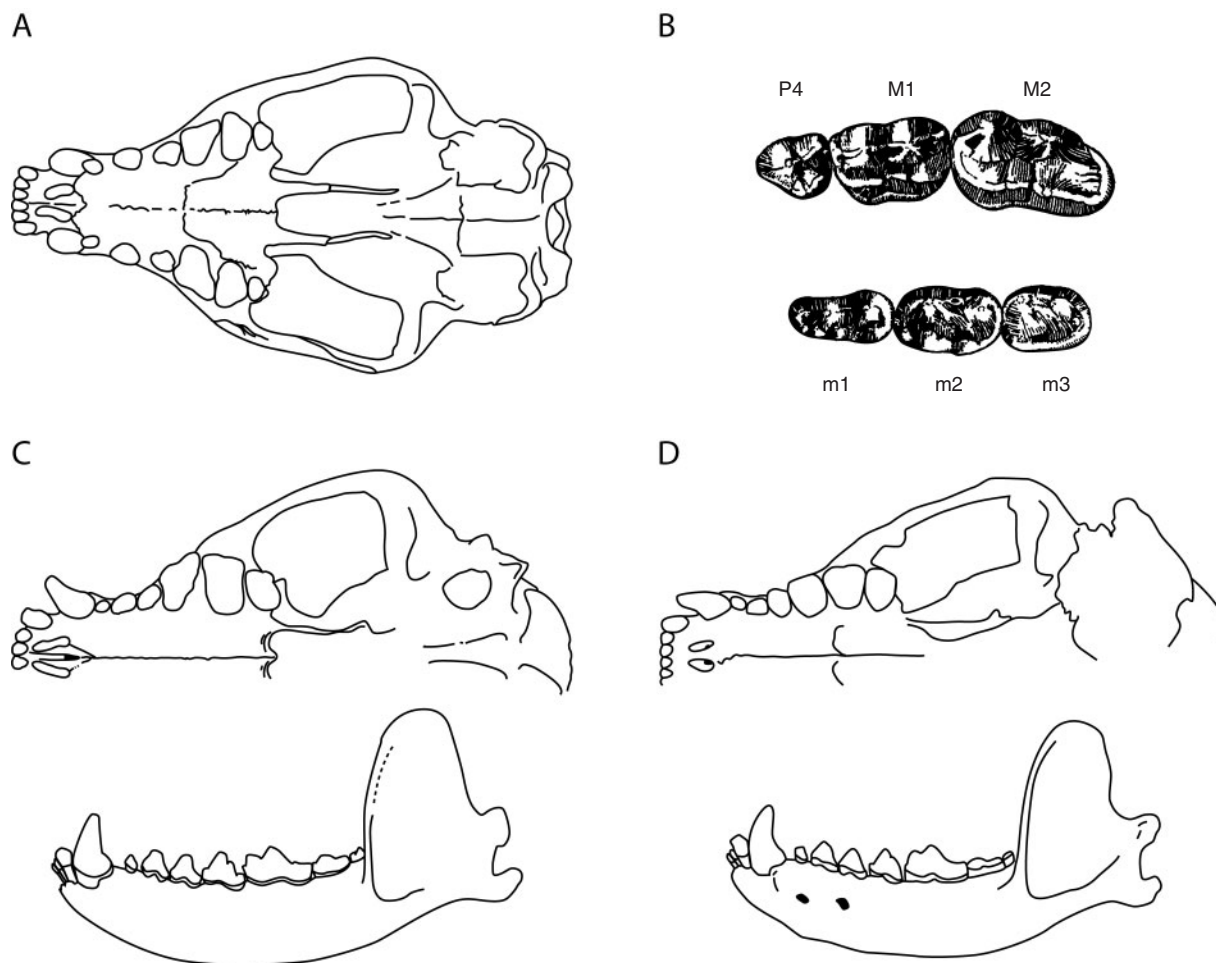


Fig. 6 Convergence among hypocarnivores. (**A**) Palatal view of skull of the extant viverrid, *Arctictis binturong*, (**B**) Occlusal view of the upper and lower cheek teeth of an ursine bear (teeth labeled as in Fig. 2). Palatal view of skulls and lateral view of mandibles of (**C**) extinct canid, *Phlaocyon leucosteus*, and (**D**) the extant raccoon, *Procyon lotor*. All skulls are drawn to approximately the same condylobasal length. (A) from Gregory and Hellman (1939), (B) from Hunt (1998b), (C) from Wang et al. (1999), and (D) from Wortman and Matthew (1899).

the binturong (*Arctictis binturong*), also exhibits a hypocarnivorous dentition with sub-quadrate upper carnassials (Fig. 6A) and a relatively equal division of the lower carnassial into talonid and trigonid, as do some of the smaller palm civets (e.g., *Paradoxurus, Paguma*) (Gregory and Hellman 1939), and the red panda (*Ailurus fulgens*).

In the early Miocene of North America, several members of the second canid subfamily. Borophaginae, evolved in the direction of hypocarnivory (Wang et al. 1999). Although not to the degree seen in the raccoon, the extinct canid *Phlaocyon leucosteus* (Fig. 6C) had broad upper carnassials and expanded, square-shaped postcarnassial molars (Wortman and Matthew 1899). Relative to the older *Prohesperocyon* (Fig. 5A and B), the shift in relative proportion between slicing and grinding functions is dramatic and clearly indicative of a dietary shift towards nonvertebrate foods including fruits. This same shift occurred at least three times among Oligocene and Miocene canids (*Oxetocyon, Phlaocyon, Cynarctus*) (Wang et al. 1999), contributing to the greatest taxonomic and ecomorphological diversity of coexisting canids ever known from any continent. Approximately 30 million years ago, at least 25 canid species co-occurred on the continent (Wang et al. 1999), as opposed to a mere seven today. At this time, hesperocyonine and borophagine canids were fulfilling a wide variety of ecological roles, spanning the full range of hypocarnivory to hypercarnivory. By the late Miocene, mustelids and procyonids had diversified in North America and replaced the hypocarnivorous canids.

