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Evolution of hypercarnivory: the effect of specialization on morphological and taxonomic diversity

Jill A. Holliday and Scott J. Steppan

Abstract.—The effects of specialization on subsequent morphological evolution are poorly understood. Specialization has been implicated in both adaptive radiations that result from key innovations and evolutionary ''dead ends,'' where specialized characteristics appear to limit subsequent evolutionary options. Despite much theoretical debate, however, empirical studies remain infrequent. In this paper, we use sister-group comparisons to evaluate the effect of morphological specialization to a particular ecological niche, hypercarnivory, on subsequent taxonomic and morphological diversity. Six sets of sister groups are identified in which one clade exhibits hypercarnivorous characteristics and the sister clade does not. Comparison results are summed across the categories ''hypercarnivore'' and ''sister group.'' We also evaluate whether increasing degrees of specialization are correlated with decreasing phenotypic variation. Results presented here indicate that specialization to hypercarnivory has no effect on taxonomic diversity, but a strong effect on subsequent morphological diversity related to the jaws and dentition, and that increasing specialization does not correlate with morphological diversity except in the most specialized saber-toothed taxa, which exhibit higher variance than less specialized morphs, possibly due to selection on other characteristics.

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Introduction

The effect of specialization on subsequent taxonomic and morphological evolution is fundamentally important to the tempo and mode of evolution and the role of adaptation in macroevolution (e.g., Futuyma and Moreno 1988; Janz et al. 2001). However, there is little consensus as to how specialization affects diversity: does it act to increase or decrease rates of cladogenesis? How does specialization affect probability of extinction? Does it constrain further adaptation? Certainly, much attention has been given to the possibility that particular specializations may promote taxonomic diversification; that is, a morphological or behavioral specialization may act as a key innovation, leading to an increase in rates of cladogenesis (Liem 1973; Mitter et al. 1988; Farrell et al. 1991; Hodges and Arnold 1995; de Queiroz 1999; Dodd et al. 1999), but empirical studies have produced contrasting results. Some workers have found that specialization increases taxonomic diversity (e.g., Liem 1973; Mitter et al. 1988; Farrell et al. 1991; Hodges and Arnold 1995; de Queiroz 1998; Dodd et al. 1999), some report the opposite pattern (e.g., Price and Carr 2000), and others find no effect at all (e.g., Wiegmann et al. 1993; de Queiroz 1999; Janz et al. 2001).

Despite numerous studies of the effect of specialization on taxonomic diversification, studies of its effects on subsequent morphological diversity (disparity) are few. In a theoretical context, many workers have suggested that possession of certain morphological character states may reduce the ability to attain certain other states (Lauder 1981; Smith et al. 1985; Emerson 1988; Futuyma and Moreno 1988; Werdelin 1996; Donoghue and Ree 2000; Wagner and Schwenk 2000), implying that the subsequent evolutionary trajectories of some specialized taxa may be limited. At its extreme, therefore, specialization could act as a dead end (Moran 1988; Janz et al. 2001), limiting morphological diversification and potentially reducing rates of cladogenesis or, alternatively, increasing extinction rates as specialized taxa reduce their ability to adapt to changing conditions. However, few studies have directly identified and tested effects of specialization on subsequent phenotypic change (but see Liem 1973; Moran 1988; Warheit et al. 1999).

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We determined the effect of dental and cranial specialization to a meat-only diet, hypercarnivory, on subsequent morphological and taxonomic diversity in mammalian carnivores. We used an explicitly phylogenetic approach and applied it to repeated convergences on hypercarnivory, increasing our statistical power by evaluating results from multiple sister groups. We specifically tested the hypotheses that (1) hypercarnivores have lower taxonomic and craniodental morphological diversity than do their sister groups and (2) increasing specialization leads to lower morphological diversity. To test these hypotheses, we quantified and compared diversity between hypercarnivore clades and their primitively nonhypercarnivorous sister groups. The advantage of using sister groups is that both groups (when their stem lineages are included) have by definition had equal time to diversify. We used both species counts and the methods of Slowinski and Guyer (1993) to assess taxonomic diversity. We compared morphological diversities (disparities) by comparing variances of factor scores obtained from principal-components analysis (Foote 1992, 1993; Wills et al. 1994) and by comparing the differences in average frequency of character change between categories (Sanderson 1993). Finally, we used discriminant function analysis to assign ''degrees of specialization'' to hypercarnivores and compared the disparity values of different levels of specialization.

The Order Carnivora

The order Carnivora is composed of 11 extant and two extinct families of meat-eating mammals. The diagnostic character for Carnivora is the carnassial pair, the fourth upper premolar and first lower molar, which in this group have been modified as shearing blades for effective slicing of meat. Although the shearing carnassials are a synapomorphy for this group, members of Carnivora, hereafter called carnivorans, have diversified to occupy a wide range of ecological niches, and include highly carnivorous clades such as cats (Felidae) and weasels and martens (Mustelidae), generalists like the dogs and foxes (Canidae), insectivores like the mongoose (Herpestidae), omnivores like the bears (Ursidae) and raccoons (Procyonidae), and strict herbivores such as the giant panda. Variation in ecology is strongly reflected in the dentition (Van Valkenburgh 1989), so a more omnivorous/frugivorous diet is accompanied by a relative increase in grinding surfaces whereas a more highly carnivorous diet is reflected by a relative decrease in grinding surfaces and an increase in shearing edges.

Because of the tight correlation between dentition and ecology, dental characters can be used effectively to infer aspects of the diet or ecological niche. Van Valkenburgh (1988, 1989) showed that variables including relative blade length, canine tooth shape, premolar size and shape, and grinding area of the lower molars distinguished between dietary types in extant carnivores. She compared guild compositions of carnivoran communities, concluding that each guild comprised a broadly similar set of morphotypes occupying a limited number of ecological niches (Van Valkenburgh 1988, 1989). There is thus a substantial overlap in certain regions of morphospace (Crusafont-Pairo and Truyols-Santonja 1956; Radinsky 1982; Van Valkenburgh 1988, 1989) resulting from convergence of unrelated taxa to similar ecomorphological types, including meat-specialists, bone-crackers/scavengers, omnivores, and generalists (Van Valkenburgh 1988; Werdelin 1996). Such iterative evolution produces natural replicates and is conducive for comparative study.

Of the recognized carnivoran ecomorphs, the niche of the meat specialist, or hypercarnivore, is associated with a diet comprising more than 70% meat, in contrast to the generalist (Van Valkenburgh 1988, 1989), which may eat 50–60% meat with vegetable matter and invertebrates making up the remainder of the diet. Ecological specialization to hypercarnivory is associated morphologically with specific changes in the skull and dentition that include a relative lengthening of the shearing edges, composed of the trigon of the upper fourth premolar and the trigonid of the lower first molar, and reduction or loss of the postcarnassial dentition, the second and third lower molars and first and second upper molars, teeth used for chewing or grinding food (Van Valkenburgh 1989; Hunt 1998). The facial

portion of the skull frequently shortens as well, an alteration thought related to maintaining high bite force (Van Valkenburgh and Ruff 1987; Radinsky 1981a,b; Biknevicius and Van Valkenburgh 1996). Although the absence of dietary data for many fossil taxa suggests that the term ''hypercarnivore-morph'' may be more appropriate, in this paper those taxa with morphological characteristics consistent with a hypercarnivorous diet will be called ''hypercarnivores.'' Figure 1A illustrates a generalized carnivoran with a ''typical'' tooth formula; individual cusps are labeled. Figure 1B–D illustrates hypercarnivorous modifications in order of increasing specialization. Certain extant and extinct members of such diverse lineages as mustelids (weasels and stoats), viverrids (civets and genets), canids (dogs and foxes), hyaenids (hyenas), amphicyonids (extinct bear-dogs), and ursids (bears) have all evolved phenotypes characteristic of hypercarnivory (Van Valkenburgh 1991; Biknevicius and Van Valkenburgh 1996; Werdelin 1996), although the most extreme cases appear to be in the families Felidae (cats) and Nimravidae (extinct, noncat saber-tooths). Taxa trending toward hypercarnivory are frequently referred to as ''cat-like'' (Martin 1989; Hunt 1996, 1998; Baskin 1998), a descriptor that reflects the distinctive adaptations of felids for this niche.

In a study of evolution of hypercarnivory in the family Canidae, Van Valkenburgh (1991) commented on the low apparent variability in the cranial and dental morphologies of felids and nimravids relative to canids, and suggested that this was possibly due to the extreme specialization to hypercarnivory in the former two groups. Lack of variation in felid craniodental characteristics has been noted qualitatively by many authors (e.g., Radinsky 1981a,b; Flynn et al. 1988), but few have attempted to quantify this phenomenon or to ascertain cause and effect. Quantitative evaluations of felid diversity have been generally limited to within family or genus (e.g., Glass and Martin 1978; Werdelin 1983; Kieser and Groeneveld 1991; O'Regan 2002) or, if among families, have dealt primarily with relative positioning of groups in morphospace (e.g., Glass and Martin 1978; Radinsky 1981a,b, 1982; Werdelin 1983; Van Valkenburgh 1991) or body-size correlates (Van Valkenburgh 1990; Gittleman and Purvis 1998; Gardezi and da Silva 1999).

There are, of course, various reasons why any particular clade might not exhibit certain morphologies, including lack of genetic variation, functional constraint, stabilizing selection, or competition (Smith et al. 1985; Brooks and McLennan 1991). Additional causes may include intrinsically low rates of evolution or a recent rapid radiation (Schluter 2000), either of which might suggest a pattern of constraint but actually reflect a lack of time. Another possibility is sampling bias, where alternative morphotypes may exist but occur in geographic areas where sampling is rare or nonexistent. Any study of the evolution of a character therefore benefits from the inclusion of as many different groups as possible that have evolved the trait of interest. We evaluated six separate clades of hypercarnivorous taxa for which phylogenies are available in the literature. By including a variety of groups, we were able to mitigate the effects of phylogeny and thus evaluate the effects of the specialization itself. Furthermore, because different hypercarnivorous taxa exhibit varying *degrees* of specialization, we could also assess the effects of increasing specialization on character change and morphological diversity.

