The purpose of this study was to analyze temporal and spatial distribution of Middle and Late Miocene carnivore fossil species to test whether species’ distribution is influenced by systematic position, feeding adaptations, or body size.

Carnivores are a monophyletic group that originated no later than the Paleocene. They are characterized by carnassial teeth used in dividing meat, skin, and other soft but tough foods (Biknevicius and Van Valkenburgh 1996; Wyss and Flynn 1993). Carnivores generally retain primitive mammalian heterodont dentition, and this has enabled an array of feeding adaptations ranging from herbivory to carnivory.

Dentition provides a useful indicator of dietary adaptations and can be used to reconstruct dietary preferences of extinct species (Butler 1946; Crusafont-Pairó and Truyols-Santonja 1956). Using ecomorphology, paleontologists study ecological aspects of extinct carnivores that reveal paleocommunity structure (Palmqvist et al. 1999; Van Valkenburgh 1988, 1989; Viranta and Andrews 1995), prey–predator relationships (Palmqvist et al. 1996), and evolutionary trends (Viranta 1996; Werdelin 1996). One of the most striking patterns in carnivore evolution is iterative evolution, that is, evolution of the same ecomorphologies in different evolutionary lineages repetitively over time (Martin 1989; Van Valkenburgh 1991; Werdelin 1996).

Hypercarnivores are specialized predators characterized by loss of grinding surfaces and emphasis on cutting surface in their dentition. This is best exemplified by cats (Felidae), which probably have practiced hypercarnivory since their origin in the Early Miocene (Hunt 1998a). From the
Middle Miocene onward, they all have had blade-like carnassials and no grinding surface on their post-carnassial dentition. A similar dentition (accompanied by saber-like canines) is characteristic of the archaic family Nimravidae. A comparable dentition supplemented with bone-breaking premolars is typical of many hyaenids (Hyaenidae) and the extinct Percrocutidae, which probably differed from the hypercarnivores in their ecology. By means of bone-breaking premolars, they were able to use carcasses effectively, and some may have been scavengers rather than active hunters (Werdelin and Solounias 1991). Hypercarnivores also have evolved in Canidae (Van Valkenburgh 1991), Ursidae (Kurtén 1967), Amphicyonidae (Hunt 1998b), Mustelidae (Baskin 1998, and references therein), Hyaenidae (Werdelin and Solounias 1991), and Viverridae (Cryptoprocta—Köhnecke and Leonhardt 1986).

Many carnivores are active predators but maintain the ability to supplement their diet with vegetable matter. They maintain both slicing carnassials and grinding molars. These ecomorphs are common in all carnivore families, except for felids, nimravids, and percrocutids. A few forms have developed bone-breaking adaptations by enlarging the surface of molars rather than enlarging premolars, as in hyaenids (Werdelin 1989).

Lineages within the Ursidae, Amphicyonidae, Mustelidae, Procyonidae, and Canidae have produced mainly omnivorous forms that gain significant energy from sources other than meat. Few species are as herbivorous as the giant panda (Ailuropoda melanoleuca). Dental adaptations toward a more herbivorous diet include emphasis on molar grinding surface with reduction of trigonid of the lower carnassial and a decrease in premolar size.

Hypercarnivores are present in many terrestrial ecosystems, although they are more speciose in the tropics and where prey diversity is high (Van Valkenburgh 1991), while the omnivorous carnivores occur mainly in forested areas with heterogeneous environments (Viranta and Andrews 1995).

**Materials and Methods**

Data for this study were obtained from 2 separate databases that use the structure evolution of terrestrial ecosystems designed by John Damuth (Damuth in litt.). This structure includes locality and species tables, which are combined in species–locality lists. The public version of the database Neogene of the Old World (Fortelius et al. 1996a, 1996b), as of 25 March 1999, was used for the Eurasian record, and a separate database using the commercial software package Paradox was used for the North American record. The latter is based on the volume edited by Janis et al. (1998; data sets are available on request). A current version of the Neogene of the Old World database is also available on the Internet (www.helsinki.fi/science/now).

For higher classification I followed Wyss and Flynn (1993). Relationships of Miocene carnivore species are subject to little debate. The simocyonine group remains controversial and is placed in the Procyonidae in this study.