Larger hypocarnivores are rare in the history of the Carnivora, evolving relatively late (Mio-Pliocene) in one subfamily (Ursinae) within the bear family, Ursidae (Hunt 1998b) and among Pliocene South American procyonids (*Chapalmalania* sp.) (Marshall 1977). Extant ursids have a distinctive craniodental and postcranial morphology that is relatively conserved within the family. Salient features include large body size, plantigrade to subplantigrade limb posture, robust skeletons, large heads with elongate rostra, reduced premolars, and enlarged molars (Ewer 1973). Like the smaller hypocarnivores, they have expanded postcarnassial molars relative to their carnassials, but the expansion results in molars that are rectangular and elongate mesiodistally rather than quadrate (Hunt 1998b; Sacco and Van Valkenburgh 2004) (Fig. 6B). Moreover, the largest upper molar in ursids is M2 as opposed to M1 in the procyonids and canids. Except for the insectivorous sloth bear and herbivorous panda, there is relatively little variation in overall dental morphology among ursine bears. For example,

both the highly carnivorous polar bear and extinct short-faced bear, *Arctodus simus*, have dentitions that differ little from those of more omnivorous bears, although the latter species had a short, broad snout like that of hypercanivores (Kurten and Anderson 1980). The absence of greater craniodental specialization in carnivorous ursids may reflect the fact that ursids tend to take prey that are small relative to their own body size and also rely on nonvertebrate foods for at least part of the year (Sacco and Van Valkenburgh 2004).

The most hypocarnivorous of ursids and perhaps carnivorans is the herbivorous giant panda, *Ailuropoda melanoleuca*. As expected, the panda has relatively large grinding molars, but also has deep, rigid mandibles, and enhanced mechanical advantage of jaw adductor muscles relative to other bears (Sacco and Van Valkenburgh 2004). In these last two features, the panda is more similar to hypercarnivorous canids that take large prey, where these traits are associated with increased bite forces and higher masticatory loads (Van Valkenburgh and Koepfli 1993). In the panda, the amplification of bite force in association with massive crushing molar teeth is an adaptation to the problem of feeding on extremely fibrous, tough bamboo with bunodont rather than hypsodont teeth, such as those of ungulates and glires (rodents, lagomorphs). As carnivorans, they have short digestive tracts without an associated fermentation chamber. Consequently, it is critical that the bamboo be thoroughly masticated prior to swallowing so as to maximize digestive efficiency.

## Hypercarnivores

Evolution has produced at least four different sorts of mammalian hypercarnivores again and again, exemplified by two kinds of felids (with sabertooth or conical canine teeth), large canids, and hyaenids. Hereafter these will be referred to as ''cats'' or cat-like, wolf-like, and hyena-like, respectively. Although these forms all share features that unite them as hypercarnivores, they also differ in significant ways that reflect differences in predatory style (slashing versus crushing killing bite), diet (bone consumption), and phylogeny. Nevertheless, their diets overlap extensively with each representing a different way to ''skin the cat''.

### Cat-like ecomorphs

The first type of hypercarnivorous carnivoran to appear in the fossil record is somewhat surprisingly quite extreme, a sabertooth cat-like species. Appearing suddenly in the late Eocene (*circa* 37 ma) in both North America and Asia (Bryant 1991;

Peigne et al. 2000), these members of the extinct family Nimravidae, were already highly specialized cat-like predators with elongate, mediolaterally compressed canine teeth, and retractile claws (Fig. 7A). Like all cat-like species, the nimravid *Dinictis* had lost its postcarnassial grinding dentition as well as the crushing basin-like talonid on the lower carnassials. The rostrum is foreshortened, enhancing the mechanical advantage of the jaw adductors (temporalis, masseter) for bites made with the canine teeth, and reducing torsional stresses on the cranium during uneven canine tooth loading (Covey and Greaves 1994). However, *Dinictis* also shows some features peculiar to having saber-like canines. The anterior dentition (incisors) is large and procumbent in a curved arcade that allowed use of the incisors in feeding with the jaws near closure as well as during prey capture. *Dinictis* also shows a slight ventral elongation of the anterior mandible that develops into a large flange in some later sabertooths, both nimravid and felid. The function of the flange may have been protection for the upper canines, when the jaws are closed and/or increased dorsoventral buttressing of the symphyseal area to resist high bite forces (Therrien 2005). However, this is uncertain as not all



**Fig. 7** Convergence among sabertooth "cats". Lateral views of (**A**) the nimravid, *Dinictis felina*, (**B**) the nimravid *Eusmilus sicarius*, (**C**) the felid *Smilodon fatalis*, and (**D**) the felid *Homotherium serus*. All skulls are drawn to approximately the same condylobasal length. (A–D) from Emerson and Radinsky (1980).

sabertooth "cats" have a flange and it is progressively reduced in the *Smilodon* lineage.

In *Dinictis* and all sabertooths, the major site of insertion for the temporalis muscle, the coronoid process of the mandible, is reduced considerably relative to that seen in extant felids (Emerson and Radinsky 1980). This affects bite mechanics in two opposing ways. On the one hand, it reduces the mechanical advantage of the temporalis by shortening the lever arm provided by a tall coronoid process. On the other, it reduces the degree of stretch of the muscle fibers when the jaws are opened widely, to clear the canine tips, thus allowing the muscle to maintain a greater force capability to initiate closure. For sabertooths, the ability to open their jaws widely was critical for the use of the canines, and in addition to reduction of the coronoid process, they display other features that enhance gape, such as an upwardly rotated face and laterally displaced angular process on the dentary (Emerson and Radinsky 1980).