Methods

Definition

Because identification of a hypercarnivorous taxon is partly a subjective decision, opinions may vary between workers. In a broad sense, the designation ''hypercarnivore'' has been used to describe taxa that have increased the slicing component of the dentition relative to the grinding component (Van Valkenburgh 1991). However, taxa that fit this overall categorization can be further subdivided according to relative robustness (widening) of the premolars (Van Valkenburgh 1991). In combination with the features of elongated blade, reduced postcarnassial teeth, and a shortened face, normal-sized or narrowed premolars produces the ''cat-like'' phenotype. In contrast, relative broadening of the

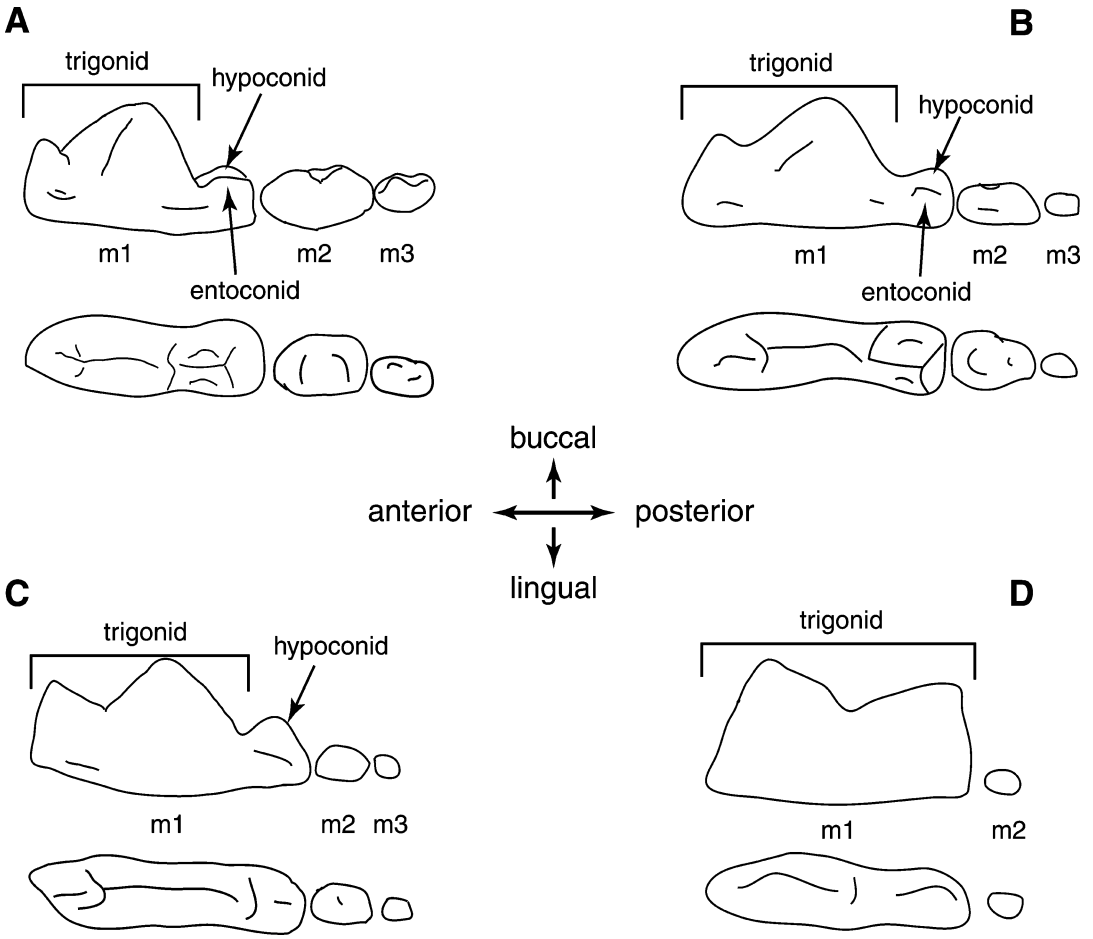

FIGURE 1. A, Generalist dentition. The talonid is basined, with the hypoconid and entoconid cusps roughly equal in size. Note that the m2 and m3 are unreduced. B, Dentition trending toward hypercarnivory. The shearing blade is slightly elongate, and the hypoconid and entoconid are unequal in size (hypoconid is larger). The m2 and m3 are somewhat reduced in size. C, Trenchant talonid. The shearing blade is elongate, and the hypoconid is enlarged and medial, whereas the entoconid is completely reduced. The m2 and m3 are reduced. D, Note the absence of a talonid, including loss of the hypoconid and entoconid. The shearing blade extends the entire length of the m1, the m2 is reduced or absent, and the m3 is absent.

premolars appears to be an alternative trajectory that leads not to a truly cat-like condition but toward more hyena-like (bone-cracking) characteristics (Van Valkenburgh 1991). Although end-members of these groupings (e.g., felids vs. hyaenines) are easily differentiated, gradations between groups can be subtle, as can be the difference between a generalist with hypercarnivorous tendencies and a hypercarnivore (e.g., between some ancestors and descendants). To reduce the necessity for arbitrary judgments, for this study we established a minimum definition of a hypercarnivore in order to more objectively differentiate between cat-like, hyena-like, and transitional forms. The following combination of characteristics was therefore considered minimally diagnostic when evaluating putatively hypercarnivorous taxa for inclusion in this study: trigonid not less than 70% of the length of the m1, width of the fourth lower premolar not greater than 60% of its length, entoconid and hypoconid unequal.

Given the above qualifications, it is important to note that hypercarnivorous clades in this study were recognized on the basis of being *basally* hypercarnivorous. Therefore, if the first two branches for a given clade were hypercarnivorous, the entire group was considered so, because hypercarnivory was estab-

lished as the ancestral condition. Any evolution of the phenotype subsequent to that ancestral condition was then considered part of the total diversity of that clade.

Taxa and Phylogenies

Hypercarnivorous taxa were initially identified through literature searches for taxa described as hypercarnivorous or highly predaceous. Diet (where known) and dental formula were also taken into account. Besides all members of the families Felidae and Nimravidae, taxa described by various workers as hypercarnivorous include the hyaenid genera *Chasmaporthetes*, *Hyaenictis*, and *Lycyaena* (Werdelin and Solounias 1991); members of the Simpsonian subfamily Mustelinae (now recognized as paraphyletic), especially the genus *Mustela* (Ewer 1973; King 1989); the viverrid *Cryptoprocta ferox* (Wozencraft 1984, 1989; Werdelin 1996); and hesperocyonine canids of the genera *Enhydrocyon*, *Ectopocynus*, and *Parenhydrocyon* (Van Valkenburgh 1991; Wang 1994). Additional taxa identified include the ''paleomustelids'' *Megalictis* and *Oligobunis* (Baskin 1998), as well as certain borophagine canids including *Euoplocyon*, *Epicyon*, *Osteoborus*, and *Borophagus* (Wang et al. 1999); the amphicyonids *Daphoenictis* (Martin 1989), *Temnocyon*, and *Mammocyon* (Van Valkenburgh 1991, 1999); and the ursids *Hemicyon johnhenryi* (Van Valkenburgh 1991), *Cephalogale*, and *Phoberocyon* (Van Valkenburgh 1999).

A literature search for species-level, character-based phylogenies for these taxa and their sister groups produced mixed results. In some cases, character-based phylogenies are not available and these taxa were consequently excluded from study (e.g., amphicyonids, ursids, and paleomustelids). In those cases where multiple phylogenies were available, we critically examined the possibilities and chose the better-supported tree based on criteria that included use of a data matrix, type and amount of evidence (molecular vs. morphological, kind and number of morphological or molecular characters, appropriateness of gene or genes used), and congruence with alternative phylogenies. Sister groups were identified from available higher-level analyses; however, in several cases (e.g., *Mustela*, Felidae), there is significant disagreement regarding the appropriate sister taxon. When a definitive sister group could not be determined, analyses were repeated with several alternative sister groups. Two groups that contain hypercarnivorous taxa, the borophagine canids and the ''paleomustelids,'' were not included in diversity comparisons but were included in degree-of-specialization analyses. Borophagines, which trend strongly toward a bone-crushing phenotype, did not meet our working definition of hypercarnivores and were consequently excluded from sister-group comparisons. However, the distinctive bone-crushing modifications of the group were useful in determining relative positioning in morphospace and in assigning degrees of specialization for other taxa being evaluated. In addition, there is a substantial range of variation within the ''bone-crushing'' specialization of borophagines, and although sampling was incomplete, the placement of specific taxa such as the derived *Euoplocyon* was of general interest. Paleomustelids did not meet the criteria set out for phylogenies (none available were based on a data matrix), but because these taxa have been repeatedly described as very specialized to the hypercarnivore niche (Baskin 1998), their position in morphospace relative to other hypercarnivores was of interest.

Six sets of sister groups did meet the criteria for inclusion in this study, in that all met the minimum requirements for a hypercarnivore and a species-level phylogeny was available. These sister-group sets are the clades Felidae/Hyaenidae, *Mustela/Galictis-Ictonyx-Pteronura-Lontra-Enhydra-Lutra-Amblonyx-Aonyx*, *Philotrox-Sunkahetanka-Enhydrocyon/Cynodesmus*, *Cryptoprocta/Eupleres-Fossa*, *Chasmaporthetes-Lycyaena-Hyaenictis/Palinhyaena-Ikelohyaena-Belbus-Leecyaena*(*Hyaena*)*-Parahyaena-Hyaena-Pliocrocuta-Pachycrocuta-Adcrocuta-Crocuta* (hereafter designated *Palinhyaena-Crocuta* [Werdelin and Solounias 1991]), and Nimravidae/Aeluroidea. Phylogenies used are shown in Appendix A.