The Evolution of Terrestrial Ecosystems database structure allows incorporation of ecomorphic characters and ecologic interpretations for taxa. Two of the data fields, body mass and the 3rd diet category, were used for the carnivores. Body mass estimates are calculated based on morphologic structures known to correlate with body mass, and they are expressed as species means in kilograms. Most of the body mass estimates for carnivores were calculated by me. All of the estimates used are based on the length of the lower carnassial. Equations for various families were used to calculate body mass estimates for fossil representatives of extant families (Van Valkenburgh 1991). For members of extinct families, the equation for the closest living analog or one based on all carnivore families was used. Thus, the felid equation was used for nimravids and the ursid equation was used for amphicyonids (Viranta 1996). The recent hyaenid family is depauparate with only 4 species, so no equation is available for them. I used the all-carnivore equation for hyaenids and percrocutids (apparent close relatives of hyaenids—Werdelin and Solounias 1991).

This study explores the temporal range of species; I thus used only species that appeared and disappeared during the Middle and Late Mio-
cena. All species that appeared before, or continued to live after, the period were omitted.

Taxonomic information at the level of superfamily was coded separately. All species were members of either the Arctoidea, Canidae, or Feloidea (Table 1).

Taxa were combined into 3 categories: small (<10 kg body mass), medium (10–60 kg), and large (>60 kg; Table 1). This split places small carnivores from the size of least weasels (Mustela rixosa) to the size of red foxes (Vulpes vulpes) in the 1st category. The 2nd category, medium size, includes animals the size of typical larger canids such as coyotes (Canis latrans) and even wolves (Canis lupus). The 3rd category includes large carnivores, such as brown bears (Ursus arctos) or large pantherine felids (Panthera onca, Panthera tigris, and Panthera leo) in the modern fauna. Although large carnivores are rare now, many carnivores of the Miocene, especially machairodontine felid and amphicyonid species, were large.

Carnivore species were classified into 6 dietary categories: hypercarnivorous (meat only), mesocarnivorous (meat), bone breakers (meat and bone), omnivorous, insectivorous, and piscivorous. The latter 2 categories were omitted because of small sample sizes, and analyses were conducted on the species in the first 4 categories (Table 1).

The term hypercarnivore indicates primary groups with the emphasis on slicing surface in their dentition. In modern Canidae, the raccoon dog (Nyctereutes procyonoides) has a lower carnassial with a large crushing trigonid and short anterior blade or talonid and has a very opportunistic, omnivorous diet (Kauhala et al. 1998). The mesocarnivorous red fox (V. vulpes) has both the well-developed trigonid and talonid and is a hunter that uses a variety of food sources (Henry 1986). The gray wolf (C. lupus) is a hypercarnivore with emphasis on the trigonid in the lower carnassial (Van Valkenburgh 1991).

In the manner of Crusafont-Pairo and Truyols-Santonja (1956), Martin (1989), and Palmqvist et al. (1999), the relationship between the trigonid and talonid in the lower carnassial, along with molar number and morphology, was used to estimate the diet of the extinct carnivores. Carnivores with lengthened trigonids were classified as hypercarnivores. Enlarged posterior premolars with a conical shape or enlarged molars with heavy wear were indicative of bone breaking (see Werdelin 1989). Mesocarnivores were carnivores with an equal emphasis on slicing (talonid) and grinding (trigonid) parts of the carnassial. Omnivores had shortened trigonid and usually well-developed post-carnassial dentition. Given the well-established form–function relationship of the carnivore dentition, this method is widely used.

Some analyses combined species of the 4 diet categories into 2 groups to test for interactions between distribution and reliance on meat. This compared meat-dependant hypercarnivores and bone breakers with less meat-dependant mesocarnivorous and omnivorous taxa.

Fossil localities were placed in the common and widely used biochronological systems: North American land mammal ages (Tedford et al. 1987) and Mammalian Neogene units for Europe (Mein in litt.; Steininger et al. 1989). Average duration of a North American land mammal age biochron during the Middle and Late Miocene is 1.37 × 10^6 years (SD = 0.45). During the same time, the average length for a Mammalian Neogene unit is 1.38 × 10^6 years (SD = 0.65). I used North American land mammal age and European mammalian Neogene biochrons as time scales. To ease comparison between the 2 areas, I calculated midpoints for each unit (Fig. 1).