In addition to the relatively reduced mechanical advantage of the jaw adductors, they also appear to have been relatively smaller than in conical-toothed felids. The zygomatic arches are less widely spaced and areas of origin of both the masseter and temporalis are reduced relative to extant felids (Emerson and Radinsky 1980). This suggests that sabertooths may have had weaker bites than conical-toothed cats but there are other features that may have compensated. For example, the mastoid processes are enlarged; these served as attachment sites for head-depressing musculature that could have assisted closure of the jaws (Akersten 1985; Anton et al. 2004b). Moreover, their carnassials are positioned closer to the jaw joint and the temporalis fibers are more vertically oriented, both of which would improve mechanical advantage (Emerson and Radinsky 1980). Finally, the robust architecture of their dentary bones suggests that they were subjected to heavy loads, supporting high bite forces (Biknevicius and Van Valkenburgh 1996; Therrien 2005).

The convergence in form between nimravid and felid sabertooths is striking and probably reflects the extreme requirements of this highly specialized morphology. Elongate canines demand large gape, which in turn produces a cascade of related adaptations (procumbent incisors, reduced coronoid, and mechanical advantage of the temporalis, reorientation of the temporalis, recruitment of head-depressing musculature). All sabertooths share these features to varying degrees, even though the shapes of their canines may differ substantially. Elongation of the canine teeth appears to be the first step in
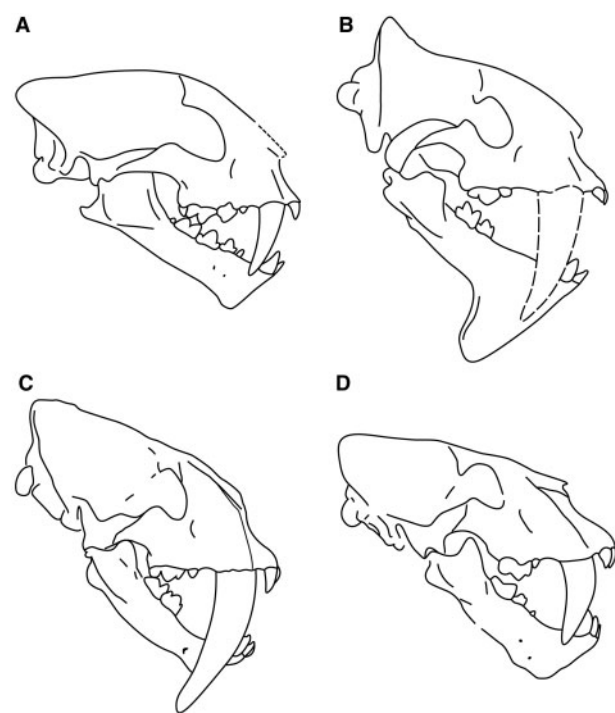
the evolutionary trajectory as exemplified by *Machairodus aphanistus*, a Miocene felid from Spain that displays saber-like canine teeth in combination with a primitive cranio-mandibular morphology (Anton et al. 2004a). Among felids, two sabertooth forms are recognized, dirk-toothed and scimitar-toothed (Martin 1989). Dirk-toothed cats, such as *Smilodon fatalis* (Fig. 7C), have upper canines that are very long, narrow mesiodistally, slightly recurved, with minimal or no serrations. Scimitar-toothed sabercats, such as *Homotherium* (Fig. 7D), have shorter upper canines that are relatively broader mesiodistally and often bear coarse serrations (Van Valkenburgh and Ruff 1987).

Notably, the two ecomorphs of the canines seem to have hunted differently, with dirk-toothed cats having shorter, robust limbs indicative of ambush attack and scimitar-toothed forms having longer, more gracile limbs suggestive of hunting by short-distance pursuit (Martin 1989; Anyonge 1996). Both probably killed similarly, using a ''canine-shear bite'' (Akersten 1985) in which lower canines were anchored into the prey and the upper sabers driven downward by the combined action of jaw-adducting and head-depressing musculature. A rearward pull would then remove a substantial quantity of tissue and create a serious wound. One or two canine-shear bites to the throat could easily sever major vessels, rapidly killing the prey. The throat is favored over the abdomen as the preferred site of attack because of the presence of vulnerable vital vessels and the reduced likelihood of the teeth encountering bone and breaking (Emerson and Radinsky 1980; Van Valkenburgh 2001a; Salesa et al. 2005).

The repeated evolution of sabertooth ecomorphs in carnivorans (nimravids, felids), as well as creodonts (*Machaeroides*) and marsupials (*Thylacosmilus*) over the past 45 million years is evidence of the success of the design. But for what? What advantage did the elongate teeth provide that compensated for the associated apparent losses in biomechanical efficiency of muscle systems and the increased vulnerability to tooth fracture? The most widely accepted answer is that the saber-like canines allowed individuals to take larger prey relative to their body size, thus providing them with a wider range of potential prey (Emerson and Radinsky 1980). Recently, it was suggested that sabertooth predators were also able to kill relatively quickly, reducing the risk of injury to the cat itself (Salesa et al. 2005, 2006b).

Nimravids dominate the cat-like ecomorph niche in the late Eocene and Oligocene but are gradually replaced by felids in the Miocene. The earliest felid, *Proailurus*, appeared about 25 million years ago in the Old World, and like the first nimravid, is already easily recognizable as a cat. The tooth row is shortened by loss of the postcarnassial molars and a diminution of anterior premolars, the canine teeth are enlarged and relatively round in cross-section, and the rostrum is short (Fig. 8A). Felids change relatively little over their evolutionary history; the tooth row shortens further, the zygomatic arches expand laterally, the brain enlarges, and the occiput becomes broader and taller (Radinsky 1982) (Fig. 8B). They are very effective killers, combining strong teeth and jaws with flexible forelimbs and retractile claws to dispatch prey with one or a few crushing bites.

The evolutionary success of the cat-like ecomorph is supported by the independent evolution of cat-like ecomorphs in at least four other families, three caniform and one feliform. In the early Miocene of North America, prior to the arrival of felids from the old world, cat-like canids (*Ectopcynus*, *Enhydrocyon*) and mustelids (*Megalictis*) appeared, some of which were leopard-sized (Wang 1994; Baskin 1998) (Fig. 8C and D). Similarly in the Miocene of the Old World, short-faced cat-like forms appeared among amphicyonids (*Brachycyon*) and large mustelids (*Eomellivora*, *Ekorus*) (Werdelin 1996, 2003). Even among viverrids, two very feline looking species with retractile claws arose on Madagascar, the extinct *Cryptoprocta spelea* (about 30 kg) (Goodman et al. 2004), and the extant fossa, *C. ferox* (7–12 kg). With the exception of *Cryptoprocta*, none of these cat-like forms are quite as extreme in the reduction of the tooth row as are nimravids and felids, but they all share the foreshortened rostra, enlarged canines, and carnassials with trigonids that are at least 70% of total m1 length (Van Valkenburgh 1991).