Sister Groups

Felidae/Hyaenidae.—Relationships among the feliform carnivore families—Felidae, Hyaeni-

dae, Viverridae, and Herpestidae—have been notoriously difficult to ascertain. The hypercarnivorous family Felidae is most commonly recognized as sister to the family Hyaenidae (Wozencraft 1989; Wyss and Flynn 1993; Bininda-Emonds et al. 1999), although other workers have found support for a sister-group relationship with the insectivore/omnivore/generalist group Viverridae (Hunt 1987; Hunt and Tedford 1993) or all other feliforms (Flynn and Nedbal 1998). Use of Hyaenidae may be considered a relatively conservative comparison, because Hyaenidae has less diversity than either of the alternative sister groups (Flynn et al. 1988). However, it should be noted that a hypercarnivorous clade (*Chasmaporthetes-Lycyaena-Hyaenictis*) is nested within the hyaenids as well. Because of the lack of consensus regarding the appropriate sister taxon, we performed two comparisons for Felidae, one against Hyaenidae and one against Viverridae. Within Felidae, the relationships among the various genera and species have likewise been problematic. The phylogeny we used is a composite based on the phylogenies of Mattern and McLennan (2000) for crown-group felids and of Neff (1982), Turner and Anton (1997), and Martin (1998a) for machairodontines. Consensus for the ancestry of felids leads from *Proailurus*, which exhibits a trenchant talonid and two lower molars, to *Pseudaelurus*, which has a much reduced talonid and a reduced m2, to the clade comprising Felinae + Machairodontinae, which has lost the m2 as well as the talonid and has devoted the entire lower carnassial to slicing (see Ginsburg 1983; Hunt 1996, 1998; Martin 1998b). The species-level phylogeny for Hyaenidae is from Werdelin and Solounias (1991).

Chasmaporthetes-Lycyaena-Hyaenictis/Palinhyaena-Crocuta.—Within Hyaenidae, tendencies toward increased carnivory first appear in generalist forms such as *Ictitherium*, *Thalassictis*, *Hyaenotherium*, and *Hyaenictitherium*. Recognizably hypercarnivorous taxa are present in the clade composed of the genera *Chasmaporthetes-Lycyaena-Hyaenictis*. These taxa have been described as cursorial and somewhat ''cat-like'' (Werdelin and Solounias 1991). Their sister clade paralleled the development of certain of these hypercarnivorous characteristics in the evolution of a trenchant heel and loss of the m2 in some taxa (Werdelin and Solounias 1991, 1996), but members of the *Palinhyaena-Crocuta* clade trend strongly toward bone-cracking modifications (e.g., premolar width >60% of premolar length), and extant hyaenids in this group are known to occupy a scavenging/bone-cracking niche (Ewer 1973; Nowak 1999) in contrast to the apparently highly predaceous tendencies of *Chasmaporthetes-Lycyaena-Hyaenictis*. We follow Werdelin and Solounias (1991) in recognizing these groups as monophyletic with distinctly different ecologies, acknowledging that the taxa in the *Palinhyaena-Crocuta* clade have become specialists in their own right.

Philotrox-Sunkahetanka-Enhydrocyon/Cynodesmus.—Within the hesperocyonine canids, the clade identified as hypercarnivorous comprises the genera *Enhydrocyon*, *Philotrox*, and *Sunkahetanka*. The four species of *Enhydrocyon* are clearly hypercarnivorous relative to earlier hesperocyonines—*Enhydrocyon crassidens* has been described as the most derived hesperocyonine for this niche. However, *Philotrox* and *Sunkahetanka* also exhibit modifications characteristic of hypercarnivory, along with other characteristics consistent with bone-crushing habits. In Wang's (1994) cladogram, *Sunkahetanka* and *Philotrox* are successive outgroups to *Enhydrocyon*, thus establishing hypercarnivory as the basal condition for this clade. We therefore included these taxa in a hypercarnivorous clade and contrast them to a sister group composed of the two-species nonhypercarnivorous genus *Cynodesmus*. Although the immediate outgroup to this *Philotrox-Sunkahetanka-Enhydrocyon/Cynodesmus* clade, *Mesocyon*, has also been described by some workers (Van Valkenburgh 1991; Wang 1994) as hypercarnivorous, its tendencies are very slight, and it does not meet our criteria: *Mesocyon* retains a strongly basined talonid and well-developed postcarnassial teeth (m2 and m3) and has a relative blade length of less than 70%.

Cryptoprocta/Eupleres-Fossa.—*Cryptoprocta* is a monotypic genus in the family Viverridae (Wozencraft 1984) whose phylogenetic affinities have been problematic. There is ongoing work regarding the relationships of viverrids

(e.g., Veron and Catzeflis 1993; Veron 1995; Veron and Heard 1999); however, these phylogenies have limited taxon and character sampling and are not adequate for our purposes. The most robust phylogeny for viverrids presently available, and that based on the widest sampling, is that of Wozencraft (1984), wherein the two taxa *Eupleres goudotii* and *Fossa fossana* are the sister group to *Cryptoprocta ferox*.

Mustela/Galictis-Ictonyx-Pteronura-Lontra-Enhydra-Lutra-Amblonyx-Aonyx.—*Mustela* is a highly predaceous genus of small carnivores in the family Mustelidae (Ewer 1973; King 1989). Despite a great deal of recent attention that has included both molecular and morphological analyses (Bryant et al. 1993; Masuda and Yoshida 1994; Dragoo and Honeycutt 1997; Koepfli and Wayne 1998), intrafamilial relationships remain contentious. As a result, we used several alternative phylogenies (Bryant et al. 1993; Dragoo and Honeycutt 1997; Koepfli and Wayne 2003) and evaluated results for each group in turn.

Nimravidae/Aeluroidea.—In contrast to the large number of phylogenetic hypotheses proposed for extant Mustelidae, the extinct sabertoothed family, Nimravidae, is relatively impoverished. Of the phylogenies available, only those of Bryant (1996) for Nimravinae and Geraads and Gulec (1997) for Barbourofelinae meet the criteria for inclusion. We grafted these nonoverlapping phylogenies together to create a single composite tree for use in our study. The relationship of Nimravidae to other carnivoran taxa is also not well established, and various workers place nimravids basal to all of Carnivora (Neff 1983) or to Canidae (Flynn et al. 1988), or sister to Felidae (Martin 1980) and Feliformia (Baskin 1981). Bryant (1991) and Wyss and Flynn (1993) evaluated the various hypotheses and attempted to obtain a better resolution by incorporating additional evidence. Both concluded that the best (if weakly) supported hypothesis is that Nimravidae is sister to the aeluroid carnivorans, an opinion followed here.

Taxonomic Diversity

Several methods are available for comparison of taxonomic diversity and determination of whether rates of cladogenesis have been affected by a given trait. The simplest is a binomial sign test (Sokal and Rohlf 1994), which allows direct comparison of species diversity between sister groups. Species are counted and the group (hypercarnivorous vs. nonhypercarnivorous) with more species receives a plus sign; the group with fewer species receives a minus. The numbers of signs across all groups under study are then contrasted under a null hypothesis of no significant difference. A more complex alternative is that set forth by Slowinski and Guyer (1993). Their method, which incorporates a model of random speciation and extinction, uses Fisher's combined probability test (Sokal and Rohlf 1994) to determine whether certain traits have caused significantly higher diversity. This approach has been applied in evaluations of species diversity for both plants (Hodges and Arnold 1995; Dodd et al. 1999; Smith 2001) and animals (Gardezi and da Silva 1999).

We obtained species counts from the primary literature (see Table 1 for references) for all six sister-group pairs under study and applied both tests against the null hypothesis that specialization to hypercarnivory had no effect on the subsequent diversification of an affected clade. The most common alternative hypothesis is that specialization to hypercarnivory, as with many other kinds of resource specialization, should reduce subsequent cladogenesis. However, this may not be the case. Using matrix representation to create supertrees for all extant carnivoran taxa, Bininda-Emonds et al. (1999) tested for adaptive radiations under the methods of Nee et al. (1995). Contrary to the argument that specialization should negatively affect cladogenesis, their results suggested that both *Mustela* and Felidae may have undergone more speciation events than would be expected by chance (Bininda-Emonds et al. 1999), although, for Felidae at least, this result may be an artifact of a high rate of extinction in the sister group (Hyaenidae). Because the effects of specialization on taxonomic diversity are uncertain, we performed one-tailed tests in the direction of decreased species diversity and then repeated the tests in the direction of increased species diversity.

TABLE 1. Taxonomic diversity. References for species counts are as follows: Hesperocyoninae: Wang (1994); Mustelidae, Viverridae, and Herpestidae: Nowak (1999); Hyaenidae: Werdelin and Solounias (1991); Felidae: Nowak (1999), Berta and Galiano (1983), Martin (1998a), Ginsburg (1983), Turner and Anton (1997), Berta (1987), Hemmer (1978), Glass and Martin (1978), Werdelin (1985), Hunt (1996); Nimravidae: Bryant (1996), Geraads and Gulec (1997).

Hypercarnivore	No. of species	Sister group	No. of species
Felidae	86	Hyaenidae	69
Hyaenidae: *Chasmaporthetes/Lycyaena/Hyaenictis*	15	Hyaenidae: *Crocuta/Palinhyaena*	15
Nimravidae	24	Felidae/Hyaenidae/Viverridae/Herpestidae	228
Canidae: Hesperocyoninae *Enhydrocyon/Philotrox/Sunkahetanka*	6	Canidae: Hesperocyoninae *Cynodesmus*	2
Viverridae: *Cryptoprocta*	1	Viverridae: *Eupleres/Fossa*	2
Mustelidae: *Mustela*	17	Mustelidae: *Galictis/Ictonyx/Pteronura/Lontra/Enhydra/Lutra/Amblonyx/Aonyx*	26

Morphological Diversity

Data Collection.—Cranial and dental material in the collections of the American Museum of Natural History, the Field Museum, the Florida Museum of Natural History, and the Natural History Museum, London, was measured for our study. Appendix B lists species name, collection number, and museum for each specimen. Measurements were taken to the nearest 0.01 mm with digital calipers. Where only a single specimen was available for a species, measurements were repeated two to three times, and the mean taken of those measurements. Where multiple specimens were available, two to four specimens were measured, and those measurements were used to obtain a mean for the species. Where information regarding sex was available and species were known to be sexually dimorphic (e.g., *Mustela*, some felids), only males were included in the data set.

