

The morphological diversification of carnivores in North America

Gina D. Wesley-Hunt

Abstract.—The evolutionary history of a clade has traditionally been studied through phylogenetics, and taxonomic diversity has been used as a crude proxy for morphological diversity. However, morphological diversification—beyond counting taxa—can provide a very different view of a clade's evolutionary history and allows the investigation of patterns and timing of morphological evolution.

In this paper I use dentition to document the pattern of morphological and taxonomic diversification of Carnivoramorpha and mammalian meat eaters in North America. Using the dentition permits ecological inferences to be made, because teeth and diet are closely related. I present a method developed to describe the entire dentition of the Carnivoramorpha and other mammalian meat eaters (Creodonta). Morphological diversification is measured by dental disparity, using the mean pairwise dissimilarity among species.

I test the following hypotheses: (1) Morphological diversification was suppressed relative to taxonomic diversification, early in the evolutionary history of Carnivoramorpha; and (2) once an efficient system for consuming meat evolved, the dental system remained relatively unchanged.

The first hypothesis is rejected. Taxonomic and morphological diversity increase together through the clade's early evolution. There is no evidence of a morphological release in the carnivoramorphan with the demise of creodonts. The second hypothesis is supported. The ecological group "mammalian meat eaters" rapidly diversified morphologically and reached its maximum disparity early in its history, after which the dental system remained relatively unchanged.

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Introduction

Morphological diversity, in conjunction with taxonomic diversity, provides a powerful tool to interpret the evolutionary processes underlying the patterns of biodiversity. The principal purpose of this study is to quantify and test hypotheses of the morphological and taxonomic diversification of the clade Carnivoramorpha, and the ecological group carnivores (terrestrial eutherian mammal meat eaters), by using the North American fossil record (Carnivoramorpha is operationally defined as Carnivora and the fossil taxa within "Miacoidea" [Wyss and Flynn 1993]).

Traditional methods of documenting diversity are measurements of taxon richness. However, taxonomic and morphological diversity can represent different aspects of biodiversity and do not necessarily covary (Foote 1993, 1997). Morphological diversity has the potential to describe ecological diversity (i.e., the number of ways to make a living) and changes in ecological structure over time, and to help

identify extinction processes, such as selective versus random extinctions (Foote 1993). In order to fully describe biological variety, both taxonomic and morphological diversity must be measured. As stated by Van Valkenburgh and Janis (1993: p. 340), "It is time we stopped simply counting taxa and tracking their numbers over time, and began looking at them, measuring them and estimating their ecological roles. Without this added perspective, our conclusions concerning diversification over evolutionary time remain incomplete." This is the first study to comprehensively quantify the dental morphological diversification of North American "ecological carnivores" and the clade Carnivoramorpha over their entire evolutionary history.

Prior morphological diversification studies have primarily focused on invertebrate clades (Foote 1997; Ciampaglio et al. 2001). A small minority of studies address other taxonomic groups; for example, angiosperms (Lupia 1999) and "ungulates" (Jernvall et al. 1996). If

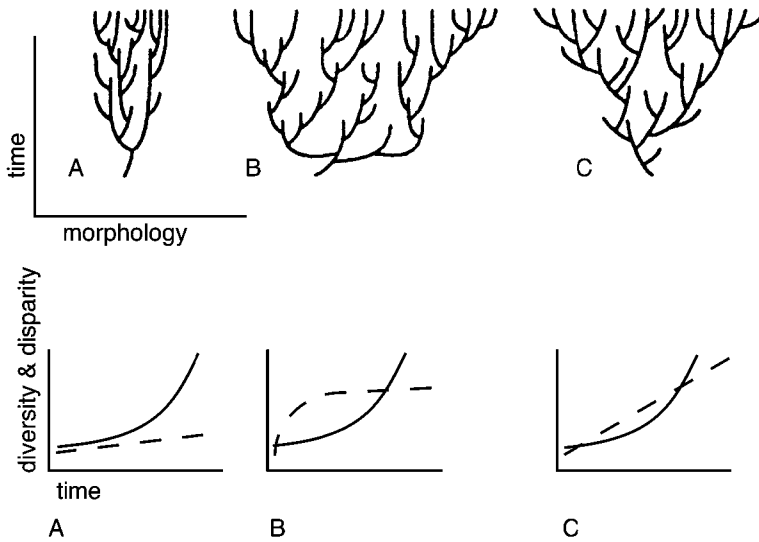


FIGURE 1. Top, Idealized diversity patterns (modified from Fig. 1 of Foote 1993: p. 192). Bottom, Predicted diversity and disparity curves over time (solid line, taxonomic diversity; dashed line, morphological disparity). A, Morphologic evolution is constrained. Taxonomic diversification is not accompanied by morphologic diversification. B, Morphological steps are large early in the clade's history. Morphological diversity may continue to increase, but steps are smaller. Morphologic diversification outstrips taxonomic diversification. C, No constraint on morphological evolution, no trend in morphological step size. Morphologic diversification is concordant with taxonomic diversification.

the conclusions drawn from these studies are to be applied to our understanding of large-scale processes and patterns of evolution, more studies must be done on different groups with different ecologies (Lupia 1999).

Diversification of a clade can follow one of three simplified, or idealized, patterns (Fig. 1) (Foote 1993). (A) Taxonomic diversity increases more rapidly than morphological diversity, indicating possible morphological constraints. (B) Morphological diversity increases more rapidly than taxonomic diversity. Later in the clade's evolutionary history taxonomic diversity may increase, filling in the existing morphospace. This pattern would satisfy the classic definition of an adaptive radiation—the rapid occupation of morphospace (Simpson 1953; Foote 1993). Or (C), taxonomic and morphological diversification are relatively concordant, and there is no apparent limit on morphological evolution. The pattern of diversification in the majority of clades studied approximate pattern B, in which morphological diversity increases rapidly and outstrips taxonomic diversity (Foote 1997). Disparity is a commonly used measure of morphological diversity, and it quantifies the amount of dis-

persion (or the degree of dissimilarity) among forms in morphospace (Roy and Foote 1997).

When Carnivoramorpha first emerged in the Paleocene they were not the only group of terrestrial meat-eating mammals present. The Creodonta (oxyaenids and hyaenodontids) were also present and, judging from their dentitions, many were specialized meat eaters and must be included in any study addressing the evolution of mammalian carnivory. In North America few creodonts survived past the Eocene, and all were extinct by the late Oligocene (Gunnell 1998). The taxonomic decline of Creodonta and the end of the Eocene coincided with the beginning of the radiation of Carnivora, and the origination of most modern families. Regardless of whether this was taxonomic displacement or replacement this pattern has generated the hypothesis that the diversification of carnivorans was suppressed by the incumbent creodonts early in their history (Van Valkenburgh 1999).

Taking a step beyond the diversification of a clade, how does an ecological group diversify, divide resources, and evolve the structure we see today? Ecology has been inferred from morphological patterns of diversification in

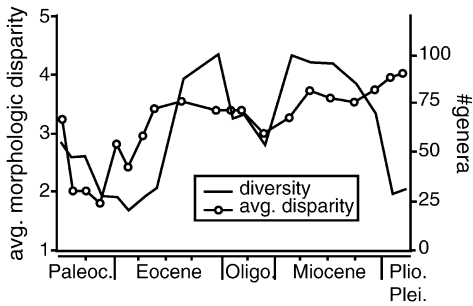


FIGURE 2. North American “ungulates.” Taxonomic diversity (number of genera sampled) and morphologic disparity (average pairwise disparity) over time. Modified from Jernvall et al. 2000.

previous studies (see, e.g., Van Valkenburgh 1988, 1989 for carnivores; Foote 1996b for cretoids; Jernvall et al. 1996, 2000 for ungulates). Such inferences can be made *if* the characters used are functionally significant as well as relevant (Foote 1997; Roy and Foote 1997). Dental morphology provides a good indicator of diet and ecology in living mammals because teeth are directly involved in the consumption of food (Lucas 1979; Van Valkenburgh 1989; Jernvall et al. 1996). By using modern analogs, the ecology and diet of fossil carnivoramorphans have been inferred from dental morphology in several studies (including but not limited to: Crusafont-Pairó and Truyols-Santonja 1956; Van Valen 1969; Van Valkenburgh 1987, 1989, 1991, 1996; Biknevicius and Van Valkenburgh 1996; Werdelin 1996). The functional significance of the characters used in this study is discussed in the Appendix.

Jernvall et al. (1996, 2000) used morphological diversity measures to address the dental diversification of herbivory in “ungulates” (he includes Artiodactyla, Perissodactyla, and Condylarthra). This non-monophyletic group of herbivores responded to a dramatically changing ecosystem resulting from climate changes through the Cenozoic. During this time, North America transformed from a generally subtropical, closed forest to a more open savanna-like environment with expansive grasslands (Jacobs et al. 1999; Willis and McElwain 2002). The resulting pattern (Fig. 2) is a generally concordant increase in average disparity and taxonomic diversity, although disparity increases slightly before taxonomic diversity (Jernvall et al. 2000). If this pattern is

indicative of an ecological group (herbivores) tracking a changing resource (flora), what pattern would emerge from an ecological group consuming a stable resource? Van Valkenburgh (1988) suggested that carnivore dental morphologies have not changed over their long histories because the functional requirements of eating flesh remain relatively constant over time—e.g., the physical and biological properties of skin, flesh, and bone have not altered drastically over the Cenozoic. Thus carnivoramorphans and creodonts provide an opportunity to study the diversification of an ecological group (carnivores) consuming a stable resource (vertebrate fauna).