### Hyena-like ecomorphs

Spotted hyenas (*Crocuta crocuta*) are examplar bone-cracking hypercarnivores. Bone-crackers break bones with their premolars and are distinguished from less-specialized bone-crushers, such as wolves, that break bones with their post-carnassial molars (Werdelin 1989). Despite the fact that the mechanical advantage of the jaw-adducting musculature is greater at the molars, using premolars to crack bones allows larger bones to be consumed because of increased gape farther from the jaw joint (Ewer 1973). Limb bones are a valuable food resource as they often contain blood and fat-rich marrow. Bone meal is up to 40% organic matter and hyenas digest bones thoroughly (Kruuk 1972). One cost of bone-cracking is a higher frequency of tooth fracture as shown by comparative studies of tooth
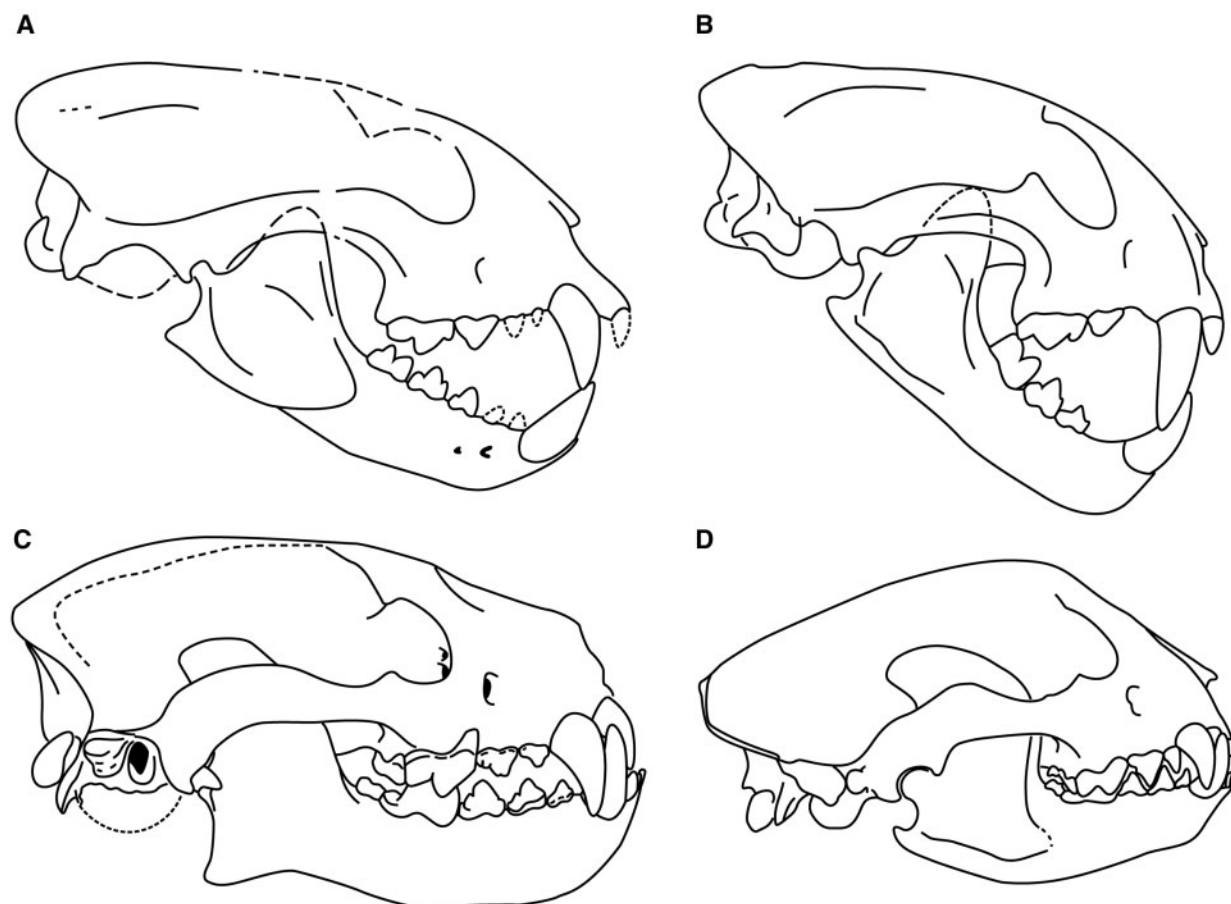
**Fig. 8** Convergence among cat-like hypercarnivores. Lateral views of (**A**) the earliest felid, *Proailurus lemanensis*, (**B**) the extant clouded leopard, *Neofelis nebulosa*, (**C**) the extinct canid *Enhydrocyon sp.*, and (**D**) the extinct mustelid *Megalictis ferox*. All skulls are drawn to approximately the same condylobasal length. (A) and (B) from Radinsky (1982); (C) from Wang (1994); (D) from Hunt and Skolnick (1996).

breakage in large carnivorans (Van Valkenburgh 1988a; Van Valkenburgh and Hertel 1993). Nevertheless, hypercarnivorous bone-crackers evolved at least three times in the Carnivora, once among the Caniformia, in the borophagine canids (Wang et al. 1999), and twice among the Feliformia in the hyaenids and percrocutids (Werdelin and Solounias 1991).