Western Eurasia was defined as the continent and adjacent islands west of 60°E. For those data, I used quadrants based on latitudinal and longitudinal lines, rather than faunal similarities or other paleobiological conditions. The lines are selected to match major observed contrasts between eastern and western Europe as well as the Mediterranean region and northern Europe (Fortelius and Hokkanen 2001). Four quadrants are recognized: northwest (the area covering north of 45°N and west of 20°E), southwest (south of 45°N and west of 20°E), northeast (north of 45°N and east of 20°E), and southeast (south of 45°N and east of 20°E).

Coordinates or exact geographic locations were not available in our database for North America; thus, these localities were assigned to provinces. Provinces are biogeographic regions that are distinct from neighboring areas in faunal composition (Tedford et al. 1987; Van Valkenburgh and Janis 1993). Provinces included in this study are the Pacific Northwest (Washington and Oregon), California coast (central and coastal California), Gulf Coast (Texas Gulf Coast,
Table 1.—Number of species in each dietary and size category of middle and late Miocene carnivores for North America and western Eurasia.

<table>
<thead>
<tr>
<th>Family</th>
<th>Omnivores</th>
<th>Mesocarnivores</th>
<th>Hypercarnivores</th>
<th>Bone-breakers</th>
<th>Small (&lt;10 kg)</th>
<th>Medium (10–60 kg)</th>
<th>Large (&gt;60 kg)</th>
<th>Timespan Mean</th>
<th>SD</th>
<th>Maximum range Mean</th>
<th>SD</th>
</tr>
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<td></td>
<td></td>
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<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
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<td>2</td>
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<td>1.52</td>
<td>2.00</td>
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<td>0</td>
<td>1.92</td>
<td>1.16</td>
<td>1.17</td>
<td>0.39</td>
</tr>
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Fig. 1.—Diversity and completeness of fossil record of large mammals (ungulates and carnivores) in the Middle and Late Miocene of North America and Eurasia. Records appear to represent the faunas well, except for the 2 diversity crashes in North America. These diversity crashes are probably real, although the fact that the records are incomplete adds to their magnitude. Circles indicate completeness index (CI in legend); diamonds indicate sample size ($n$ in legend).

Florida, parts of Louisiana, Mississippi, and southern East Coast including parts of Georgia and North and South Carolina), the northern Great Basin (southeastern California, Nevada, and southwestern Utah), the southern Great Basin (Arizona, New Mexico, the Texas Big Bend area, southwestern Colorado, and northern Mexico), the southern Great Plains (Texas and Oklahoma panhandles), the central Great Plains (Nebraska, South Dakota, Wyoming, Kansas, most of Utah, and northern and northeastern Colorado), the northern Great Plains (Montana, North Dakota, and western Canada), and the East Coast (north of the Carolinas). Quadrants of western Eurasia are comparable in geographic size to the North American provinces.

Completeness of the ungulate and carnivore fossil record through the Middle and Late Miocene was considered using a conservative completeness index ($CI_{bda}$) introduced by Barry et al. (1995) and Maas et al. (1995). It was calculated as $CI_{bda} = (N_{bd}/(N_{bd} + N_d))$, where $N_{bd}$ is the number of species present before, during, and after the given interval and $N_d$ is the number of species absent in the interval, but present before and after it (termed range-through species). In a complete absence of range-through species ($N_d = 0$), $CI_{bda}$ equals 1 and the interval is considered to be well sampled. The lower the index, the less complete the sample.

For each species, distribution in numbers of provinces or quadrants of occurrence in different time intervals was analyzed. Maximum distribution of a species was the greatest number of provinces or quadrants counted at any time during its existence. This method should correlate with actual distribution and provide a good estimation of maximum range.