In addition to discussing the diversification of Creodonta and Carnivoramorpha in North America (Analysis 1), I test two specific hypotheses: (1) Morphological diversification was limited, relative to taxonomic diversification, early in the evolutionary history of the clade Carnivoramorpha—approximating pattern A in Figure 1 (Analysis 2); and (2) Once an efficient system for consuming meat evolved, the dental system remained relatively unchanged (Analysis 3). This hypothesis predicts that no significant change in disparity or occupied area of morphospace will occur within the ecological group “carnivores” over the Cenozoic. I will test these hypotheses by quantifying the dental form (see Appendix), calculate morphological disparity, and compare the resulting relationship between taxonomic diversity and morphological disparity to the idealized patterns of diversification (Fig. 1).

Methods

This paper introduces a quantitative method that describes the entire dentition of carnivores, capturing its functional complexity and heterogeneity. The carnivoran tooth row comprises four functional regions with differing roles in food processing: (1) incisors and canines, (2) premolars, (3) carnassials, and (4) postcarnassial molars (Van Valkenburgh 1989). The 17 morphological characters presented in the appendix describe the functional features of these regions as well as body size. Many of these characters have been documented in previous studies to correlate with

functional aspects of the tooth row. The characters are comprehensive and applicable to all terrestrial carnivorous taxa, both living and extinct, and regardless of taxonomic affiliation. This allows the extinct group, Creodonta, to be included. Moreover, taking the nature of the fossil record into account, the characters also accommodate incomplete specimens, composite material from several individuals, and crushed and distorted specimens. To increase the information captured while maintaining applicability, qualitative as well as quantitative characters were included and treated as discrete characters. Although this meant losing information due to binning quantitative data, it increased the power of the method to describe a large range of morphological variation and large patterns in evolutionary history.

Quantifying Form.—The 17 characters described in the Appendix, include 64 character states. The criteria used to divide continuous quantitative characters into discrete categories are discussed for each applicable character. All quantitative characters are based on measurement averages. Because this method describes shape, the 11 characters that are a morphocline (small, medium, and large) are ordered to preserve the linear information in size. Body size is included as a character, and it may also be present secondarily (allometry) in other shape characters. Size is an important indicator of ecology and is a factor in the differences between taxa (MacNab 1971, 1989; Gittleman 1986; Carbone et al. 1999); therefore, the influence of size in the characters is not avoided.

Calculating Disparity.—Two methods of measuring dissimilarity were used to quantify separate properties of morphologic diversity: mean pairwise dissimilarity between species (referred to in this study as “disparity”) (Foote 1992), and volume of occupied morphospace (Wagner 1996). The first measure, mean pairwise dissimilarity (disparity), was calculated for each taxonomic pair as the total number of character state mismatches divided by number of characters compared (Foote 1992). For binary and unordered multistate characters, the difference between taxa is zero for matches and one for mismatches.

TABLE 1. Association between the first three principal coordinates (PCO) and morphological characters. The p -values indicate degree of association. For binary characters, strength of association was determined by Mann-Whitney U -test. For ordered and unordered characters, strength of association was determined by Kruskal-Wallis test.

Character	PCO 1	PCO 2	PCO 3
1	<0.05	<0.001	<0.0001
2	<0.0001		<0.0001
3	<0.0001	<0.05	<0.001
4	<0.001	<0.0001	
5	<0.0001	<0.05	
6	<0.05	<0.05	<0.05
7		<0.0001	
8	<0.0001	<0.0001	<0.0001
9	<0.0001	<0.0001	<0.0001
10	<0.05	<0.0001	<0.05
11	<0.0001	<0.0001	
12	<0.0001	<0.0001	
13	<0.0001	<0.0001	<0.05
14	<0.0001	<0.05	<0.0001
15			
16	<0.0001	<0.0001	<0.0001
17	<0.001	<0.0001	<0.05

Ordered multistate characters were rescaled so that the maximum difference was one. Therefore, all characters had equal weight (Foote 1992), but all character state transformations were not equal; as a result, some dissimilarity information was lost (see discussion below and Table 1). Mean pairwise dissimilarity was used as a dissimilarity metric because it is robust to sample size; which is important when dealing with carnivores which have low population densities and sometimes irregular preservation potential, compared to other trophic levels. In addition, this measure can easily be applied to discrete characters (Foote 1992; Lupia 1999; Ciampaglio et al. 2001).

The standard error of the average dissimilarity in each interval was estimated by using the standard deviation of the distribution of bootstrapped values (1000 replicates) (Sokal and Rohlf 1995). Using the estimated standard error, a t -test tested for significant differences in disparity between intervals. A principal coordinate analysis was performed on the distance matrix of the entire sample to calculate the location of each taxon in morphospace by using the loadings of the first two axes. I chose a principal coordinate analysis because it can accommodate discrete characters and missing

data. Non-applicable or missing data can cause triangular inequalities in raw distances among taxa, implying that nonidentical taxa actually are identical. Theoretically, this can distort eigenvectors. However, use of Kirkpatrick and Lofsvold's (1992) "squeeze routine" showed that negative eigenvectors had no effect on the primary pattern.

The association between the 17 characters and the first three principal coordinates were calculated (Table 1) because principal coordinates are derived from a distance matrix and not the raw morphological data. The Mann-Whitney *U*-test was used for binary characters and the Kruskal-Wallis test was used for multistate ordered and unordered characters. Although there is a high degree of association between the majority of characters and principal coordinate axes (PCO), in some of the multistate characters one or two of the character states drive the association. Character 15 (cusp shape) is the only character without a significant association with any of the axes. Character 7 (shape of the upper carnassial) is associated only with the second axis (PCO 2).

The second measure of morphological dissimilarity used is the volume of occupied morphospace. This measure is defined by the geometric means of the ranges along the first three axes of the principal coordinate analysis (Wagner 1996). Although this measure is sensitive to sample size, this effect is reduced in this study because morphospace is defined by all taxa included in the study, and not independently in individual time intervals (Foote 1991; Wagner 1996).

Sampling.—Taxonomic sampling was done at the genus level, incorporating only fully ossified adults of terrestrial carnivoramorphans and creodonts from North America (including Mexico). North America is where carnivoramorphans first appear in the fossil record, probably where the initial radiation occurred (Flynn and Wesley 2005), and the fossil record of carnivores is excellent. Genera rather than species were used because the method was not designed to capture the minor differences between species, and because the species-level systematics is not uniformly resolved across the taxa analyzed. For accuracy, only specimens or high-quality casts were used for cod-

ing. One complete, representative specimen was used for each genus when possible. If available, multiple specimens were studied (up to ten) to insure that the representative was not aberrant. If significant within-species variation existed and four or more characters would be coded differently, multiple representatives for that genus were used. A composite representative was created if all characters could not be coded from a single specimen in a genus. Taxonomy from Wang (1994), Wang et al. (1999), and Janis et al. (1998) was used. A total of 106 genera were sampled over the 65 million years of the Cenozoic. To prevent a modern bias in the last interval, only those modern taxa that occur in the fossil record two or more million years ago were included. The only genera excluded as a result were *Alopex*, *Gulo*, and *Conepatus*. Taxonomic age ranges follow those of Alroy (2002) and assume presence in intervals between first and last occurrences. Taxonomic diversity was measured as the quantity of sampled genera present in each interval.

Analyses.—Three separate analyses were performed: The first included all taxa sampled in Carnivoramorphia and Creodonta (106 taxa); the second included only Carnivoramorphia (95 taxa); and the third analysis included a subset of the total sample (Carnivoramorphia and Creodonta) that consists only of taxa with a linear upper carnassial (i.e., hypercarnivores; 72 taxa). Hypercarnivores are defined as taxa that consume almost entirely vertebrate flesh, and they are characterized by specialized dentition in which the primary function is slicing (Van Valkenburgh 1991). It is important to note that this group of hypercarnivores is not a monophyletic clade. Regardless of monophyly, the relationship between morphological disparity and taxonomic diversity holds important information. For example, maximum disparity occurring at low diversity suggests a different ecological structure than when maximum disparity occurs at high diversity.

Results and Discussion

Diversification of Creodonta and Carnivoramorphia: Analysis 1

Results.—(Figs. 3, 4). The total sample was included (all 106 carnivoramorphans and cre-

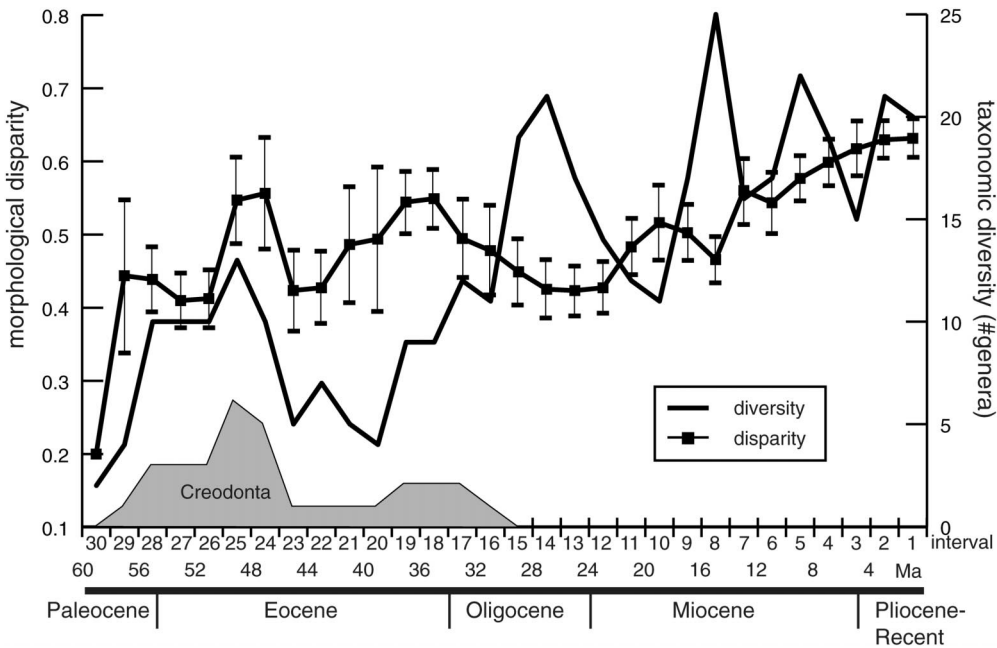


FIGURE 3. Analysis 1: composite of carnivoramorphans and creodonts. Mean pairwise morphological disparity and taxonomic diversity curves over the Cenozoic. Diversity is measured as number of genera sampled. Error bars are based on bootstrap resampling of taxa within intervals and are one standard deviation above and below mean disparity. (Timescale from Berggren et al. 1995.)