Bone crackers are characterized by some of the same features mentioned earlier in cat-like species (Figs 8 and 9). As can be seen in both the extant spotted hyena (Fig. 9A) and extinct borophagine dog, *Borophagus*, (Fig. 9B), their snouts are somewhat shortened to increase the mechanical advantage of jaw-closing muscles. Postcarnassial molars are reduced in size and number, but unlike the cat-like species, the premolars are relatively massive and conical in shape. In addition, the skull displays a prominent sagittal crest that rises behind the orbits giving the skull a dome-like profile. The high sagittal crest reflects the expansion of attachment area of the primary jaw adductor muscles (temporalis). In addition, the dome-shape appears to strengthen the skull by dissipating compressive forces that occur during bone-cracking (Werdelin 1989). Similarly, in response to high loads placed on the jaws during bone-cracking, the dentaries are deep dorsoventrally with relatively thick cortical bone (Biknevicius and Ruff 1992). Even the microstructure of the teeth has been modified in ways that resist fracture; enamel prisms are layered in a highly complex architecture that resists propagation of cracks (Stefan and Rensberger 1999). In addition to breaking large bones, the powerful teeth and jaws of hyenas also allow them to dispatch carcasses rapidly. For example, Kruuk (1972) observed a single hyena consume a small Thomson's gazelle (estimated mass of 2.5 kg) in less than 2 min, and saw 21 hyenas finish a 220 kg zebra mare and her 150 kg foal in 36 min.

Although bone-cracking borophagines and hyaenids have similarly shaped skulls, there are key

differences between them in their dentition and inferred feeding behavior (Werdelin 1989). Whereas hyenas crack bones between their upper and lower third premolars, tooth wear patterns indicate that borophagines did so between upper carnassial (P4) and lower fourth premolar and carnassial (m1). The hyena arrangement seems "better" in that the slicing function of the carnassials is not compromised as it is in borophagines. Borophagines exhibit heavy wear on their carnassials due to their involvement in bone eating. Werdelin (1989) suggested that the borophagine condition is largely the result of a phylogenetic constraint imposed by their descent from canids that retained substantial postcarnassial molars. As a consequence, the carnassials are situated farther forward in the jaw and fall within the region of maximum bite force production based on a trade-off between maximizing mechanical advantage of muscles and avoiding excessive tensile stress on the jaw joint of the balancing side (approximately halfway between the jaw joint and



Fig. 9 Convergence among bone-cracking hypercarnivores. Lateral views of (A) the spotted hyena, Crocuta crocuta, and (B) the extinct borophagine canid, Borophagus secundus. (A) and (B) from Van Valkenburgh and Jenkins (2002).

lower canine tooth) (Greaves 1983). Postcarnassial molars were reduced early in the history of hyenas and consequently, the carnassial is positioned behind the region of maximum bite force. Despite the blunting of their carnassials, the genus Borophagus includes eight species and persisted for 10 million years in North America (Wang et al. 1999). Carnassials appear to be most important for cutting thick skin and opening carcasses (Van Valkenburgh 1996), and the blunted carnassials of Borophagus suggest it may have scavenged much more frequently than do extant hyenas (Werdelin 1989).

### Wolf-like ecomorphs

Gray wolves, dholes (Cuon alpinus), and African wild dogs (Lycaon pictus) are hypercarnivorous canids that usually take prey that is at least 45% of their own mass, and often larger than themselves (Van Valkenburgh and Koepfli 1993). The elusive South American bush dog (Speothos venaticus) also appears to fall within this grouping, but its natural history is much less well understood. Relative to other canids, these four species have relatively broader snouts, greater mechanical advantage of the jaw adductors, deeper jaws, enlarged anterior teeth (canines, incisors), reduced postcarnassial grinding molars, and elongate blades (trigonids) on their lower m1 (Van Valkenburgh and Koepfli 1993). Notably, the m1 talonid has also become blade-like as opposed to basin-like in all but the wolf, and is referred to as a "trenchant heel" (Wortman and Matthew 1899). The effect of the trenchant heel is to lengthen the blade, presumably allowing a longer cut for a given bite. Several of these features (broader snouts, deeper jaws, jaw muscle leverage, enlarged anterior dentition) are adaptations used in pulling down large prey with jaws alone and are also characteristic of spotted hyenas. Unlike felids or nimravids, whose forelimbs grasp and hold prey, canids and hyaenids must kill with jaws and teeth alone as they have lost the ability to supinate their paws (Ewer 1973; Andersson and Werdelin 2003; Andersson 2004). Often working in groups, they overcome prey using multiple sets of jaws, some holding while others make the kill. During the kill, skulls and teeth are loaded heavily and in response, anterior teeth are robust, dentary bones are deep dorsoventrally, thereby resisting bending stresses, and the snout is broad and so resists torsional stresses imposed by uneven loading at the canines (Van Valkenburgh and Koepfli 1993). Assisting in feeding are the carnassials that have large trigonid blades and trenchant heels, and bite force is
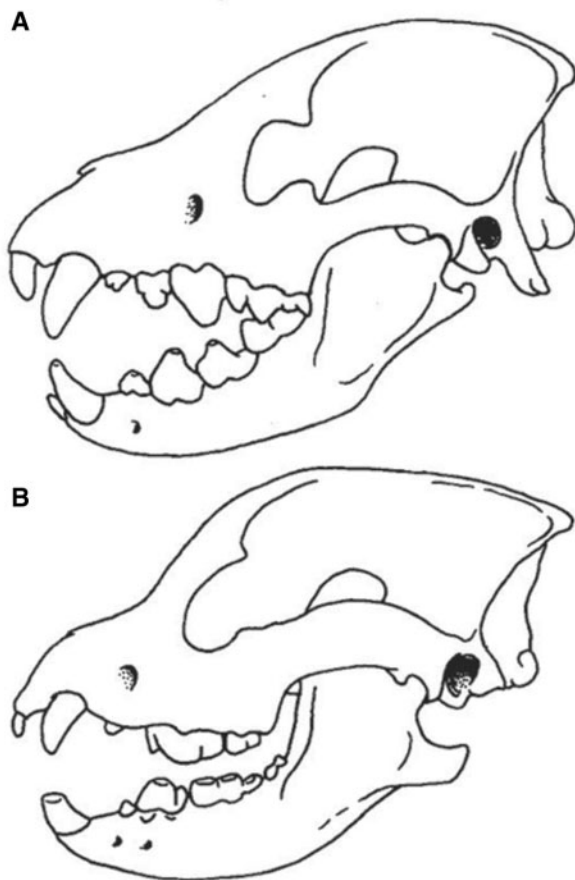
enhanced by reduction of the length of the tooth row (diminution of postcarnassial molars) that shortens the distance from the jaw joint to the canines. In contrast to cat-like and hyena-like ecomorphs, postcarnassial reduction is not as extreme and these teeth function in bone-crushing (Biknevicius and Ruff 1992), and unlike the condition in the hyena-like ecomorphs, the premolars remain relatively narrow buccolingually.