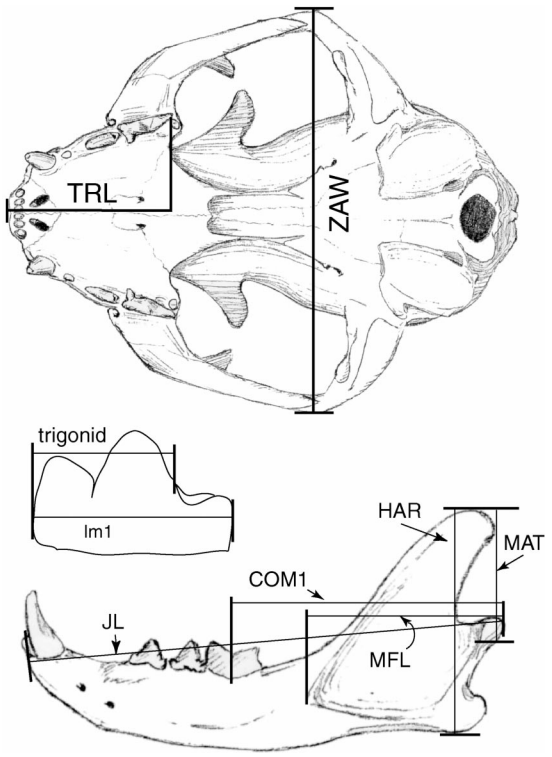

FIGURE 2. Representative cranial and dental measurements used in morphological analyses. JL, jaw length; TRL, tooth-row length; ZAW, zygomatic-arch width; lm1, length of M1; trigonid, trigonid length; HAR, height of ascending ramus; MAT, distance from condyloid process to coronoid process; MFL, distance from condyle to front of masseteric fossa; COM1, distance from carnassial notch to condyle.

Measurements.—We measured 290 specimens for the following distances (Fig. 2): jaw length (JL), tooth-row length (TRL), zygomatic-arch width (ZAW), length of P4 (lP4), length of M1 (lM1), length of M2 (lM2), length of p3 (lp3), width of p3 (wp3), length of p4 (lp4), width of p4 (wp4), length of m1 (lm1), width of m1 (wm1), length of m2 (lm2), length of m3 (lm3), trigonid length (m1 trigonid), height of ascending ramus (HAR), distance from condyloid process to coronoid process (MAT), distance from condyle to front of masseteric fossa (MFL), and distance from carnassial notch to condyle (COM1). The variables JL, TRL, ZAW, MAT, MFL, and COM1 are from Radinsky (1981a,b). For hesperocyonine canids, we used the published data of Wang (1994).

The following eight shape or proportion variables were derived from the original measurements. These variables were used for both disparity analyses and character mapping and are based in part on those of Van Valkenburgh (1988, 1989): relative blade length (RBL, defined as trigonid/lm1), grinding surface length relative to tooth-row length (GSL/TRL, GSL defined as lp3 + lp4 + lm1 + lm2 + lm3 − trigonid), shape of the m1 (m1 shape, wm1/lm1), shape of the p4 (p4 shape, wp4/lp4), shape of the p3 (p3 shape, wp3/lp3), ratio of lM1 to lP4 (M1/P4), m1 length relative to tooth-row length (lm1/TRL), and grinding surface length relative to m1 length (lm1/GSL). Of these, the variables RBL and p4 shape have previously been shown to differentiate effectively between dietary types in carnivorans (Van Valkenburgh 1988, 1989). Van Valkenburgh (1988, 1989) also used an area measure, TGA (total grinding area), which we have modified to a linear measure, GSL. Like TGA, GSL denotes the relative amount of grinding surfaces in the tooth row. Relative blade length is generally used as an indicator of highly carnivorous taxa, because hypercarnivores increase the size of the trigonid relative to the length of the entire m1. Shape of both the p3 and the p4 is indicative of bone in the diet, because wider premolars indicate a more durophagous dietary niche in taxa that have reduced the postcarnassial dentition (Van Valkenburgh 1988, 1989; Werdelin 1989; Werdelin and Solounias 1991). As mentioned above, widening of the premolars in conjunction with elongation of the shearing blade can be considered an alternative trajectory for hypercarnivorous specialization. M1/P4 is a partial measure of the postcarnassial dentition and therefore an indicator of the relative amount of postcarnassial surface area; m1 shape, estimated by dividing the width of the m1 by its length, is representative of an emphasis on slicing as the tooth narrows. GSL/TRL indicates the proportion of the teeth in the jaw not devoted to slicing; GSL is standardized by the upper tooth row because carnivoran jaw lengths are independent of skull length and neither is a reliable standard at a level higher than family (Van Valkenburgh 1990). lm1/GSL likewise indicates the proportion of postcanine tooth surface area taken up by the lower carnassial. lm1/TRL is essentially a measure of the length of the face standardized to body size (as indicated by m1 length; Gingerich 1974; Van Valkenburgh 1988; Werdelin and Solounias 1991): the face tends to shorten as taxa become more highly carnivorous and the position of the carnassials is altered to maintain high bite force (Radinsky 1981a,b; Van Valkenburgh and Ruff 1987; Biknevicius and Van Valkenburgh 1996).

In addition to the above eight characters, the following 19 shape or proportion measures were used for character mapping but not multivariate analyses: P4 shape, blade/GSL, lp3/lm1, lp4/lm1, lm1/JL, MFL/JL, MAT/HAR, MFL/COM1, lm1/MAT, TRL/ZAW, ZAW/JL, lm1/ZAW, (lM1 + lM2)/P4, MAM/HAR, and (discrete characters) shape of the m1 talonid basin (Van Valkenburgh 1988), position of carnassial (Van Valkenburgh 1988), position of P4 protocone, shape of protocone, and presence or absence of the m2.

Data Preparation: Missing Data.—Many of these data come from fossil material, so some proportion will be missing in most groups (total original missing cells ranged from 50% in hyaenids to 28% in Felidae). Because some of our statistical methods require that all cells contain values, however, we treated missing data as follows: For disparity analyses involving PCA, individual taxa with >50% missing data were excluded from analysis. Missing data in the remaining taxa were handled either by replacement with the group mean or by replacement using regression based on another highly correlated character. Replacement values for individual measurements were calculated on the basis of family or generic-level means and regression. Where correlation analysis did not indicate any good correlate for a particular variable, missing data for that measure were of necessity replaced by the overall mean. Because results from separate analyses by the two methods did not differ substantially, we report only those based on replacement by regression. For analyses involving character mapping, taxa with missing values were excluded for that character.

Variance.—Distributions of all variables

were evaluated prior to analyses, and transformations were performed as appropriate. To compare disparities between hypercarnivores and their sister groups, we performed principal components analysis (PCA) based on correlation matrices of the above-listed variables and analyzed differences in variance for the categories ''hypercarnivore'' and ''sister'' in each of the six sets of sister taxa. To obtain disparity values, we calculated the total variance for each member of each hypercarnivore–sister group pair by determining the variance of its factor scores (eigenvalues) for the first five eigenvectors. Five factors were generally sufficient to explain >90% of the variation in a set of data. Values thus obtained were then scaled by the amount of variance explained by each vector, and scaled values summed to create a single composite disparity score for each member of the set. Each of the six pairs of sister groups was analyzed separately because of a concern that strong loadings for particular variables in some pairs of sister groups could unduly influence the apparent variance in other groups, masking taxon-specific variation (see also Warheit et al. 1999). However, categorical disparity results did not change when all data were analyzed in a single large set, although individual results for sister pairs did change slightly. Variance was chosen as a representative disparity measure because it is relatively insensitive to sampling (Foote 1992, 1997). Total values for each taxon set for each category were then contrasted by Wilcoxon Rank Sums against a null model of no difference.

Character Mapping.—An alternative measure of evolutionary rate, frequency of character change, is calculated as the number of independent derivations of any given character state divided by the number of branches on a tree (Sanderson 1993). Up to 27 characters were mapped onto phylogenetic trees for groups under study, and frequency of change for each character was determined for each sister clade. Frequency of change was averaged over all characters for each member of the sister-group pairs. Incomplete sampling (either missing taxa or missing characters) prevented inclusion of all 27 characters in some groups. In these situations, the average was calculated from the characters available. Results by category (hypercarnivore, sister) were pooled and evaluated with Wilcoxon Rank Sums.

Degree of Specialization.—As noted above, hypercarnivorous taxa can be subdivided generally into ''cat-like'' and ''hyaena-like'' morphotypes on the basis of robustness of the premolars. However, the stages of evolution of a hypercarnivorous phenotype are not discrete but can better be viewed as grades on a continuum. Thus, we combined all hypercarnivorous taxa into a single data set and evaluated the position of each specimen in a single, ''hypercarnivore'' morphospace. Initial data exploration consisted of examination of two- and three-dimensional graphs of combinations of original variables as well as plots of PC factor scores for the combined data set based on the eight variables listed in Figure 2. Distributions of all variables were examined prior to analysis and transformations performed as necessary.

Because our intent was to assign each specimen to a specific degree of specialization within hypercarnivores overall, some sense of relative position in space of each specimen was necessary. Thus, the following were designated as ''reference'' taxa and assigned levels of specialization a priori: *Proailurus* (= level 3), *Pseudaelurus* (= level 4), *Felis* (= level 5), and *Hyaena* (= level 7). These taxa have distinct specializations (hyena = bone) or known degrees of development relative to each other (*Proailurus* → *Pseudaelurus* → *Felis*) (Radinsky 1982; Ginsburg 1983; Hunt 1998), and were used as identifiers to provide reference (positional) information for the remaining taxa. This enabled us to determine the appropriate number of levels and to assign the remaining specimens to levels on the basis of clustering and spacing around these reference taxa. Hyenas (level 7) were included as indicators of taxa with bone-eating tendencies, thus allowing us to distinguish between cat-like and hyena-like morphs. However, this numeric designation is only an identifier and is not meant to imply a position along a continuum of change; this level was not included in analyses of disparity based on degree of specialization.