odonts) and intervals were 2 Myr. Average disparity generally increased over the Cenozoic, and taxonomic diversification was generally concordant with morphological diversification (Fig. 3). During the trend of increasing morphological disparity, there were two points at which a large increase in disparity occurred between consecutive intervals (significant at the level of 0.10: t -test: $t = 1.70, 1.90$; $p < 0.10$). These jumps in disparity occurred between Intervals 26 and 25 (52–48 Ma) and between Intervals 8 and 7 (16–12 Ma; see Analysis 2). Both increases in disparity were due to the appearance of large, hypercarnivorous forms (Fig. 4, quadrant 2—the morphospace is partitioned into four quadrants by the zero axes; refer to caption of Fig. 4 for explanation). In Interval 25 (50–48 Ma), hypercarnivorous eutherian mammal forms first appeared in the North American record, represented solely by large-bodied oxyaenid creodonts (Fig. 4, quadrant 2). The decrease in disparity during the middle Eocene (Intervals 23 and 22: 46–42 Ma) was due to the extinction of the hypercarnivorous oxyaenid creodonts. Disparity increased again in Interval 21 with

the appearance of the hypercarnivorous hyaenodontid creodonts and a reduction to five genera. It is not until Interval 19 (38 Ma), near the end of the Eocene, that a hypercarnivorous member of Carnivora appeared in the fossil record of North America. Although low in diversity, the few creodonts that were present in the second half of the Eocene were hypercarnivorous, and they continued as large, specialized predators until 30 Ma (Interval 15), when they disappeared from the North American record. The creodonts shared the hypercarnivorous morphospace (quadrant 2) with carnivorans for approximately 8 Myr (Intervals 19–16: 38–30 Ma). Before the Miocene, the only form to even marginally occupy quadrant 4 of the morphospace, which today is filled with generalists such as raccoons and bears, was an oxyaenid creodont (*Oxyaena*; Interval 28). *Oxyaena* occupied an area of the morphospace close to that of the Pleistocene ursid *Arctodus*.

Discussion.—It is not known whether creodonts were actively displaced by competitive interaction with carnivoramorphans or whether, instead, the pattern of increasing

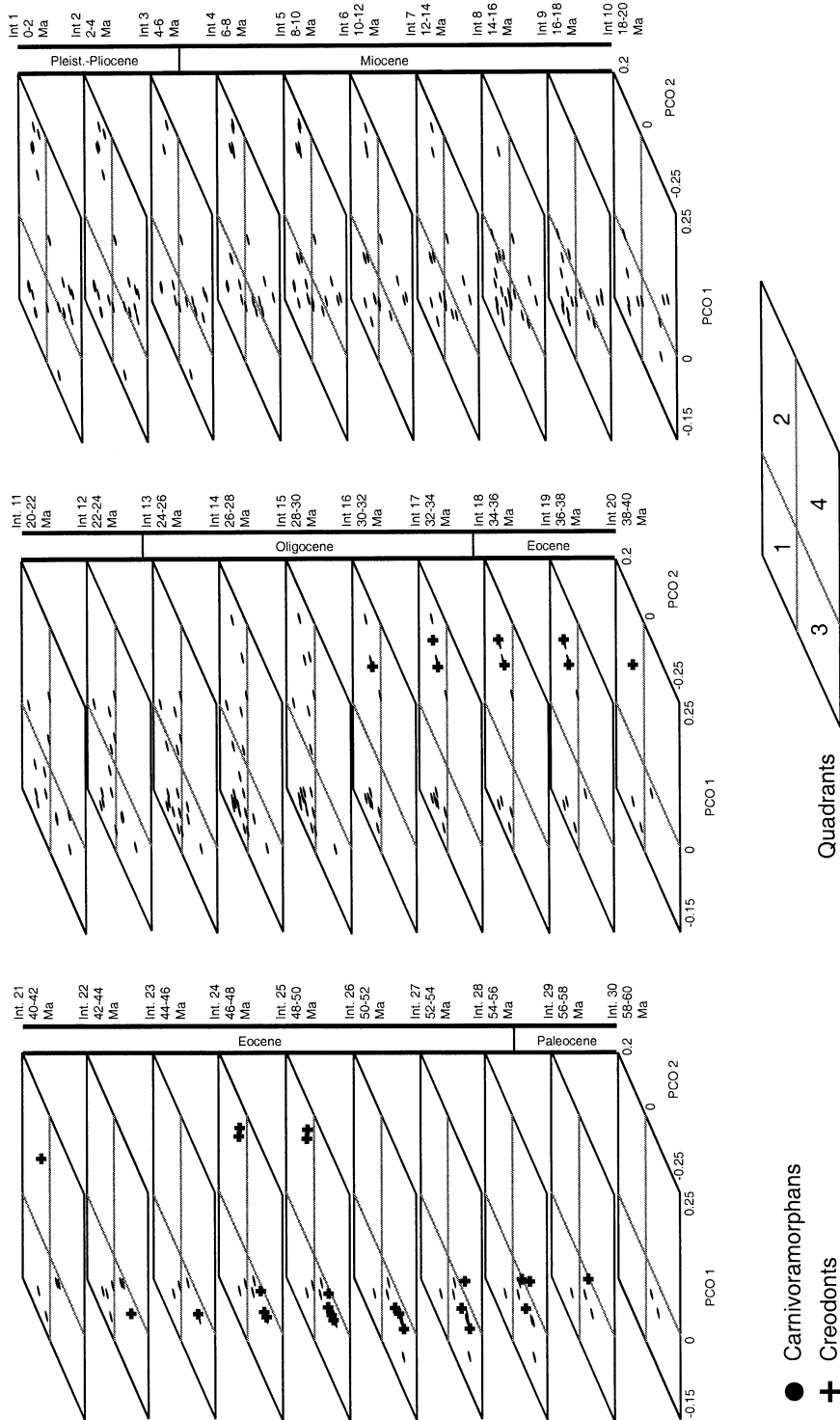


FIGURE 4. Analysis 1: carnivoramorphans and creodonts. Pattern of morphospace occupation through the Cenozoic, based on first two principal coordinates. Morphospace is divided into four quadrants by 0 axes; quadrants are numbered to facilitate discussion. Hypercarnivorous, felid-like taxa appear in quadrant 2. The majority of canids occupy quadrant 1, and more-generalized procyonids and ursids are found low in quadrants 3 and 4. (Timescale from Berggren et al. 1995.)

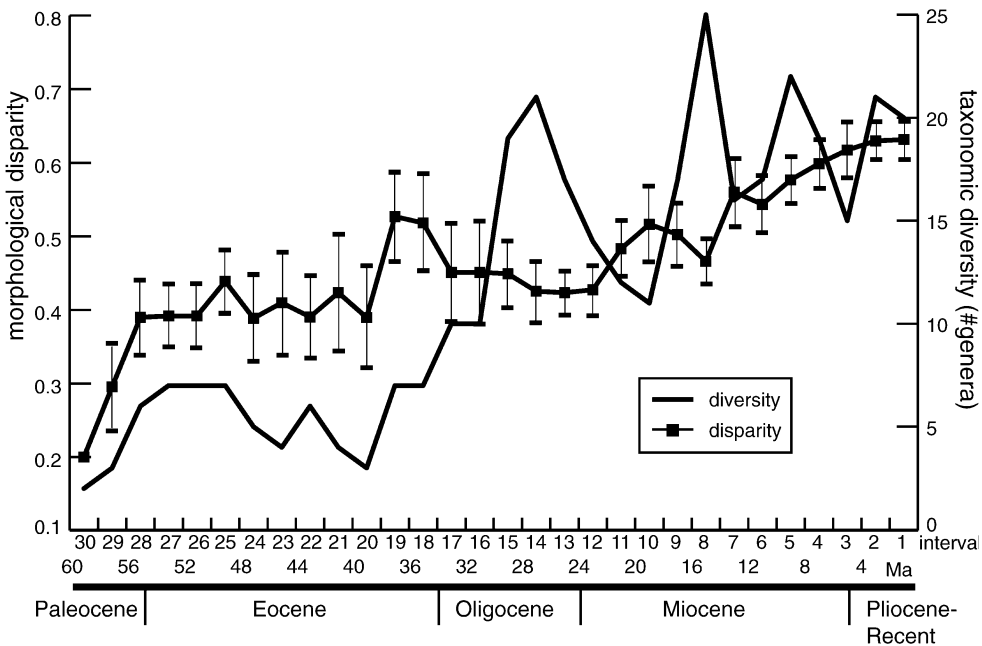


FIGURE 5. Analysis 2: carnivoramorphans only. Mean pairwise morphological disparity and taxonomic diversity curves over the Cenozoic. Diversity is measured as number of genera sampled. Error bars calculated as in Figure 3. (Timescale from Berggren et al. 1995.)

carnivoramorphan taxonomic diversity was the result of passive replacement, due to chance or some other factor such as climate change (Van Valkenburgh 1999). It has been proposed that the taxonomic diversity of carnivoramorphans was suppressed by the incumbent creodonts (Van Valkenburgh 1999). During Intervals 21–15 (40–28 Ma) quadrant 2 of the morphospace continues to be occupied by creodonts and is joined by another felid-like creodont and carnivoramorphans in Interval 19. Therefore, the increase in disparity immediately following the decrease in creodont taxonomic diversity was caused by carnivoramorphans expanding into the only area of morphospace still occupied by a creodont. The decline of the creodonts in North America, however, does not appear to have had a strong effect on carnivoramorphan disparity levels—there was no morphological release. Although carnivoramorphans may have been taxonomically suppressed, they do not appear to have been morphologically suppressed by the presence of creodonts. To further test the hypothesis that morphological diversification was suppressed or limited by the presence of

Creodonta, I conducted a second analysis focusing solely on carnivoramorphans.