Given that the wolf-like ecomorph is not as extreme in its skull and dental modifications as the hyena-like and cat-like ecomorphs, it is not surprising that it evolved multiple times in at least five families of carnivorans, including one feliform (Hyaenidae) and four caniforms (Canidae, Ursidae, Amphicyonidae, Ailuridae), although not all of these have been as cursorial as modern forms (see subsequently). The convergence in overall form is quite striking despite phylogenetic distance. For example, the wolf-like ursid *Phoberocyon* (Fig. 10C) retains relatively substantial postcarnassial molars, but its enlarged carnassial with a trenchant heel and deep mandible are very similar to those of the gray wolf (Fig. 10B) and the borophagine canid, *Epicyon saveus* (Fig. 10A). Wolf-like hyenas dominated the family in the Miocene of the Old World, prior to the arrival of canids from North America (Werdelin and Solounias 1991). These taxa tended to reduce postcarnassial molars to a greater degree than that seen among other wolf-like forms, while lengthening their premolars (Fig. 10D). Thus, in their wolf-like phase, hyenas forfeited or at least lessened their bone-crushing abilities, and then subsequently evolved bone-cracking abilities in the Plio-Pleistocene.
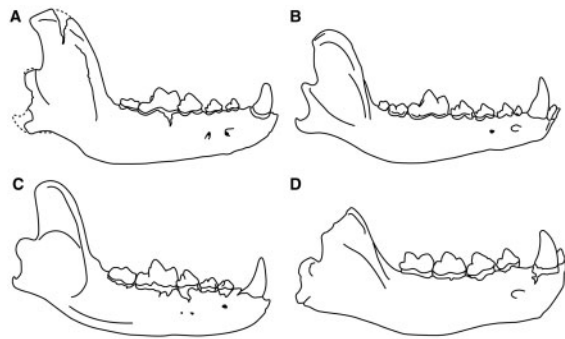


Fig. 10 Convergence among wolf-like hypercarnivores. Lateral views and occlusal views of the dentaries of (**A**) the extinct borophagine canid, *Epicyon haydeni*, (**B**) the extant gray wolf *Canis lupus*, (**C**) the extinct hemicyonine ursid, *Phoberocyon johnhenryi* and (**D**) the extinct hyaenid *Chasmoporthetes ossifragus*. All mandibles are drawn to the approximately the same length. (A) from Wang et al. (1999); (B) from Miles-Gilbert (1980); (C) from White (1947); (D) from Kurten and Anderson (1980).

## Patterns of ecomorphological evolution in the carnivora

A summary table of the evolution of various dietary ecomorphs among families (Table 1) reveals variation among families in the extent of diversification over their evolutionary histories. Mesocarnivory is the basal condition and appears in at least nine of the 12 families. Percrocutids are too poorly known to be certain of their ecomorphological diversity. Nimravids and felids, however, have good fossil records, and as yet, no known mesocarnivorous forms. Both these cat-like families are already highly specialized when they first appear in the fossil record, having largely lost their postcarnassial teeth and greatly foreshortened their skulls (Radinsky 1982; Holliday and Steppan 2004). Given that evolutionary reversals are unlikely (Dollo's law), it seems that their options in terms of returning to a more omnivorous diet were limited as grinding teeth were vestigial or completely absent. Interestingly, the last survivors of the Oligocene radiation of nimravids (e.g., *Nimravus, Pogonodon*) had less specialized lower carnassials with short talonids, suggesting a possible dietary shift that proved unsuccessful (Van Valkenburgh 1991). Postcarnassial molars do occasionally reappear in lynxes, but they are single-rooted pegs with minimal function (Werdelin 1987b). Alternatively, a bone-cracking function potentially could have evolved in felids or nimravids by premolar expansion as occurred in the hyaenids, but this did not happen. An expansion of the

Table 1 The incidence of evolution of various ecomorphs (>7 kg) within carnivoran families

| Family | Hypo | Meso | Cat-like | Hyper Hyena-like | Wolf-like |
|---|---|---|---|---|---|
| Canidae | + | + | + | + | + |
| Ursidae | + | + | | | + |
| Amphicyonidae | | + | | | + |
| Ailuridae | + | + | | | + |
| Procyonidae | + | + | | | |
| Mustelidae | + | + | + | | |
| Felidae | | ? | + | | |
| Nimravidae | | ? | + | | |
| Hyaenidae | + | + | | + | + |
| Percrocutidae | | ? | | + | |
| Herpestidae | | + | + | | |
| Viverridae | + | + | | | |

+ indicates the presence of at least one species within a particular ecomorph.
? indicates uncertainty due to a limited fossil record. For explanation of the ecomorphs, see text.

premolar row would lengthen the jaw, reducing bite force at the canines. In felids and nimravids, the ability of the canine teeth to produce an effective killing bite was never compromised by modifications that might have broadened their diet. Given the evolutionary persistence of cat-like forms, it appears to be a highly successful morphotype, and selection to produce less specialized forms may be weak or absent (Van Valkenburgh 1991).