After assigning each specimen to a level, taxon assignments and the original eight var-

TABLE 2. Disparity values obtained for each set of sister groups. Disparity was calculated as the sum of the scaled variance of the first five factor scores obtained from PCA.

Hypercarnivore	Disparity	Sister group	Disparity
Felidae	46.20	Hyaenidae	116.66
Hyaenidae: *Chasmaporthetes/Lycyaena/Hyaenictis*	44.91	Hyaenidae: *Crocuta/Palinhyaena*	109.95
Nimravidae	90.65	Felidae/Hyaenidae/Viverridae/Herpestidae	79.01
Canidae: Hesperocyoninae *Enhydrocyon/Philotrox/Sunkahetanka*	84.53	Canidae: Hesperocyoninae *Cynodesmus*	180.56
Viverridae: *Cryptoprocta ferox*	21.47	Viverridae: *Eupleres/Fossa*	107.64
Mustelidae: *Mustela*	36.87	Mustelidae: *Galictis/Ictonyx/Pteronura/Lontra/Enhydra/Lutra/Amblonyx/Aonyx*	117.60

iables were entered into a discriminant function analysis (DFA). Unlike PCA, which is an objective method used to identify that combination of variables that explain the maximal amount of variation along successive orthogonal axes, DFA is used to find the combination of variables that most clearly distinguishes between previously defined categories (in this case, degrees of specialization), so that the probability of misclassification when placing individuals into categories is minimized (Dillon and Goldstein 1984). The accuracy and stability of the classifications is assessed by using jack-knifing. Because levels were being compared with each other, it was important that they be as well-supported as possible. A small number of taxa could not be unequivocally assigned to a specific degree of specialization, which made their a priori assignments for DFA necessarily somewhat arbitrary. Because the functions used by DFA to discriminate between categories is based on the membership in those categories, we performed successive iterations of DFA and made adjustments to taxon assignments until we could obtain high accuracy upon resampling while still maintaining correspondence with the natural divisions observed in PC plots. The final percentage of correct assignments was 98.6% for fit based on original assignments and 96% for cross-validated data.

Disparity Based on Degree of Specialization.—Methods for determining disparity values based on degree of specialization are identical to those set out for comparison of sister-group sets, but rather than comparing the variances of the members of a pair of sister groups, we performed a single PCA including all hypercarnivorous taxa and then determined scaled variance for each level of degree of specialization. Disparity values thus obtained were plotted against degree of specialization to determine whether degree of specialization and disparity were correlated.

Results

Taxonomic Diversity

Species counts for the six sets of hypercarnivores are shown in Table 1. Neither a sign test nor the method of Slowinski and Guyer (1993) yielded a significant difference in taxonomic diversity between hypercarnivores and their sister groups. Most sister-group sets were roughly equivalent, with hypercarnivorous Felidae and hesperocyonine canids exhibiting slightly greater taxonomic diversity and Viverridae and *Mustela* slightly lower diversity. Species counts for the hypercarnivorous *Chasmaporthetes-Lycyaena-Hyaenictis* and the bone-cracking *Palinhyaena-Crocuta* were equal. The only hypercarnivorous taxon that showed any notable difference in taxonomic diversity relative to its sister group was Nimravidae, a group whose relatively basal position in the carnivoran phylogeny places it as sister to all of Aeluroidea. Setting aeluroid diversity equal to one (the opposite extreme for sister-group comparisons) did not alter these results.

Morphological Diversity

Variance.—Hypercarnivores show significantly lower morphological diversity than do their sister groups ($p < 0.01$, Wilcoxon Rank Sums; Table 2, Fig. 3), and these results are ro-

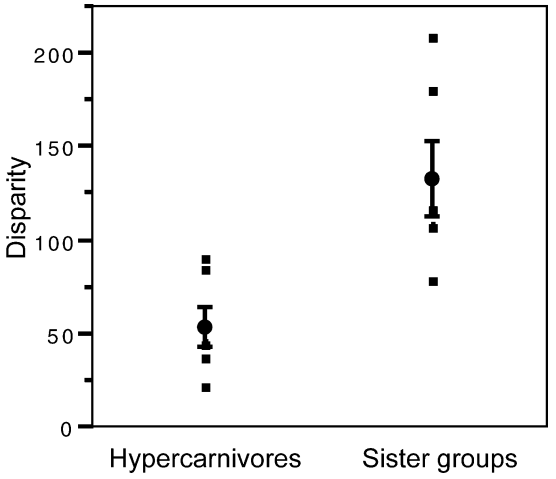

FIGURE 3. Average disparity for six clades of hypercarnivorous taxa and their respective sister groups. Disparity is the sum of the scaled variances of the first five factor scores obtained from PCA of the eight variables representative of skull and dental morphology illustrated in Figure 2. Wilcoxon Rank Sums $p < 0.01$.

bust to perturbations of the various data sets (e.g., different included variables, data transformations, inclusion or exclusion of questionable taxa, alternative sister groups). Method of replacement of missing values also had no effect on the results of the analyses. Exclusion of *Proteles cristatus*, the highly derived aardwolf, from sister-group analyses for felids and hyaenids did not affect the significance of the results overall, although it did result in roughly equivalent disparity values for felids and hyaenids. Comparisons of felids with an alternative sister clade (viverrids), also did not affect our results: felids are relatively lower and viverrids relatively higher in disparity when compared with each other. Exclusion of both felids and nimravids and their sister groups from the pooled values also did not affect the results, which remained significant at $p < 0.02$. Nimravidae, the saber-toothed noncat family, was the only group of the six that showed disparity equivalent to or higher than that of its sister taxon.

Frequency of Change.—Average frequency of change was calculated for six sets of hypercarnivore/sister pairs. We found that the two categories, hypercarnivore versus sister, were significantly different for the two groups ($p < 0.037$, Wilcoxon Rank Sums). Of the six, all hypercarnivore clades except Nimravidae showed lower frequency of change relative to their sister group. Congruent with comparisons of variance, the family Nimravidae exhibited a higher frequency of change relative to its sister taxon; this value was the second-highest frequency of change of any clade evaluated (Table 3, Fig. 4).

Degree of Specialization.—Six categories of specialization were identified for hypercarnivorous taxa, ranging from the somewhat specialized hesperocyonine canid genera *Philotrox-Sunkahetanka-Enhydrocyon* through highly specialized saber-toothed taxa. A two-dimensional plot based on the shape variables of RBL and GSL to TRL indicates placement of key specimens and is coded by degree of specialization (Fig. 5) rather than taxon. Although the assignment of taxa to a particular degree of specialization was, as much as possible,

TABLE 3. Average frequency of change obtained for each set of sister groups, calculated as the number of independent derivations of a character state/number of nodes on the phylogeny.

Hypercarnivore	Average frequency of change	Sister group	Average frequency of change
Felidae	0.1370	Hyaenidae	0.1841
Hyaenidae: *Chasmaporthetes/Lycaena/Hyaenictis*	0.1206	Hyaenidae: *Crocuta/Palinhyaena*	0.1637
Nimravidae	0.2289	Felidae/Hyaenidae/Viverridae/Herpestidae	0.1838
Canidae: Hesperocyoninae *Enhydrocyon/Philotrox/Sunkahetanka*	0.0714	Canidae: Hesperocyoninae *Cynodesmus*	0.1786
Viverridae: *Cryptoprocta ferox*	0	Viverridae: *Eupleres/Fossa*	0.3182
Mustelidae: *Mustela*	0.1607	Mustelidae: *Galictis/Ictonyx/Pteronura/Lontra/Enhydra Pteronura/Lontra/Enhydra/Lutra/Amblonyx/Aonyx*	0.2195

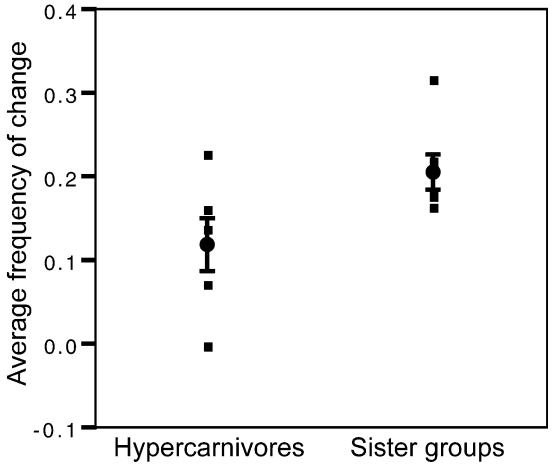

FIGURE 4. Average frequency of change for six clades of hypercarnivorous taxa and their respective sister groups. Nimravids are the uppermost symbol in the left column. Wilcoxon Rank Sums $p < 0.04$.