Diversification of Carnivoramorpha: Analysis 2

Results.—(Table 2, Figs. 5–9). This analysis includes only Carnivoramorpha, and 2-Myr intervals are used. Although I present the disparity and diversity patterns of Carnivoramorpha over the entire Cenozoic, only Intervals 30–18 (60–34 Ma) from the Paleocene through the Eocene are used to test the hypothesis of early diversification patterns. North America has by far the most complete Paleocene and Eocene record of carnivoramorphans of any continent and is an excellent model for the initial diversification of the clade. During the latest Eocene and Oligocene the Carnivoramorpha became much more global in distribution, and North America is no longer an accurate estimate of the clade's total diversity.

The shape of the disparity and diversity curves during the Paleocene and Eocene does not support the hypothesis that morphological diversification is delayed early in the

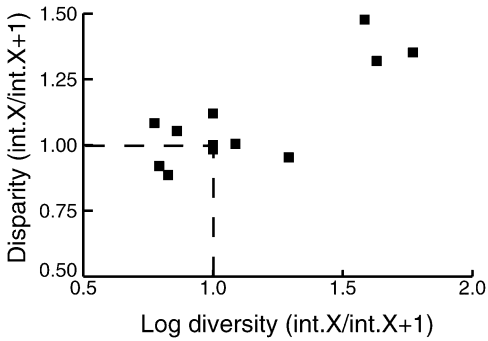


FIGURE 6. First Differences, Analysis 2: Carnivoramorpha. Changes in disparity and diversity between successive intervals (Gould and Calloway 1980; Foote 1994). The correlation between increases (decreases) in disparity and increases (decreases) in diversity is significant (Spearman $r = 0.573$, $p = 0.0572$).

clade's evolutionary history relative to taxonomic diversity. Rather, morphological diversification appears to increase in step with taxonomic diversification. To test this pattern more rigorously, I measured the correlation between the first differences (changes between successive intervals) of disparity and diversity (Gould and Calloway 1980; Foote 1994) (Fig. 6). The correlation between increases (decreases) in disparity and increases (decreases) in diversity is significant (Spearman $r = 0.573$, $p = 0.0572$) and the general pattern is consistent with concordant morphological and taxonomic diversification. Spearman rank correlation was used because it is nonparametric and does not assume a normal distribution. The hypothesis that carnivoramorpha were morphologically limited relative to taxonomic diversification early in its evolutionary history can be rejected.

In only one instance did disparity increase dramatically between consecutive intervals (see Table 2 for p -values). As stated earlier, this large increase in disparity occurred between Intervals 8 and 7 (16–12 Ma; t -test: $t = 1.70$, $p < 0.10$). Although a non-saber-toothed feliform was present in Interval 8, the increase in disparity did not occur until Interval 7, as a result of the appearance of a large, saber-toothed, hypercarnivorous feliform and the extinction of intermediates in quadrant 1 and 3 (Fig. 4). The volume of occupied morphospace did not change between these intervals (Fig. 7).

Within the general trend of increasing disparity and volume of occupied morphospace in carnivoramorphan evolution, there are smaller perturbations. High disparity in the late Eocene was due to the appearance of felid-like hypercarnivores occupying a new quadrant of morphospace (Fig. 4, quadrant 2). After this peak, disparity decreased while taxonomic diversity increased, indicating an increase in morphological intermediates. The continued increase in the volume of occupied morphospace (Fig. 7) suggests that although most taxonomic originations occurred within the existing morphospace, there were also originations around the edges. The disparity late in the Oligocene (Interval 13) was substantially lower than the disparity in the late Eocene (Interval 19). During the early Miocene (Intervals 13–10; 26–18 Ma), disparity levels increased steadily from the Oligocene minimum, while taxonomic diversity decreased owing to increased extinction intensity and decreased origination intensity (Fig. 8). The volume of occupied morphospace did not change during this period, with the exception of a large decrease during Interval 10 (20–18 Ma). The combination of a local peak in disparity and a local minimum in occupied morphospace during Interval 10 indicates that morphological extremes and intermediates were going extinct. Disparity continued to increase through the Miocene and Pliocene, although the volume of occupied morphospace remained relatively static, showing only a slight increase. Disparity levels in the Pliocene (Intervals 1 and 2; 4–0 Ma) were significantly higher than the disparity in the middle Eocene (Interval 21; 42 Ma) (t -test: $t = 2.50$; $p < 0.02$).

Discussion.—The increase in disparity through the early Miocene occurs during a time when no feliforms were present in North America. The hypercarnivorous nimravid feliforms were extinct in North America after Interval 14 (26 Ma) and felids did not arrive in North America until the early middle Miocene (Interval 8; 16 Ma). It has been suggested that canids evolved hypercarnivorous morphologies because feliforms were absent during this period (the “cat-gap,” Intervals 13–9; 26–16 Ma) (Van Valkenburgh 1991). The data pre-

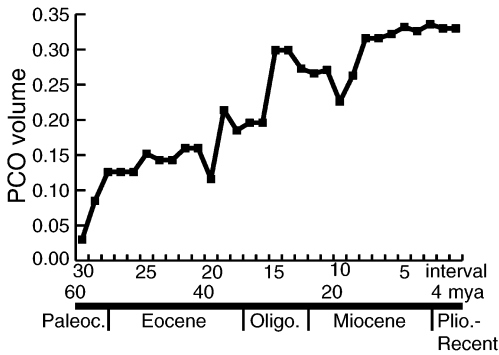


FIGURE 7. Volume of occupied morphospace over time, Analysis 2: Carnivoramorpha. Volume calculated as geometric means of the ranges along the first three axes of the principal coordinate (PCO) analysis for each interval (Wagner 1996). PCO loadings are based on total taxonomic sample.

sented here do not support this hypothesis. In the calculated morphospace, extreme hypercarnivores (e.g., felids, nimravids) occupy the right side of quadrant 2, whereas hypercarnivorous canids occupy only the left margin of quadrant 2. Canids never occupy the area of morphospace in which felids, nimravids, and hypercarnivorous creodonts are found. More pertinent to the issue at hand, however, is that most of these hypercarnivorous canids were present *before* the disappearance of the nimravids, and all went extinct before the appearance of felids. Following the extinction of nimravids, only three taxa originated in the margin of quadrant 2 of morphospace, two of which were relatively small in body size (<21.5 kg—see character 17). The third taxon, the hypercarnivorous mustelid *Aelurocyon*, was much larger (<50 kg) and appears just above the lower border of quadrant 2 in Interval 13. This could be an example of a lineage evolving, albeit only marginally, to exploit open morphospace, but it also went extinct well before the appearance of felids. After the extinction of the hypercarnivorous canids in Interval 10, the left half of quadrant 2 was never reoccupied. *Chasmaporthetes*, an extinct hyaenid, occupied a position near this abandoned area of morphospace but was closer to the felid-occupied morphospace. In the last two intervals of the “cat-gap” (Intervals 10 and 9; 20–16 Ma) quadrant 2 was completely empty, with the exception of *Euplocyon* at the

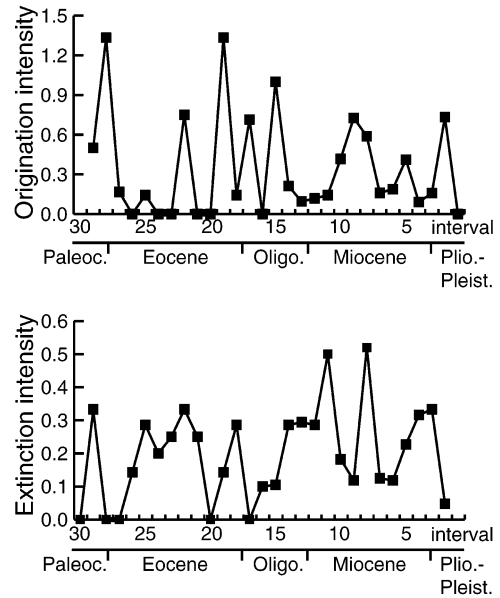


FIGURE 8. Origination and extinction intensity over time, Analysis 2: Carnivoramorpha. Origination intensity is the number of originations in an interval divided by the diversity of the preceding interval. Extinction intensity is the number of taxa in interval X that do not survive to the next interval X - 1, divided by the diversity in interval X.

left margin of the quadrant. There was a progressive and marked decrease in hypercarnivorous forms during the “cat-gap.” Intervals 14–11 (28–20 Ma) are characterized by above average extinction intensities and below average origination intensities. Interval 10 (20 Ma) was marked by an increase in origination intensity, and Interval 9 (18 Ma) showed a decrease in extinction intensity and a large increase in origination intensity. Nonetheless, despite increased origination intensities and decreased extinction intensities near the end of the “cat-gap” (Intervals 10–9; 20–16 Ma), there was still no substantial invasion of hypercarnivorous morphospace until the immigration of felids into North America. I then tested for a significant difference in body size distributions between consecutive intervals during the “cat-gap” (Fig. 9) (paired t -test: $t = 1.394$, $p = 0.1968$; and $t = 0.589$, $p = 0.5973$) and found no statistically significant correlation between body size and extinction among the carnivorous forms (taxa with a linear upper fourth premolar).