Although my focus has been on feeding adaptations, there are functional associations between postcranial adaptations and killing behavior that should be mentioned. Cat-like ecomorphs are always characterized by the retention of the ability to supinate their forelimbs, usually in association with retractile claws. Even the most cursorial of felids, the cheetah, retains this ability. This linkage likely results from the advantages provided by holding hold prey somewhat still with grappling limbs, while a relatively precise killing bite is made with elongate canine teeth. Among wolf-like and hyena-like ecomorphs, the association between limb morphology and killing mode is less constrained. Many of these species, including all extant forms, evolved a cursorial morphology, in which elbow joints are limited to fore-aft movements, but other extinct taxa (e.g., borophagine dogs, amphicyonids, ailurids) retained some supinatory ability (Andersson and Werdelin 2003;Andersson 2004; Salesa et al. 2006a), and in one instance, evolved a false thumb used in climbing (the ailurid, *Simocyon battaleri*, Salesa et al. 2006a). These less cursorial wolf-like and hyena-like forms were especially diverse in the Miocene of North America, and their presence might reflect the exceptional species richness of browsing ungulates (Janis et al. 2004) in association with a mixed vegetation structure that did not require extreme cursoriality for hunting success (Andersson and Werdelin 2003).

The appearance of cat-like and wolf-like forms among families that tend to be more mesocarnivorous, such as canids and mustelids, is not distributed evenly over their evolutionary history. In at least two instances, their evolution seems to have occurred in response to ecological opportunity, such as in the absence or near absence of nimravids or felids. The first instance occurred in North America approximately 30–20 ma, during an interval when previously dominant hypercarnivorous predators, nimravid cat-like ecomorphs and wolf-like hyaenodontid creodonts, declined in diversity, finally becoming extinct (Van Valkenburgh 1991). Between 29 and 24 ma, three genera of 10–20 kg, short-snouted hesperocyonine canids with trenchant-heeled

lower carnassials evolved *in situ*, and two genera of hypercarnivorous amphicyonids immigrated from the Old World (*Temnocyon* and *Mammocyon*) (Hunt 1998a). The hypercarnivorous canids subsequently declined in diversity but additional hypercarnivorous taxa appeared in the form of giant mustelids (e.g., *Aelurocyon*) and a hemicyonine ursid (*Phoberocyon*). Notably, this flurry of unusual hypercarnivores occurred largely during a time when both nimravids and felids were absent from North America (Van Valkenburgh 1991; Wesley-Hunt 2005). This "cat gap" (Hunt and Joeckel 1988) lasted from about 25 to 17 ma, at which time the first felids immigrated to the New World. Felids then steadily diversified, reaching a continental maximum of seven genera about one million years ago.

The second example of a burst of evolution of hypercarnivores in a typically more mesocarnivorous family involves canids in South America. Canids first appeared in South America approximately 2.5 ma ago by immigration from North America via the Panamanian isthmus. They arrived on a continent devoid of hypercarnivores, except for a gigantic phorusrhacoid ground bird (Marshall 1977). Canids rapidly diversified by evolution *in situ* and further immigration, reaching a maximum of eight genera (16 species) in the late Pleistocene (Berta 1987). Of these, seven had moderately or well-developed trenchant heels on their lower carnassial, and Berta (1988) suggested that the feature arose independently in two lineages. Over the same time span, felids arrived in South America but diversified little. Why the canids outpaced the felids in the evolution of large hypercarnivores in South America is not clear. It may be that canids arrived significantly earlier than felids and rapidly filled available ecospace, thus inhibiting felid diversification and further immigration. At the end of the Pleistocene, all the hypercarnivorous South American canids but one disappeared as did the largest felid, *Smilodon*. Notably, none of the South American hypercarnivorous canids ever migrated successfully to North America. Throughout the Pleistocene, hypercarnivore diversity in North America was high, with as many as six felids, one wolf-like hyena, and a wolf-like canid present. Thus, the bloom of hypercarnivorous canids in South America appears to have been a classic example of evolutionary opportunism.

The history of carnivorous mammals is characterized by a pattern of rises and falls in which formerly dominant clades of large hypercarnivores declined and were replaced by new taxa that converged along similar

morphological lines (Van Valkenburgh 1999). In a survey of seven such turnover events from Old and New World faunas, only three were likely a result of active competitive replacement based on temporal overlap of similarly sized ecomorphs in both clades (Van Valkenburgh 1999). The others all appeared to represent examples of evolutionary opportunism as described for the South American canids. Whatever the cause, the repeated, relatively rapid filling of large hypercarnivore ecospace suggests it is an attractive dietary specialization that augments fitness. Indeed, of the 12 families of carnivorans surveyed here, only one, the procyonids, is not known to have evolved hypercarnivory at least once (Table 1).

## Advantages and disadvantages of hypercarnivory

Meat exceeds plant and arthropod foods in energy content and ease and speed of digestion. Consequently, that alone favors the evolution of hypercarnivory. Carnivorous diets are associated with higher basal rates of metabolism, faster growth rates, and higher fecundity in carnivorans (McNab 1989; Munoz-Garcia and Williams 2005). Consequently, if ecological conditions, such as an already high diversity of predators, do not inhibit the evolution of hypercarnivory, mesocarnivorous species are expected to evolve in that direction.

Nevertheless, there are a number of costs, both short-term and long-term, to becoming a hypercarnivore, especially one that takes relatively large prey. Predation can be a risky business especially when prey is large relative to predator. Serious injury and death resulting from the actions of struggling or escaping prey have been observed in African wild dogs (Creel and Creel 2002), lions (Schaller 1972), and gray wolves (Rausch 1967; Mech and Nelson 1990; Smith et al. 2006). Less serious, but still costly and more likely, are risks of fracturing teeth. A survey of nine species of large carnivorans revealed that one out of every four individuals had at least one broken tooth, and most of these were canines (Van Valkenburgh 1988a). Fracture rates are higher among bone-crackers, and among more carnivorous species compared with omnivorous ones (Van Valkenburgh, manuscript in preparation). In addition to these costs incurred by hunting and feeding, there are perils associated with competition among hypercarnivores. Dangerous intraspecific and interspecific conflicts among predators over carcasses occur regularly, as well as mortality due to intraguild predation (Palomares and Caro 1999; Van Valkenburgh 2001b; Donadio and Buskirk 2006).