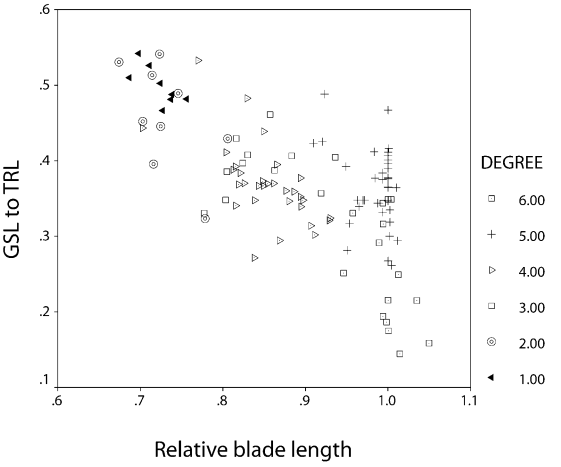

FIGURE 5. Plot of proportional variables indicating positioning of taxa in morphospace when coded by degree of specialization. Relative blade length is calculated as the length of the trigonid (shearing blade) relative to the length of the entire m1 and reflects the amount of meat in the diet. GSL/TRL is a measure of tooth surfaces not devoted to slicing relative to the length of the face. Degrees 1 and 2 represent taxa that are relatively less specialized (e.g., mustelids and hesperocyonine canids). Degree 6 represents taxa that are relatively more specialized and is composed exclusively of felid and nimravid saber-toothed taxa.

phylogeny free, taxa did tend to fall strongly into groupings consistent with phylogeny. Thus, hesperocyonine canids constituted all but one member of level 1, whereas mustelids made up all members of level 2. Levels 3 and 4 were more diverse and included saber-toothed taxa, viverrids, felids, and hyaenids, but level 5 was composed entirely of members of Felidae (both Felinae and Machairodontinae), and level 6 was made up of saber-tooths from both Felidae and Nimravidae. Assignments of particular species to degrees of specialization are shown in Table 4.

Disparity by Degree of Specialization.—Disparity values obtained by summing the variance of the first three factor scores for each de-

TABLE 4. Degree of specialization was assigned on the basis of evaluation of location in principal components space and a priori designations in combination with discriminant function analysis. A total of 109 individual specimens were evaluated; the following list is condensed where genera or families did not vary.

Level 1	Level 2	Level 3	Level 4	Level 5	Level 6
Mustela putorius	*Mustela altaica*	*Dinictis felina*	*Pseudaelurus*	Felinae	*Smilodon*
Enhydrocyon basilatus	*Mustela felipei*	*Lycyaena*	*Nimravides galiani*	*Nimravides catacopis*	*Xenosmilus hodsonae*
Enhydrocyon crassidens	*Mustela frenata*	*Proailurus*	*Cryptoprocta ferox*	*Paramachairodus*	*Barbourofelis*
Enhydrocyon pahinsintewakpa	*Mustela kathiah*		*Pogonodon*		*Eusmilus*
Philotrox condoni	*Mustela nigripes*		*Dinictis cyclops*		*Hoplophoneus occidentalis*
Sunkahetanka geringiensis	*Mustela nivalis*		*Hoplophoneus oharrai*		
	Mustela sibirica		*Hoplophoneus primaevus*		
	Mustela vison		*Nanosmilus kurteni*		
			Nimravus brachyops		
			Nimravus gomphodus		

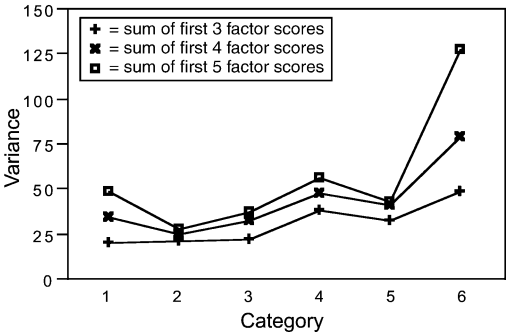

FIGURE 6. Disparity for different degrees of specialization to hypercarnivory, ranging from less (1) to more (6) specialized. Degree 1 is composed of hesperocyonine canids and one mustelid. Degree 2 is exclusively members of *Mustela*. Degree 3 is composed of *Proailurus*, *Cryptoprocta*, hyaenids, and some felids and nimravids. Degree 4 includes *Pseudaelurus* and some felids and nimravids. Degree 5 is exclusively felines and some machairodontines. Degree 6 is composed of machairodontine and nimravid sabertooths. Note the discontinuously high variance of degree 6 relative to degrees 1–5.

gree of specialization show a distinct positive correlation between variance and increasing specialization. However, this correlation becomes nonsignificant as successive factor scores are added to the sum (Fig. 6). Level 6, composed exclusively of saber-toothed taxa, is noteworthy in that disparity is higher than that seen in any of the other specialist groups, and this result does not change even when level 6 is partitioned by nimravids or machairodontines (felid saber-tooths). Nimravids in level 6 score particularly high for disparity values, although their disparity remains comparatively low relative to those of ''generalist'' families also evaluated (Viverridae and Mustelidae).

Discussion

Our results show that morphological specialization to hypercarnivory strongly affects morphological but not taxonomic diversity. Discordance between levels of taxonomic and morphological diversification has been addressed previously by several workers (e.g., Foote 1993; Roy and Foote 1997; Eble 2000) and, depending on the direction of the difference, may be explained as a result of diffusion through morphospace, morphospace packing, or selective extinction. In this case, the lack of an effect on species number is likely a result of continued subdivision of the available resources, possibly by body size (see, e.g., Dayan et al. 1989, 1990), even as the structure of the feeding apparatus is maintained. On a larger scale, however, it is surprising that subsequent evolution has not produced a greater diversity of form in the time since the specialization appeared. The hypercarnivore clades in this study are identified under a criterion of being basally hypercarnivorous; it is certainly not a requirement for the clade as a whole. Their lower morphological diversity is also not a result of lack of time: *Pseudaelurus* evolved at approximately 20 Ma, and modern felids appeared at ca. 16 Ma (Radinsky 1982). In the same time period, the sister group, Hyaenidae, diversified greatly, producing forms as varied as insectivore/omnivores, generalists, bone-cracker/scavengers, and its own version of the hypercarnivore (Werdelin and Solounias 1991, 1996). Interestingly, the presence of hypercarnivores within the basally non-hypercarnivorous hyaenid clade appears to have had only a small effect on overall morphological diversity within this group, although the alternative sister taxon, Viverridae, exhibits even higher disparity relative to felids. The clade of hypercarnivorous hyaenids, *Chasmaporthetes-Lycyaena-Hyaenictis*, is known from at least the late Miocene (Berta 1998), but although taxonomically it diversified equally with the *Palinhyaena-Crocuta* clade, all indications are that it deviated little from the meat-specialist morphotype. In contrast, although the *Palinhyaena-Crocuta* clade evolved specialists in its own right (bone-crackers), the brown and striped hyenas are arguably somewhat omnivorous in known habits (Ewer 1973; Van Valkenburgh 1989; Nowak 1999), and certainly the specialization for ingestion of bone does not appear to limit morphological disparity in the variables included in our study. Disparity for the single species of *Cryptoprocta* was calculated from six specimens, two of which are Pleistocene subspecies, but is still substantially lower than that of its sister clade *Eupleres-Fossa*: the latter taxa are highly divergent in phenotype relative to each other. In the case of *Mustela*, members of this genus occupy a highly predaceous niche that, with the exception of the extinct sea

mink, *Mustela macrodon* (Estes 1989), and *Mustela vison*, which eats fish, crabs, etc. (Ewer 1973), appears to have been retained over the past 10–15 Myr. *Mustela*'s putative sister groups include the otters and various generalist taxa. The noncat saber-toothed family, Nimravidae, had approximately 30 Myr to differentiate and all remained hypercarnivorous, whereas the last group evaluated, hypercarnivorous canids of the genera *Philotrox*, *Sunkahetanka*, and *Enhydrocyon*, exhibit disparity lower than that observed between two members of the single sister genus *Cynodesmus*.

Results from variance comparisons are supported by all comparisons of average frequency of character change, an important finding because these approaches capture distinctly different views of morphological change. Whereas disparity based on variance reflects occupied morphospace around a group mean, frequency of change has utility in assessing evolutionary flexibility or rates of change (see, e.g., McShea 2001), as represented by the number of changes in a given character state relative to the number of opportunities (branches) on the tree (Sanderson 1993). Note that, for our purposes, this measure was used explicitly to evaluate the frequency of any state change in any direction rather than a comparison of forward changes to reversals or stasis, a topic that will be addressed in a subsequent paper. Thus, not only do hypercarnivorous taxa occupy less morphospace overall than do their sister groups, they also appear to move from state to state less frequently within that space. This suggests that once taxa achieve the hypercarnivorous morphotype, they are effectively limited in their subsequent evolution. This consistent reduction in variability in five out of six clades evaluated strongly suggests the presence of a functional constraint, and this pattern is made even more interesting because of the sharp contrast with saber-toothed nimravids, a group whose high values for disparity and frequency of change suggest the possibility of an escape from such a constraint. In a combined morphospace, where nimravids consistently show high disparity relative to other taxa, the variables with the largest loadings on the first two principal components axes are m1/TRL and shape m1 on axis 1, and GSL/TRL and RBL on axis 2. Thus, nimravids are more variable in precisely those hypercarnivore characters of the greatest importance: relative size and shape of the carnassial (axis 1) and the proportion of the total tooth row used for slicing (axis 2). However, one of the more interesting results is that the two nimravid clades, Nimravinae and Barbourofelinae, do not exhibit the same patterns of variation in this combined principal components space. In the analysis described above, variance for barbourofelines was highest on the first axis, whereas variance for nimravines was highest on the second. This difference is intriguing, especially in light of suggestions that Nimravidae is paraphyletic (Neff 1983; Morales et al. 2001; Morlo et al. 2003).

Recognizing that, in most groups, hypercarnivory does strongly affect subsequent morphological flexibility, the idea that increasing specialization within the hypercarnivorous niche should be accompanied by decreasing disparity has intuitive appeal. The lack of correlation between the two is therefore an unexpected result, although it may be an artifact of the method used to assign degree of specialization. As noted previously, there were several taxa that did not fit clearly into particular categories. Such taxa were thus outliers in any grouping, and consequently they exerted relatively greater influence on disparity of the group in which they were placed. Although this had little effect on the ability of DFA to accurately classify taxa (at worst, 78–80% were still correctly reclassified), it did lead to low confidence in the fine-scale pattern of disparity between degrees of specialization, even when the categorical functions (the groups) themselves were well supported by resampling. One pattern did not change, however: level six, composed entirely of highly derived saber-toothed taxa, exhibited discontinuously high disparity levels regardless of how the groups were partitioned. This finding is consistent with the unexpectedly high values observed for nimravids for measures of variance and average frequency of change. Indeed, diversity in saber-tooths was commented on by Radinsky (1982), who noted the unexpected positioning of *Eusmilus* within canid morphospace on the first axis in his own analysis.