Disparity increased during the “cat-gap”

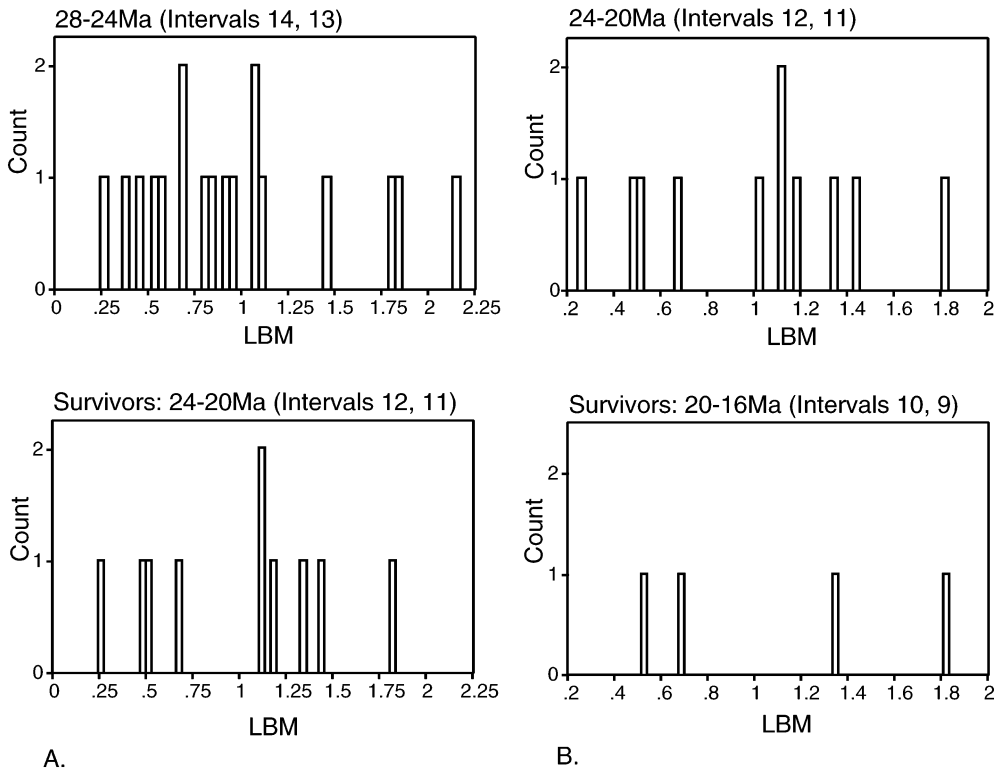


FIGURE 9. Histograms of Log Body Mass (LBM) of intervals just prior to and during the “cat-gap” (24–20 Ma). These distributions were tested for body size bias during hypercarnivore extinctions. The top histograms are LBM for all carnivorous taxa (defined as possessing a linear upper fourth premolar) present during the interval. The bottom histograms include all taxa that survived the initial interval into the following interval. The 2-Myr intervals are pooled to create a 4-Myr interval in order to increase sample size. Refer to Figure 4 for interval numbers. A paired t -test was performed to test for significant difference in body size distribution between pooled intervals. A, (top), LBM of taxa present in Intervals 14 and 13 (28–24 Ma); (bottom), LBM of taxa that survived into Intervals 12 and 11 (24–20 Ma). Body size distribution between intervals is not significantly different ($t = 1.394$, $p = 0.1968$). B, (top), LBM of taxa present in Intervals 12 and 11 (24–20 Ma); (bottom), LBM of taxa that survived into Intervals 10 and 9 (20–16 Ma). Body size distribution between intervals is not significantly different ($t = 0.589$, $p = 0.5973$).

even with the extinction of the hypercarnivorous extremes. This was due to the extinction of morphological intermediates (taxa not on the margins of morphospace) in quadrant 1, and because carnivorans began to occupy hypocarnivorous (non-meat-specialist) morphospace in the bottom of quadrant 4 for the first time in North America. Procyonids did not arrive in North America until the early Miocene, and modern ursids (e.g., Ursinae), who also occupy quadrant 4, did not arrive until the late Miocene. Extinct lineages of Ursidae were present in North America from the late Eocene through the Miocene, but they occupied an area of morphospace within quadrant 3. Amphicyonid ursoids (or “bear-dogs”) were present during this period as well but occupied morphospace generally shared with

canids (quadrant 1) and did not lie in close proximity to ursids.

The results suggest that morphological diversification was not significantly limited early in carnivoramorph evolutionary history. Instead, the diversification pattern of carnivoramorphans in North America approximates idealized pattern C (Fig. 1), characterized by concordant taxonomic and morphological diversification.

Diversification of Ecological Carnivores: Analysis 3

Results.—(Table 3, Figs. 10–13). Intervals are 4 Myr long to increase the sample in each interval. This analysis included only those taxa with a linear upper carnassial, regardless of clade membership, in order to study the evo-

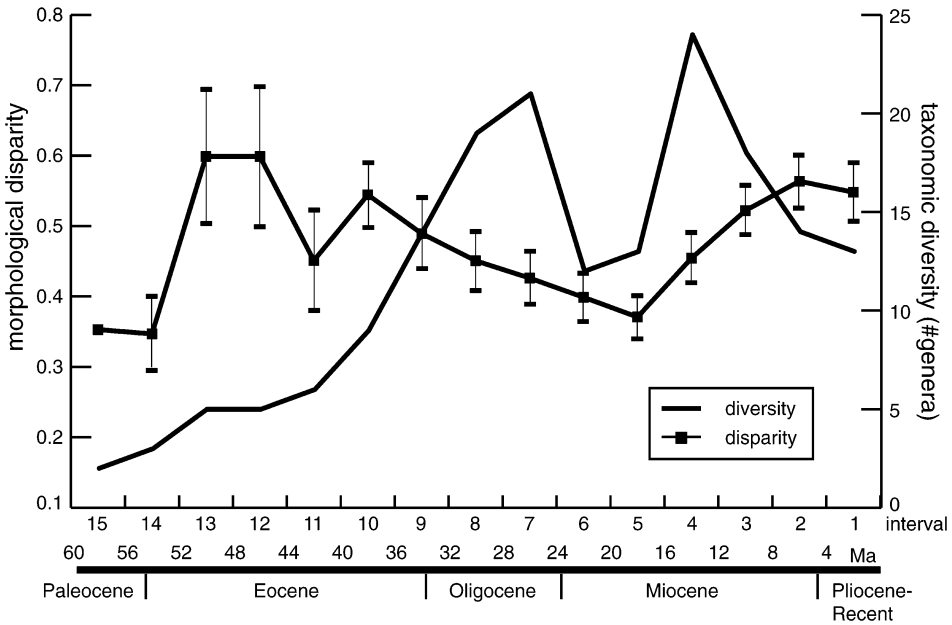


FIGURE 10. Analysis 3: ecological carnivores—only taxa with a linear upper carnassial were included. Mean pairwise morphological disparity and taxonomic diversity curves over the Cenozoic. Diversity is measured as number of genera sampled. Error bars calculated as in Figure 3. (Timescale from Berggren et al. 1995.)

lution of an ecological group, mammalian carnivores (consuming vertebrate prey). The analysis tests the hypothesis that the dental system, after its initial evolution, remained relatively unchanged, predicting that subsequent diversification will only fill in the gaps of the morphospace.

Disparity reached its maximum level early, much earlier than taxonomic diversity (Fig. 10). The initial early Eocene peak in disparity (Interval 13; 52 Ma) was followed by a general trend of decreasing disparity over the remaining intervals of the Eocene and Oligocene (Intervals 10–5; 40–16 Ma) (see Table 3 for *p*-values). Disparity did not increase again until the early middle Miocene (Interval 4; 16 Ma). The decrease in average disparity over this period was due to the proliferation of morphologically similar forms and forms filling in the gaps of the morphospace (Fig. 11).

To compare disparity with diversity, I measured the correlation of their first differences, as described in Analysis 2. Within ecological carnivores the correlation between increases (decreases) in disparity and increases (decreases) in diversity is not significant (Spearman $r = 0.2$, $p = 0.4708$); therefore, an increase

in diversity is not concordant with an increase in disparity (Fig. 12).

The volume of occupied morphospace (Fig. 13) gradually increases to a maximum at Interval 7 (28 Ma), sharply decreases during Intervals 6 and 5 (24–16 Ma), then returns to maximum levels in Interval 4 and relative stasis for the remainder of the Cenozoic. The sharp decrease in volume of occupied morphospace occurs during the “cat-gap” (Intervals 6 and 5) and coincides with the lowest disparity level after the Paleocene, indicating a small and tightly packed morphospace (Fig. 11).

The only large change in disparity between consecutive intervals occurred in the middle Miocene (Intervals 5–4; 20–12 Ma) (*t*-test: $t = 1.77$, $p < 0.10$). The initial jump in disparity at the beginning of the Eocene was not considered because the sample size of Interval 14 was too small (three taxa). The increase in disparity and occupied morphospace in Interval 4 was caused by the appearance of felids in North America, after the “cat-gap.” Over the late Eocene, Oligocene, and into the early Miocene, there was a gradual, persistent decrease in average disparity. Quadrant 1 (where most

TABLE 3. Interval \times interval significance matrix for Analysis 3 (meat eaters only). t -tests were used to test for significance differences in disparity values between intervals; standard deviation, calculated from bootstrapped values, was substituted for standard error. Shaded cells indicate successive intervals. Because of small sample size, comparisons to intervals 15 and 14 are not significant.

Interval	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1				*	**	**	**							**	
2				**	**	**	**	**						**	
3					**	**	*							**	
4	*	**			*									*	
5	**	**	**	*					**	**		**	**		
6	**	**	**							**		*	**		
7	**	**	*							**			*		
8		**													
9					**									*	
10					**	**	**							**	
11															
12					**	*								**	
13					**	**	*								
14	**	**	**	**					*	**		**			
15															

* $p < 0.10$, ** $p < 0.05$.

canids lie) became tightly packed, and hypercarnivorous canids began to fill the gap in morphospace that previously separated canids from the feliforms. Disparity levels during the late Oligocene, prior to the “cat-gap,” were significantly lower than the late Eocene peak (Interval 7, 28 Ma; Interval 10, 40 Ma; t -test: $t = 2.03$, $p < 0.05$). Minimum disparity occurred during Interval 5 (20 Ma), when all hypercarnivorous forms were absent. Disparity increased during the second half of the Miocene, as morphological intermediates in quadrant 1 went extinct and feliforms reappeared in North America.