Finally, new observations on the acquisition of hunting skills in large carnivorans reveal that it can take years for young adults to achieve the hunting success rates of their parents. For example, spotted hyenas showed a significant increase in hunting success beyond 4 years of age (Holekamp et al. 1997). Lions younger than two are unlikely to kill wildebeest or zebra (Schaller 1972), cheetahs take more than 3 years to acquire their mother's level of skill (Caro 1994), and yearling wild dogs are more of a hindrance than a help in hunting (Creel and Creel 2002). Part of the delay in acquisition of skills relates to physical development and increase in mass, but there is also a lengthy learning phase that involves both observation and practice (Stander 1992; Caro 1994). During this period of suboptimal foraging, the risk of mortality is likely to be relatively high.

There also appear to be macroevolutionary costs associated with hypercarnivory. As noted earlier, dominant clades of hypercarnivores have limited geologic lifespans in which they diversify to a maximum and then gradually decline to extinction. Given that hypercarnivores evolve repeatedly, the advantages of becoming more hypercarnivorous seemingly outweigh the disadvantages, and it is not difficult to understand why they diversify especially if the niche is relatively depauperate in species. However, what is harder to comprehend is why an apparently successful clade declines. Recently, it has been suggested that the declines are due to an increased vulnerability to species extinction as a result of large body size and high trophic level (Van Valkenburgh et al. 2004). Both of these features are associated with species that exist at relatively low densities, and small population sizes increase the probability of extinction due to stochastic events (e.g., disease, severe climatic change) (Stanley 1979; Brown and Maurer 1986).

Phylogenetic increase in body size over evolutionary timescales, or Cope's Rule, is a common phenomenon in the mammalian fossil record, and has been documented in numerous carnivoran lineages (Alroy 1998). Among predators, larger body size expands the range of potential prey sizes, reduces the risk of intraguild predation, favors victory in interspecific interference encounters, as well as improving reproductive success and thermal efficiency (Stanley 1973; Eaton 1979; Sinclair et al. 2003; Kingsolver and Pfennig, 2004; Donadio and Buskirk, 2006). What has been less well recognized is the association between increasing size and greater specialization for hypercarnivory in the carnivore fossil record. A recent study of diet and increasing body size in two extinct clades of canids,

Hesperocyoninae and Borophaginae, showed a close relationship; in both subfamilies, as body mass increased, snouts shortened, jaws deepened, carnassials enlarged, and post-carnassial grinding molars diminished (Van Valkenburgh et al. 2004). The cause of the dietary shift may be related to foraging energetics. Carbone et al. (1999) documented a significant jump in typical prey size of carnivorans above a predator mass of about 21 kg. Carnivorans above this size tend to take prey that are at least 45% of their own mass whereas those below this threshold take much smaller prey (e.g., rodents, lagomorphs, arthropods). They argued that this reflected energetic constraints imposed by tradeoffs between energy expended and energy gained in foraging. If they hunted smaller prey, carnivores larger than about 20 kg would get a caloric return on their hunting investment insufficient to maintain body condition.

To be an effective predator of large prey requires morphological specializations of the kind described in this article, some of which involve loss of part or all of a structure. For example, the tooth row is reduced and the snout is shortened. The lower carnassial becomes more specialized for slicing through loss of the talonid or its conversion to a trenchant heel. The effect of the trenchant heel is to lengthen the blade, allowing a longer cut for a given bite. In situations where rapid ingestion is favored, such as among littermates or adults feeding together on a kill, selection should favor the evolution of a longer blade and greater bite force. Notably, a study of active consumption rates (ACR, or mass consumed per unit of time actively feeding) in wolves, coyotes and grizzly bears revealed that ACR increased with sociality (wolf > coyote > bear) (Wilmers and Stahler 2002).

In the fossil canid study (Van Valkenburgh et al. 2004), evolutionary reversal to a more generalized morphology and inferred diet was extremely rare, as seems to be the case generally for structural evolution (Marshall et al. 1994). Using a sister-taxon approach, Holliday and Steppan (2004) also found that hypercarnivores were more limited in subsequent morphological evolution than were less specialized forms, supporting the rarity of reversal. Among carnivores, the combined effects of the difficulty of reversal and selection for large size and hypercarnivory act as a macroevolutionary ratchet (Van Valkenburgh 1999), limiting the future diversity of a clade as its member species become increasingly large, specialized, and less abundant (Viranta 2003; Van Valkenburgh et al. 2004). In fossil canids, the appearance of large-bodied hypercarnivores in both subfamilies was associated with a decline in average duration of species, suggesting a greater vulnerability of species to extinction. Selection at the individual level for larger size resulted in lineages that were less likely to persist and consequently, the ultimate demise of the clade.

The combination of Cope's Rule, Dollo's law, and consequent greater susceptibility to extinction results in a Cenozoic fossil record of successive dynasties of large hypercarnivores. Although the Permian record of nonmammalian synapsids (mammal-like reptiles) is not nearly as dense, a similar pattern of dynastic replacement is apparent among therapsids (Van Valkenburgh and Jenkins 2002), and should be true of dinosaurs, as well. Because the nature of the resource has been relatively stable (flesh, skin, and bones), there have been repeated experiments in the evolution of similar ecomorphs, each of which started from a phylogenetically and morphologically unique position. Thus, essential features for a given diet, such as longer cutting blades, enhanced mechanical advantage of the jaw musculature, and enlarged canine teeth evolve iteratively, reinforcing our hypotheses of function. It is hard to imagine, how we could improve on this experimental design except of course, by including observations of feeding performance in all the extinct species. Until we master time travel, we can busy ourselves with refining our understanding of the form–function relationship in carnivores through field observations and experiments. We need a better understanding of the costs of hypercarnivory, in terms of development and risks associated with competition, predation, and starvation. Finally, more complete documentation of the carnivoran fossil record, including species' morphologies and temporal and spatial distributions, as well as complete phylogenies for all the families, would allow us to test the generality of the macroevolutionary ratchet.

## Acknowledgments

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