If a hypothesis of functional constraint on characters related to the carnassial feeding apparatus can be accepted, then it follows that strong selection on some other characteristics, most obviously the canines, may have overridden this constraint in saber-toothed groups.

The results presented here suggest that there is a point as taxa evolve toward hypercarnivory where morphological flexibility becomes substantially curtailed relative to some earlier stage. In a framework of morphological change along a continuum, however, it is also apparent that there must still be alternative trajectories available to hypercarnivores at some stage in their evolution. Hypercarnivorous taxa that enhance the bone-cracking or crushing portion of their dentition (e.g., hyenas of the *Palinhyaena-Crocuta* clade, borophagines) appear to retain some measure of flexibility, although bone-crackers were not evaluated in this data set and the lower number of known occurrences make this aspect difficult to assess. Taxa that enhance the canines (saber-tooths) likewise appear to exhibit entirely different patterns of diversity relative to other cat-like hypercarnivores, as though by becoming saber-toothed they have escaped the cat phenotype. It is worth noting, however, that no hypercarnivores appear able to easily reverse to a more generalized condition—in fact, for the phylogenies used in this study, there are no known instances of the ''cat-like'' phenotype reversing to a generalist or omnivorous/insectivorous condition or even moving into a bone-cracker/scavenger niche. When degree of specialization to hypercarnivory is mapped onto the phylogenies for these groups (results not shown), movement away from a more specialized toward a less specialized condition is also an extremely rare occurrence (one mustelid, one nimravid), suggesting that there is a strong directionality to change for this phenotype.

Dollo's law, which addresses the idea of irreversibility in evolution, states that a structure, once lost, cannot be regained. Felids have received a certain amount of attention in this regard (e.g., Werdelin 1987; Russell et al. 1995) because of their extreme and, excepting lynxes, persistent reduction in the dental formula. An alternative explanation for the lower disparity observed for hypercarnivorous taxa, then, may be that it is merely a consequence of simplification via loss and reduction of compound structures: structures that do not exist will not vary. Further, if lost structures cannot be regained, then the only possible direction of change will be toward continued loss. However, this explanation alone is unsatisfactory: there is no reason why a taxon with a reduced dental formula should be less variable in the structures that remain. Additionally, not all of the taxa recognized as morphologically hypercarnivorous exhibit the very extreme specializations of felids. Hypercarnivory is recognized on the basis of a set of proportions: relative lengthening of the carnassial blade, relative shortening of the face, and relative reduction of the postcarnassial tooth row. Thus, although proportions of the skull and dentition may alter, the original structures may not be lost at all, and would thus remain available for selection to act upon in any given direction. To add to this, because sister-group comparisons evaluate differences between groups since a common ancestor, phenotypic change such as continued loss or reduction of structures over the course of the lineage will be recognized as variation within the taxon. Finally, and most importantly, the data sets used herein to calculate disparity include a number of non-dental variables. Because the diversity is measured by the total variation in all included characters, the observed disparity values cannot be considered merely a result of simplification of the dental formula. Rather, they are likely a result of both loss of structures (leading to no variation) and of lack of variation in the remaining craniodental measures as well.

As mentioned, the most obvious explanation for lower morphological diversity in multiple clades of hypercarnivores is functional constraint. A consideration of the known ecologies and behaviors of the taxa involved, however, suggests that this explanation may be an oversimplification. The taxa in this study vary in both size and degree of specialization; prey type (and hence killing method) ranges from the birds and lizards of small cats and mustelids to the larger ungulates favored by big cats. Given this potential diversity in killing

mode, it is difficult to imagine that the same functional forces are working at all levels of the size range, especially forces that are so consistently strong that they retard or prevent subsequent modification. The evolutionarily stable systems proposed by Wagner and Schwenk (2000) seem more in line, in the sense of a complex of characters that becomes more and more tightly integrated as selection acts to improve functionality of the system as a whole. Wagner and Schwenk suggested that this is brought about by ''internal selection'' on the relationships between characters, rather than selection directly on particular characteristics, and the patterns observed here certainly appear to follow this premise.

If one views the feeding apparatus as a tightly integrated functional complex from which deviation is unlikely, new questions arise: once taxa begin to trend toward hypercarnivory, is subsequent phenotypic change biased toward this niche? Is there a ''point of no return'' after which reversal or modification is not possible? Clearly, escaping is difficult, and in this case the taxa that do not exhibit lower disparity have apparently done so by evolving a very extreme alternative specialization. Is it possible that taxa can only move from a less to a more specialized condition? Mapping of degree of specialization onto phylogenies appears to indicate just such a progression, although more detailed study is needed to determine the generality of this phenomenon. More robust phylogenies for machairodontines and nimravids are sorely needed, as is a better understanding of interrelationships between aeluroids as a whole, especially fossil taxa. Such phylogenies would be of great benefit in ascertaining the most likely patterns of diversification in relation to the carnivoran feeding complex and evolution of hypercarnivorous specialization.

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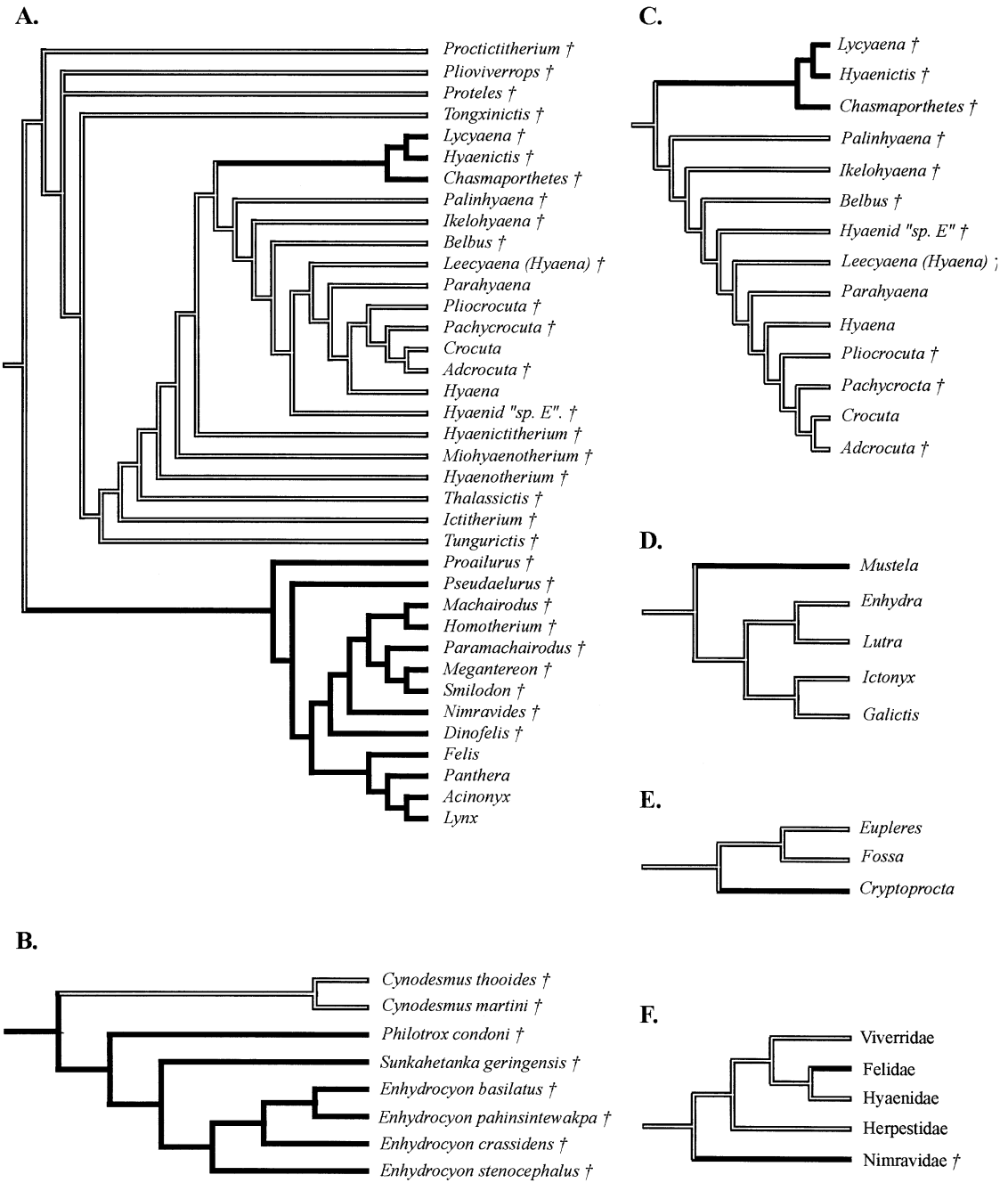
Appendix 1

Hypotheses of phylogenetic relationships for hypercarnivorous clades and their sister groups as used in this study. More-detailed, species-level phylogenies were used for frequency-of-change comparisons and are available from the authors upon request. A, Felidae/Hyaenidae. B, *Philotrox-Sunkahetanka-Enhydrocyon/Cynodesmus*. C, *Chasmaporthetes-Lycyaena-Hyaenictis/Palinhyaena-Crocuta*. D, *Mustela/Galictis-Ictonyx-Pteronura-Lontra-Enhydra-Lutra-Amblonyx-Aonyx*. E, *Cryptoprocta/Eupleres-Fossa*. F, Nimravidae/Herpestidae-Viverridae-Felidae-Hyaenidae. Extinct taxa are represented by †.

Appendix 1. Continued.



Appendix 2

Specimens

Museum abbreviations are as follows: AMNH: American Museum of Natural History; F:AM: Frick Collection, American Museum of Natural History; FMNH: Field Museum of Natural History; MCZ: Museum of Comparative Zoology, Harvard University; NHM: The Natural History Museum, London; TMM: Texas Memorial Museum; UF: University of Florida Museum of Natural History. Specimens designated P, PM, UM, UT, or UC are currently housed at the Field Museum.