Discussion.—The results of Analysis 3 support the hypothesis that once evolved, the dental system of carnivores remained relatively unchanged. Maximum disparity occurred early and the boundaries of morphospace were rapidly defined on principal coordinate (PCO) axis 1, although the volume of occupied morphospace continued to expand along PCO axes 2 and 3. With the first appearance of felids in North America (Interval 4; 16 Ma), the hypercarnivorous area of the morphospace that had been vacated by the nimravids was once again occupied. Therefore, although there was significant change in average disparity over the Cenozoic, the po-

sition of the occupied morphospace did not shift. What did change was the pattern of occupation within the boundaries of the morphospace. The results suggest that, morphologically, the number of ways terrestrial mammalian carnivores consume flesh is limited. The presence or absence of these different forms appears to be influenced by factors other than changing properties of flesh and bone in prey, instead, possibly environment or prey abundance.

Early in mammalian carnivore evolution, creodonts occupied the area of morphospace later occupied by felids and nimravids. In one case, almost the exact point of morphospace occupied by *Hyaenodon* (Interval 10; 36–40 Ma) was later occupied by a nimravid (*Hoplophonus*) and then a felid (*Lynx*). This result highlights the fact that some creodonts likely played the same ecological role in the earliest Cenozoic as felids do today. This idea was previously suggested by Van Valkenburgh (1988) and is strongly corroborated by this analysis.

Jernvall et al. (2000) documented “ungulate” morphological and taxonomic diversification by using the upper first molar to measure morphological diversity and to examine the evolution of herbivory in “ungulates.” “Ungulates” showed a general increase in av-

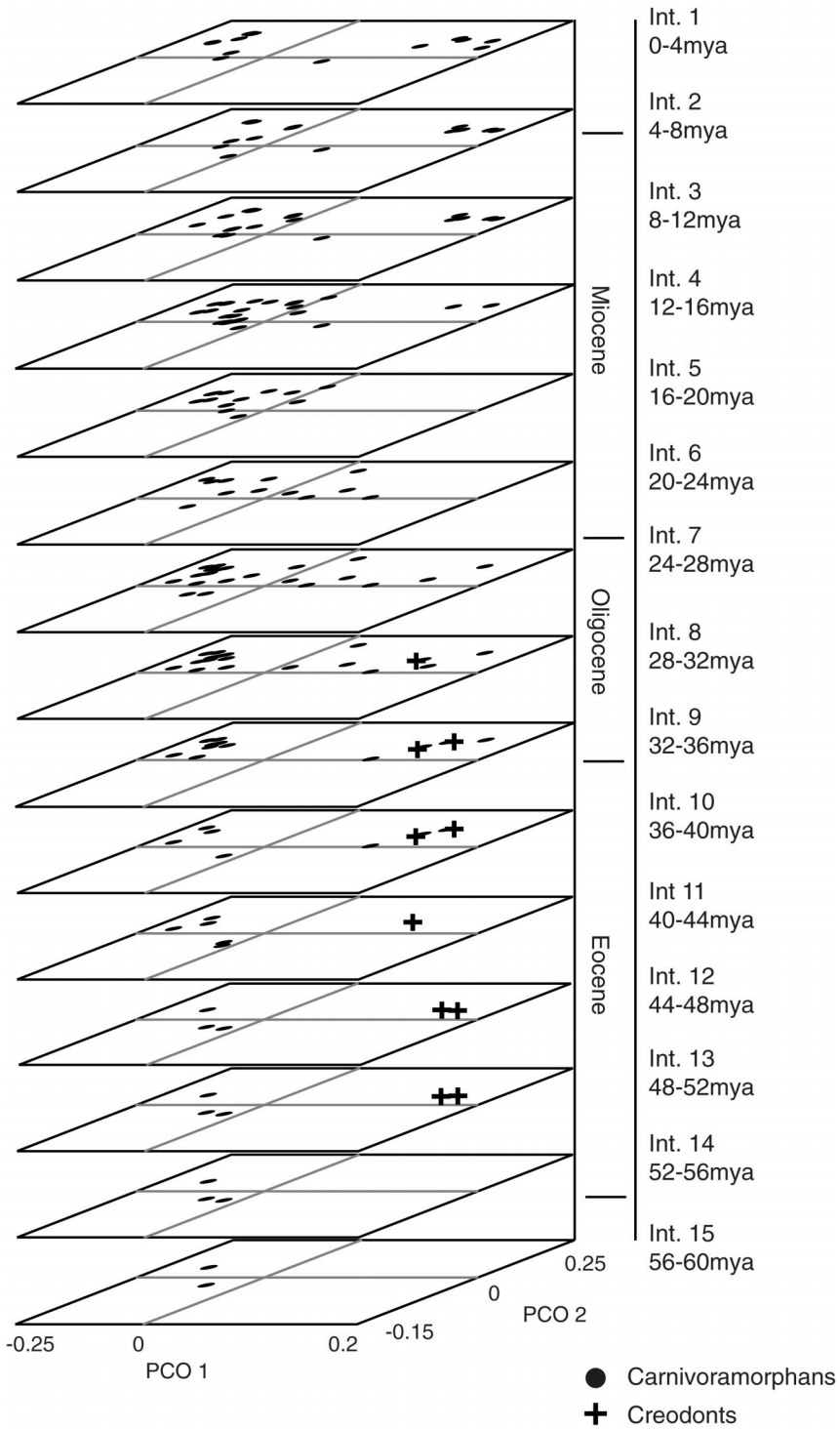


FIGURE 11. Analysis 3: ecological carnivores. Pattern of morphospace occupation through the Cenozoic, based on first two principal coordinates. (Timescale from Berggren et al. 1995.)

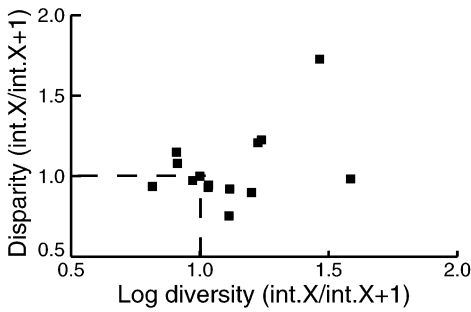


FIGURE 12. First differences, Analysis 3: ecological carnivores. Changes in disparity and diversity between successive intervals (Gould and Calloway 1980; Foote 1994). The correlation between increases (decreases) in disparity and increases (decreases) in diversity is not significant (Spearman $r = 0.2$, $p = 0.4708$).

erage disparity through the Cenozoic in North America that was generally concordant with taxonomic diversification (Fig. 2). Maximum average disparity was not attained until the Plio-Pleistocene. This is a very different pattern than is documented here in mammalian carnivores. Carnivores defined their morphospace very early in their evolutionary history and then remained relatively static. In addition, taxonomic diversity lagged well behind morphological diversification. “Ungulates” approximate the idealized history C, whereas carnivores approximate idealized history B (Fig. 1). These results are consistent with the hypothesis that “ungulates” were constantly tracking a changing resource (flora), and therefore continued to expand their morphospace, while carnivores, consuming a relatively stable resource (vertebrate flesh), filled the extent of their morphospace early on in their diversification and then remained relatively static. Both ecological groups experienced a decrease in taxonomic diversity during the Oligocene, although at different times. “Ungulate” diversity dropped at about the Eocene/Oligocene boundary (ca. 33.7 Ma), possibly because of rapid climatic cooling (Fig. 2) (Jernvall et al. 1996). Among carnivores, however, taxonomic diversity did not decrease until the end of the Oligocene (ca. 25 Ma), reaching a local minimum in the early Miocene (ca. 20 Ma). Both carnivores and “ungulates” experienced another large decrease in diversity during the end of the Miocene and the Plio-Pleistocene. There is another similar-

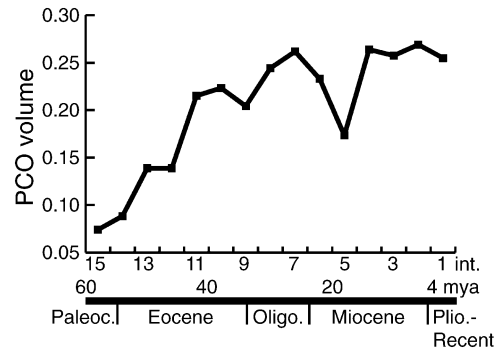


FIGURE 13. Volume of occupied morphospace over time, Analysis 3: ecological carnivores. Volume calculated as geometric means of the ranges along the first three axes of the principal coordinate (PCO) analysis for each interval (Wagner 1996). PCO loadings based on total taxonomic sample.

ity in the diversification patterns of “ungulates” and carnivores. During taxonomic diversity minima of the Oligocene in “ungulates” and early Miocene in carnivores, both groups experienced a decrease in disparity. In contrast, at the end of the Cenozoic, the decrease in diversity in both groups was paired with an increase in disparity. The extinction events occurring during the Oligocene/early Miocene therefore affected morphological extremes, whereas the extinction event at the end of the Cenozoic affected morphological intermediates and thinned the morphospace.

A large question remains as to why there was a progressive decline in hypercarnivorous carnivoramorphans during the late Oligocene/early Miocene. During this period all hypercarnivorous forms disappeared from the fossil record, including hypercarnivorous canids and mustelids, in addition to feliforms. One possible explanation is climate change. Earth was gradually cooling after the late Paleocene, and over a period spanning the Eocene/Oligocene boundary there was a dramatic climatic cooling event occurred (Graham 1999; Willis and McElwain 2002). However, ecological carnivores do not begin to decrease in diversity until the late Oligocene—a lag of approximately 9 Myr. Prey structure may offer an explanation. In the early Miocene, when carnivores were losing diversity, the number of small-bodied browsing “ungulates” was disproportionately high (Janis et al. 2000; J. Theodor personal com-

munication 2002). This change in prey structure may be connected to the decrease of morphological disparity in carnivores.