Felidae: *Acinonyx*: NHM 16573; *Dinofelis paleonca*: TMM 31181-192, TMM 31181-193; *Felis brachygnatha*: NHM16537; *Felis amnicola*: UF 1933, UF 19351, UF 19352; *Felis aurata*: AMNH 51998, AMNH 51994; *Felis badia*: FMNH 8378; *Felis bengalensis*: FMNH 62894; *Felis chaus*: FMNH 105559; *Felis colo colo*: AMNH

189394, AMNH 16695, FMNH 43291; *Felis rexroadensis*: UF 25067, UF 58308; *Felis serval*: AMNH 34767, AMNH 205151; *Felis viverrina*: FMNH 105562; *Homotherium serum*: UF 22908, UF 22909, UF 24992; *Machairodus aphanistus*: NHM 8975; *Machairodus palanderi*: F:AM 50476, F:AM 50478; *Megantereon cultridens*: AMNH 105446, NHM 49967A; *Megantereon falconeri*: NHM 16350, NHM 16557; *Megantereon hesperus*: UF 22890; *Metailurus*: F:AM China L-604, F:AM 95294; *Nimravides*: AMNH 25206, UF 24471, UF 24479, F:AM 61855, F:AM 104044; *Nimravides catacopis*: AMNH 141216, AMNH 141217; *Nimravides galiani*: UF 24462; *Panthera leo*: UF 10643, UF 10645; *Panthera onca*: UF 14765, UF 14766, UF 23685; *Panthera pardus*: AMNH 35522; *Paramachairodus ogygia*: NHM 1574; *Paramachairodus orientalis*: NHM 8959; *Proailurus lemanansis*: NHM 1646, NHM 9636, NHM 9640, AMNH 105065, AMNH 101931, AMNH 107658; *Pseudaelurus*: AMNH 18007, AMNH 27318, AMNH 27446, AMNH 27447, AMNH 61938, AMNH 62129, AMNH 62190, AMNH 62192, F:AM 61925, AMNH 27451-A, NHM 9633; *Pseudaelurus intermedius*: NHM 2375; *Pseudaelurus marshi*: F:AM 27453, F:AM 27457; *Smilodon californicus*: UF 167140, UF 167141; *Smilodon floridanus*: UF 22704, UF 22705; *Smilodon gracilis*: UF 81700; *Xenosmilus hodsonae*: UF 60000.

Nimravidae: *Barbourofelis*: P15811; *Barbourofelis fricki*: AMNH 103202, AMNH 108193, F:AM 61982; *Barbourofelis lovei*: UF 24447, UF 24429, UF 36858, UF 37052; *Barbourofelis morrisi*: AMNH 25201, F:AM 79999; *Barbourofelis whitfordi*: AMNH C38A–210, F:AM 69454, F:AM 69455; *Dinictis*: UF 155216, UF 207947; *Dinictis cyclops*: AMNH 6937; *Dinictis felina*: AMNH 38805, P12004, PM 21039; *Eusmilus*: F:AM 99259, F:AM 98189; *Eusmilus cerebralis*: AMNH 6941; *Hoplophoneus*: F:AM 69344, UC 1754; *Hoplophoneus occidentalis*: AMNH 102394; *Hoplophoneus primaevus latidens*: UM 420, UM 701; *Hoplophoneus oharrai*: AMNH 27798, AMNH 82911; *Hoplophoneus oreodontis*: AMNH 9764; *Nanosmilus kurteni*: UF 207943; *Nimravus*: F:AM 62151; *Nimravus sectator*: AMNH 12882; *Nimravus brachyops*: AMNH 6930; *Nimravus gomphodus*: AMNH 6935; *Pogonodon*: AMNH 1403, F:AM 69369, AMNH 1398; *Pogonodon platycopis*: AMNH 6938; *Sansanosmilus*: AMNH 26608; *Vampyrictis vipera*: T 3335.

Hyaenidae: *Acrocuta eximia*: AMNH 26372, NHM 8971, M8968, M9041; *Chasmaporthetes*: AMNH 99788; *Chasmaporthetes exilelus*: AMNH 26369; *Chasmaporthetes lunensis*: AMNH 10261, AMNH 26955, F:AM China 94B–1046, F:AM China 96B 1054; *Chasmaporthetes ossifragus*: AMNH 108691, AMNH 95208; *Crocuta*: NHM 16565; *Crocuta crocuta*: AMNH 187771, FMNH 98952, UF 5665; *Hyaena bosei*: NHM 1554, NHM 37133, NHM 16578; *Hyaena brunnea*: FMNH 34584; *Hyaena hyaena dubbah*: FMNH 140216; *Hyaenictitherium hyaenoides*: F:AM China 14-L344, F:AM China 14-L35, F:AM China 26-B47; *Ictitherium viverrinum*: F:AM China (G)-L100, NHM 8983, NHM 8987, NHM 8988; *Lycyaena chaeretis*: NHM 8978, NHM 8979a; *Lycyaena crusafonti*: AMNH 108175, AMNH 116120; *Lycyaena dubia*: F:AM China 52-L495, F:AM China 56-L560; *Palinhyaena reperta*: F:AM China 42-L338, F:AM China 51-L443; *Pliocrocuta perrieri*: AMNH 27756, F:AM 107766, F:AM 107767, AMNH 27757; *Pliovierrops*: AMNH 99607; *Proteles cristatus*: FMNH 127833; *Thalassictis wongii*: AMNH 20555, AMNH 20586; *Tungurictis spocki*: AMNH 26600, AMNH 26610.

Viverridae: *Arctogalidia trivirgata stigmatica*: FMNH 68709; *Chrotogale owstoni*: FMNH 41597; *Cryptoprocta ferox*: AMNH 30035, FMNH 161707, FMNH 161793, FMNH 33950, FMNH 5655; *Cryptoprocta ferox spelaea*: NHM 9949; *Eupleres goudotii*: FMNH 30492, AMNH 188211; *Fossa fossa*: AMNH 188209, AMNH 188210, FMNH 85196; *Genetta genetta senegalesis*: FMNH 140213; *Genetta maculata*: FMNH 153697; *Nandinia binotata*: FMNH 25306; *Prionodon linsang*: FMNH 8371; *Viverra zibetina picta*: FMNH 75883; *Viverricula indica babistae*: FMNH 75815, FMNH 75816.

Canidae: Hesperocyoninae: *Cynodesmus thooides*: AMNH 129531; *Ectopocynus antiquus*: AMNH 63376; *Ectopocynus simplicidens*: F:AM 25426, F:AM 25431; *Enhydrocyon basilatus*: AMNH 129549, F:AM 54072; *Enhydrocyon crassidens*: AMNH 12886, AMNH 27579, AMNH 59574; *Enhydrocyon pahinsintewakpa*: AMNH 129535; *Hesperocyon gregarious*: AMNH 9313; *Mesocyon coryphaeus*: AMNH 6859; *Mesocyon temnodon*: F:AM 63367; *Osbornodon fricki*: AMNH 27363; *Osbornodon*: AMNH 54325; *Parenhydrocyon*: AMNH 81086; *Parenhydrocyon josephi*: F:AM 54115; *Philotrox condoni*: AMNH 32796, F:AM 63383; *Prohesperocyon wilsoni*: AMNH 12712; *Sunkahetanka geringensis*: AMNH 96714.

Canidae: Borophaginae: *Aelurodon taxoides*: F:AM 61781; *Borophagus diversidens*: AMNH 67364; *Borophagus secundus*: AMNH 61640; *Epicyon haydeni*: F:AM 61461; *Epicyon saevus*: F:AM 61432; *Euoplocyon praedator*: AMNH 18261; *Euoplocyon*: AMNH 25443, AMNH 27315; *Paratomarctos euthos*: F:AM 61101; *Desmocyon thomasii*: AMNH 12874.

Mustelidae: *Arctonyx collaris*: AMNH 57373; *Eira barbara*: AMNH 128127, AMNH 29597, UF 3194; *Enhydra lutra*: UF 24196; *Galictis cuja*: AMNH 33281; *Galictis vittata*: UF 29310; *Gulo gulo*: AMNH 35054, FMNH 14026, AMNH 169501; *Ictonyx*: AMNH 165812; *Lutra canadensis*: UF 24007; *Martes americana*: UF 13212; *Martes cauvina*: UF 5642; *Martes foina*: UF 29046, AMNH 70182; *Martes pennanti*: UF 23316; *Mustela altaica*: UF 26514; *Mustela erminea*: UF 3982, UF 1417; *Mustela felipei*: AMNH 63839, FMNH 86745; *Mustela frenata*: UF 26144, UF 4779; *Mustela kathiah*: FMNH 32502, AMNH 150090; *Mustela nigripes*: AMNH 22894; *Mustela nivalis*: UF 1418; *Mustela putorius*: UF 1425, UF 14422; *Mustela sibirica*: AMNH 114878, F:AM 104392; *Mustela vison*: UF 4569, UF 4724, UF 8108; *Mydaus javanensis*: AMNH 102701; *Poecilogale albinucha*: AMNH 86491; *Taxidea taxus*: UF 384; *Vormala peregusna negans*: AMNH 60103.

"Paleo" mustelids: *Brachysypsalis*: AMNH 25295, AMNH 25299, AMNH 27307, F:AM 25284, F:AM 25363, AMNH 27424; *Megalictis*: F:AM 25430; *Megalictis ferox*: P12283, P12154, P26051, UF 23928; *Oligobunis crassivultus*: AMNH 6903, PM 537; *Oligobunis darbyi*: P25609; *Oligobunis floridanus*: MCZ 4064; *Plesictis cf. pygmaeus*: NHM 27815; *Plesiogulo marshalli*: UF 19253; *Promartes lepidus*: P12155; *Zodialestes*: F:AM 27599, F:AM 27600; *Zodialestes daimonelixensis*: P12032.