Conclusion

The pattern of morphological and taxonomic diversification of early carnivoramorphans approximates Foote's idealized pattern C (Fig. 1), in which taxonomic and morphological diversity increase together throughout the clade's evolution. Therefore, carnivoramorphans evidently were not morphologically suppressed or limited relative to taxonomic diversity early in the clade's history. This concurrent pattern of taxonomic and morphological diversification in a clade is quite rare (Foote 1997). Of the clades analyzed before this study, most exhibited an acceleration of morphological evolution early in their history, whereas taxonomic diversity remained low (pattern B) (Foote 1997).

The ecological group "carnivores" rapidly diversified morphologically and reached its maximum disparity very early in its history. The pattern of disparity in ecological carnivores suggests that once an efficient system for consuming prey was established in each taxonomic group, the dental system remained relatively unchanged. Although disparity and the volume of occupied morphospace did change over the Cenozoic, the position of the occupied morphospace never shifted, and it was primarily the pattern of occupation within the established morphospace that changed. This is in contrast to the pattern observed in eutherian mammalian herbivores, in which "ungulate" morphological diversity increased gradually and concordantly with taxonomic diversity (pattern C) (Jernvall et al. 2000). A possible explanation for the difference in diversification patterns between the two ecological groups is that while functional requirements for consuming prey have remained relatively constant over the Cenozoic, the requirements for consuming vegetation changed with each dramatic environmental shift, often because of large-scale climatic cooling during the Cenozoic. During the evolutionary history of carnivoramorphans and ecological carnivores, there was a progressive decline in the number of hypercarnivorous

forms during the early Miocene. The cause of this pattern is yet unknown and is worthy of further exploration

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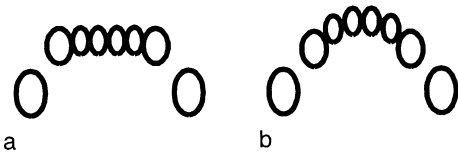
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Appendix

Character Description

1. *Incisor row: parabolic or straight* (Appendix Fig. 1). A parabolic organization allows the incisors to be used independently of the canines and because the incisors are exposed to forces in all directions; individually they are wide mediolaterally. In a straight incisor row, the teeth are buttressed by neighboring incisors and canines, and are used with the canines as one unit (Van Valkenburgh 1996).
2. *Canine: length over width*, measured at the enamel-dentine



APPENDIX FIGURE 1. Incisors. A, Straight, generally present in felids. B, Parabolic, generally present in canids.

junction. This is an ordered, continuous character. Among the carnivores sampled (fossil and Recent), the distribution is bimodal and right skewed. The continuum was divided into four categories based on two modes and to differentiate the right-skewed tail between elongate canines from the extreme morphology of saber-toothed forms: (1) <1.5 , (2) 1.5 to 1.7 , (3) >1.7 , (4) >2 . The first category includes the main mode characterizing relatively round canines. The second category includes the secondary mode and forms an intermediate group. Taxa with elongate canines are found in the third category. Taxa in the last category have extremely elongate “saber” canines.

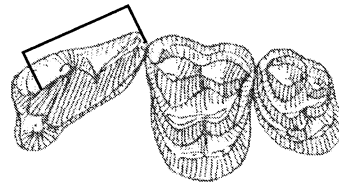
The ratio is an indicator of the mediolateral strength of the canine. A rounder canine will be better able to resist mediolateral stress than an elongate canine and may be indicative of different killing behaviors (Van Valkenburgh 1987).

3. *Number of upper premolars anterior to the carnassial*: Vestigial premolars (those that appear to be nonfunctional—a small “nub,” globular in morphology and without distinct cusps) are not included. This character is discrete and ordered. Hypercarnivorous taxa tend to have a reduced number of premolars, whereas omnivores generally retain all premolars.
4. *Largest upper premolar anterior to the carnassial: length over width*. This is an ordered, continuous character. The distribution is dispersed and bimodal among taxa sampled. The continuum was divided into three categories based on its distribution. The exact cutoff between categories was arbitrary. The three bins are defined as (1) <1.7 , (2) $\geq 1.7 < 2.5$, (3) ≥ 2.5 . The first bin describes relatively round premolars and contains the first mode. The second bin contains the second and largest mode characterizing relatively long premolars. The third bin contains few taxa and describes the extremely elongate premolar condition.

Premolars in meat eaters are used for piercing or crushing. Premolars used in crushing typically will be thick mediolaterally to withstand the resulting forces (Lucas 1979). The largest upper premolar (usually the third premolar in carnivoramorphans) can also be extremely elongate and incorporated into the shearing blade in hypercarnivorous forms.

5. *Upper premolar spacing: close or spaced*. Premolars were characterized as spaced if gaps were present between the first, second, and third upper premolars. Premolars were characterized as close under the following conditions: (1) no space between the second and third premolars; however, space may be present between the canine and the first premolar, or between the first and second premolars, but *not* both; or (2) the first *and* second premolars are vestigial.

The spacing of the upper premolars is generally indicative of the length of the snout and, in conjunction with the number of premolars (see above), can distinguish between a short snout with three premolars (raccoon) and a short snout with one premolar (domestic cat). Both the cat and the raccoon would be coded as having close upper premolars. The extant bear *Ursus arctos* is problematic in that it is coded as having both absent and close premolars, the condition



APPENDIX FIGURE 2. Blade length of upper carnassial. Length of the shearing blade (indicated) compared with the total length of the upper carnassial. In this example the blade is at least $2/3$ of total tooth length. (Modified from Fig. 49[a], *Paracynarctus kelloggii*, of Wang et al. 1999: p. 108.)

one would expect in a felid. But, when the other characters are considered, the ursid coding still reflects its omnivorous diet.

6. *Last lower premolar: length over width*. This character is ordered, continuous, and with a dispersed bimodal distribution. The continuum was divided into three categories based on its distribution; the exact cutoffs between categories were arbitrary: (1) <1.7 , (2) 1.7 to 2.15 , (3) >2.15 . The first bin includes the left tail and mode, and it loosely defines a shape that is considered “rounded” in the context of the sample. The second bin contains the right mode and the largest portion of the sample. The third bin includes the right tail and characterizes elongate lower premolars.

The lower premolars, as well as upper premolars, are used for bone crushing in different taxa. As in the upper premolars, an elongate lower last premolar can be incorporated into the shearing blade of hypercarnivorous forms.

For non-carnivoramorph meat eaters, the largest upper shearing tooth and the largest lower shearing tooth is treated as functionally equivalent to the upper and lower carnassials of carnivoramorphans because both produce the primary shearing blade of the animal.

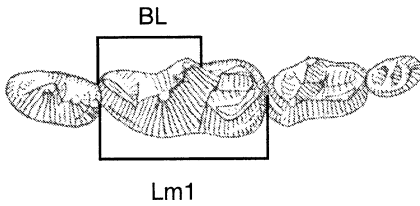
7. *Shape of the upper carnassial*: (1) square, (2) equilateral triangle, (3) an elongate triangle (approximating a right, scalene triangle), (4) linear. The shape is determined by the outline of the occlusal surface. To distinguish between a triangular and linear outline of the upper carnassial, the carnassial is classified as linear if the paracone participates in the shear and there is no shelf lingual to the paracone.

More-carnivorous taxa have a triangular or linear carnassial, increasing shear, whereas generalist taxa tend to have square carnassials or carnassials that approximate an equilateral triangle (Van Valkenburgh 1991).

8. *Blade length of upper carnassial*: length of shearing blade compared with total length of the upper carnassial. (1) no blade present, (2) the blade $1/3$ of total length, (3) the blade $1/2$ of total length, and (4) the blade $2/3$ or greater of total tooth length (Appendix Fig. 2). This character is ordered.

Categories were constructed to capture most of the diversity present without being so detailed that they cease to be useful. The shearing blade can be composed of more than the metastyle blade; often the protocone is incorporated into the shearing blade, and in some hypercarnivorous forms the entire tooth is involved. In many hypocarnivores, no blade is present.

9. *Relative blade length of lower carnassial*: ratio of the anteroposterior length of the trigonid, measured on the buccal side, over the total maximum length of the tooth (Appendix Fig. 3). This character is ordered, continuous, and bimodal in distribution. The first mode is highly dispersed and includes the majority of the sample. The second mode, which describes the hypercarnivores, has low dispersion. The dis-

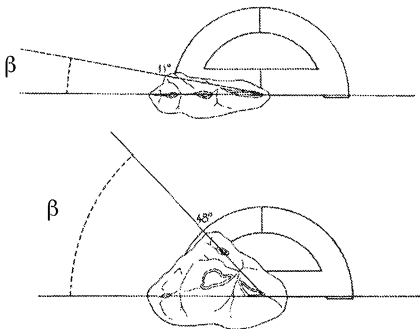


APPENDIX FIGURE 3. Relative blade length of lower carnassial. The ratio of the anteroposterior length of the trigonid (BL), measured on the buccal side, over the total maximum length of the tooth (Lm1). (Modified from Fig. 49[b], *Paracynarctus kelloggii*, of Wang et al. 1999: p. 108.)

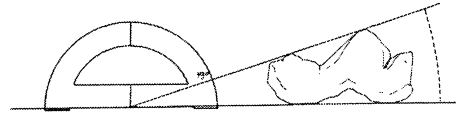
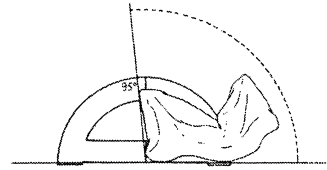
tribution is divided into five categories: (1) less than 0.6, (2) >0.6 to 0.7, (3) >0.7 to 0.8, (4) >0.8 to 0.9, (5) >0.9 . The second category contains the first mode; the fifth category contains the second (hypercarnivorous) mode.

This character was developed by Van Valkenburgh (1988, 1989) and has been shown to be a good indicator of diet among modern carnivorans. In modern taxa, carnivorans specialized for the consumption of meat are characterized by a lower carnassial dominated by the slicing blade (ratio approximating 1). This character is ordered, owing to the reduction of the talonid and an increasingly blade-dominated tooth within clades when approaching hypercarnivory (Wang 1994).

10. *Angle β , upper carnassial.* β is the angle between a line drawn from the metacone to the most anterior projection of the parastyle, and a line drawn from the metacone to the apex of the protocone, with the tooth positioned in full occlusal view (Appendix Fig. 4). This character is ordered. The distribution of β in the sample is unimodal with high dispersion and is skewed to the right. The continuum was divided into four categories based on the distribution and distinguishing the extremes: (1) $<15^\circ$, (2) 15° to 27° , (3) 28° to 38° , (4) $>38^\circ$. Category 2 includes the mode of the distribution. Category 4 contains the most hypocarnivorous taxa, whereas category 1 generally contains the specialized meat eaters.
- This character was developed by Crusafont-Pairó and Truyols-Santonja (1956). The two angles, β and α (see below), proved to be good descriptors of carnivoramorph evolution and ecological indicators.
11. *Angle α , lower carnassial.* α is the angle between a line drawn along the base of the tooth crown, above the roots, and a line



APPENDIX FIGURE 4. Angle β , upper carnassial: Top, An example of a hypercarnivore. Bottom, A hypocarnivore. (Modified from Fig. 5 in Crusafont-Pairó and Truyols-Santonja 1956: p. 318.)



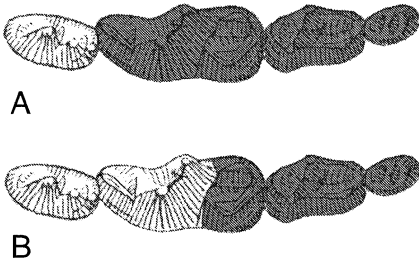
APPENDIX FIGURE 5. Angle α , lower carnassial: Top, An example of a hypercarnivore. Bottom, A hypocarnivore. (Modified from Fig. 1 in Crusafont-Pairó and Truyols-Santonja 1956: p. 315.)

drawn tangential to the protoconid and to the highest point on the talonid with the tooth positioned in full occlusal view (Appendix Fig. 5). This character is ordered. The distribution is unimodal with high dispersion and is skewed to the right. The continuum was divided into three categories based on the distribution. The boundaries reflect the curve of the distribution (delineating the mode from the tails) and a biologically significant transition to the right of the mode, where the talonid becomes very reduced—exact cutoffs between categories were arbitrary: (1) $<30^\circ$, (2) 30° to 60° , and (3) $>60^\circ$. Category 2 contains the mode of the distribution. Category 1 describes the generalists, whereas category 3 describes hypercarnivores. This character was developed by Crusafont-Pairó and Truyols-Santonja (1956).

12. *Angle γ , lower carnassial.* γ is the angle between the paralophid and protolophid of the trigonid of the lower carnassial positioned in occlusal view (Appendix Fig. 6). This character is ordered and bimodal. The first mode has high dispersion, the second mode no dispersion. The continuum was divided into four categories, delineating the first mode from the tails of the distribution, and the second mode at the extreme: (1) $<70^\circ$, (2) 70° to 130° , (3) $>130^\circ$ and $<180^\circ$, (4) equal to 180° . The second category contains the first mode; the fourth category contains the second mode. If the metaconid is absent there is no protolophid, and the angle is coded as 180° (category 4—characteristic of hypercarnivorous forms). Category 3 contains very few taxa; no taxon sampled had an angle γ between 150° and 180° . It appears that once the trigonid approaches the angle of 145° or 150° , the metaconid is lost. Hypocarnivores tend to have closed trigonids (low γ values), as do the earliest members of Carnivoramorpha.
13. *Shape of upper first molar:* (1) square or longitudinal rectangle, (2) transverse rectangle, (3) triangle, (4) absent. Shape was determined by outline of the occlusal surface. If the anteroposterior length was equal to or greater than the width,



APPENDIX FIGURE 6. Angle γ , lower carnassial: The angle between the paralophid and protolophid. (Modified from Fig. 49[b], *Paracynarctus kelloggii*, of Wang et al. 1999: p. 108.)



APPENDIX FIGURE 7. Grinding area: Total occlusal surface area of the lower molars (A) divided by the total grinding surface area (B). Shaded area is the area measured. (Modified from Fig. 49[b], *Paracynarctus kelloggii*, of Wang et al. 1999: p. 108).

it was considered square or a longitudinal rectangle. A molar that is mediolaterally wider than long, and has a hypocone or posterior shelf, was coded as a transverse rectangle. The triangle category was applied only to molars that were distinctly triangular—one lingual cusp and no hypocone, hypocone shelf, or enlarged cingulum around the protocone. If the molar is reduced, and not counted in the number of upper molars, it was coded as absent.

This character addresses the amount of grinding area on the upper tooth row, and in conjunction with other characters, describes how the upper molars are organized. In non-carnivoramorphans, in which the first upper molar may be the carnassial, the first molar posterior to the largest shearing tooth was scored.

14. *Number of upper molars.* For a molar to be considered present, its occlusal surface area must be equal to at least one-half of the surface area of the first upper molar. This character is ordered.

The reduction of molars is always associated with increasing carnivory. In non-carnivoramorphans, in which the first upper molar may be the carnassial, only molars with a grinding surface are counted. For example, a taxon in which the first molar is the carnassial and there are no molars with a grinding surface, the taxon is coded as having no molars.

15. *Cusp shape.* Cusps on the upper first molar were classified as round or sharp (from Jernvall 1995). “Sharp” is defined as a cusp that comes to a point and possesses sides with straight slopes. A “round” cusp has a rounded tip and the sides have curved slopes.

This character is somewhat subjective; therefore, only the cusps of the upper first molar are used for consistency within the sample, and the cusps are coded as round only when the condition is unambiguous. When the first molar was absent or reduced, the fourth upper premolar was used. Intermediate conditions were attributed to wear, and such cusps were therefore coded as sharp. Round cusps are more able to withstand the forces associated with crushing, whereas sharp cusps are more suited to process soft foods by piercing (Lucas 1979, Lucas and Peters 2000).

16. *Grinding area of the lower molars.* Calculated as the total occlusal surface area of the lower molars divided by the total grinding surface area (Appendix Fig. 7): (surface area of $m_1 + m_2 + m_3 \dots$) / (m_1 talonid + $m_2 + m_3$ + grinding area of p_4). This character is modified from Van Valkenburgh’s (1988, 1989) Relative Grinding Area. This character is or-

dered, continuous, bimodal in distribution, and highly skewed to the right. The continuum was divided into six categories to delineate the first mode from its immediate tails, the progressively increasing ratios, and the second mode at the extreme end characterizing no grinding area at all: (1) from 1 to 1.5, (2) >1.5 to 2, (3) >2 to 2.4, (4) >2.4 to 3, (5) >3 to 8, (6) >8. The second bin includes the mode for non-hypercarnivorous taxa. The sixth bin represents the mode of the distribution containing the hypercarnivores—all taxa with a grinding area of 0 or a grinding ratio >8.

The proportion of the molar row dedicated to grinding is much larger in generalists than in hypercarnivores (Van Valkenburgh 1989). Area measurements were taken digitally from digital images. When a portion of the lower fourth premolar formed a component of the grinding area, it was included in the denominator. In some taxa, the trigonid of the first lower molar is very low and has become a grinding surface; therefore, the total area and the grinding area are equal. Many early carnivoramorphans have high trigonids on all three of the lower molars; in such cases, only the talonids of these molars were included when calculating the grinding area.

17. *Body size* was estimated from the length of the first lower molar. This character is ordered, continuous and unimodal with high dispersion. The distribution of log body size was divided into five categories: (1) <7 kg, (2) 7 kg to 21.5 kg, (3) >21.5 kg to 50 kg, (4) >50 kg to 100 kg, (5) >100 kg. Body size estimates were derived from the regression of log body mass on log m_1 length, a calculation based on known body masses from extant carnivorans (Van Valkenburgh 1990). A different regression was used for each family to increase accuracy. For fossil carnivoramorphans that do not have living descendants, the regression for all of terrestrial Carnivora was applied. For creodonts, body size was estimated from the average length of all the lower molars (Morlo 1999).

Categories were determined in part by thresholds proposed in the literature. Carbone et al. (1999) concluded that carnivores above 21.5 kg consume only vertebrate prey close to or greater than the mass of the predator, whereas carnivores below 21.5 kg consume prey less than half of their mass and are more likely to be dietary generalists. Van Valkenburgh (1985, 1988) proposed a threshold at 7 kg based on evidence that carnivores above this mass are more likely to be competitively interactive with one another. The large body size categories were defined on the basis of gaps in the distribution (50 kg) and an arbitrary delineation at 100 kg to more finely divide the continuum. Category 2 contains the mode of the distribution, although there is a large portion of the sample below 7 kg. Log body mass is ordered because, owing to its important ecological ramifications (MacNab 1971, 1989; Gittleman 1986), it is necessary to preserve the linear relationship of the categories.

Sexual dimorphism is present in carnivorans but the intertaxon variation is minor compared with intrataxon variation. Binning the data further reduces the impact of sexual dimorphism. Although more accurate body size indicators than lower first molar length exist for carnivorans, such as head+body length and skull length, the material necessary for these measures is rare in fossil specimens (Van Valkenburgh 1990). When the most accurate body size proxy available from the literature for each taxon was used instead of the m_1 estimate, the difference in disparity values was minute.