Temporal range of each species was estimated as number of time units between 1st and last appearance. Use of these time units instead of actual time is justified, although not without problems. A majority of localities have no absolute dates associated with them. Most are placed in a North American land mammal age or Mammalian Neogene unit. There is also a theoretical foundation for use of the chronological systems. The faunal units are based on stages in evolution, and amplified faunal turnovers occur at the boundaries of units. Thus, the likelihood for extinction or origination is greater around the boundaries than in the middle of the unit. Second, the 1st and last records of species may not represent the actual origination or extinction events (Signor and Lipps 1982). Even if the real 1st record (the 1st appearance datum) were known, the date of origination is probably in a lower part of the faunal unit. Similarly the last appearance datum is not likely to represent the last individuals, so I placed extinction at the end of the unit. Possibilities for even earlier origins and later extinctions remain, but these are difficult to verify in paleontological data.

For statistical analysis, species were divided into 2 categories of maximum distribution and time span. Species that occurred in more than 2 provinces or quadrants at any time were recorded as widely distributed. The ones that never had more than a 2-province or quadrant distribution were recorded to have restricted distribution. Similarly, a species with longer than 2 time units temporal duration were long duration, whereas ones with duration of 1 or 2 units were short duration. Relationships between body mass, diet, taxonomic position (superfamily), and patterns of distribution and longevity were tested in contingency tables. Pearson chi-square statistics were performed using Systat 5.0 software (SYSTAT Inc. 1992). I also used contingency tables and Pearson chi-square to test for the independence of body mass, diet, and superfamily. Probability values that were $\leq 0.05$ were considered significant.
Finally, I extracted data on geographical ranges of the modern North American carnivores from Hall (1981) to test whether modern hypercarnivores show distribution patterns. Hall’s distribution maps take into account historical sightings and should reflect precolonial distribution. I excluded all mainly South American species (Herpailurus yaguarondi, Leopardus, Conepatus mesoleucus, Bassariscus astutus, Nasua nasua).

### RESULTS

In Middle and Late Miocene Eurasia mammalian species diversity is steady, but in North America diversity declines steadily. Decline is interrupted by 2 crashes (Fig. 1). Completeness indices are near 1 most of the time for both regions (Fig. 1). The completeness index for western Eurasia is never lower than 0.85. Two low values in the North American record are associated with diversity crashes. These occur in the late Late Barstovian (1.35 \times 10^7 years ago, CI_{bda} = 0.66) and in the late Early Hemphillian (8.0 \times 10^6, CI_{bda} = 0.80) and are likely to bias my recorded longevity for species. Some of the 1st and last appearances may have been missed for these 2 periods; however, this should apply to species in all categories equally.

Maximum geographic distribution of species is not significantly related to superfamilial membership (Table 2). In western Eurasia, members of Arctoidea, Canoidea, or Feloidea do not differ significantly from one another. Similarly, all 3 superfamilies in North America have similar patterns of large versus small maximum distribution.

Size and diet categories are related to maximum distribution, although the relationship is more pronounced and significant in western Eurasia (Tables 2 and 3). If the 2 meat-dependant groups (hypercarnivores...
### Table 3

Distribution of carnivore species by species longevity and maximum distribution of the species, related to dietary adaptation. Geographic distribution is given as number of quadrants (western Eurasia) and provinces (North America—see text) occupied by the species. Longevity is shown in biochrons (approximately 1.4 million years—see text). *P* is value for Pearson chi-square test for correlation between maximum distribution or longevity and dietary adaptation.

<table>
<thead>
<tr>
<th>Dietary adaptation</th>
<th>Omnivory</th>
<th>Mesocarnivory</th>
<th>Hypercarnivory</th>
<th>Bonebreaking</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Geographic distribution (quadrants or provinces)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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<td></td>
</tr>
<tr>
<td>≤2</td>
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<td>83</td>
<td>40</td>
<td>43</td>
</tr>
<tr>
<td>&gt;2</td>
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<td>6</td>
</tr>
<tr>
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<td></td>
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<td></td>
</tr>
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<td>33</td>
<td>15</td>
<td>17</td>
</tr>
<tr>
<td>&gt;2</td>
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<td>8</td>
<td>3</td>
<td>7</td>
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</table>

and bone breakers) are combined and compared with the 2 less meat-dependant groups (mesocarnivores and omnivores) combined, the relationship with the maximum distribution remains significant (*P* = 0.021) in western Eurasia and remains nonsignificant (*P* = 0.069) in North America.

In a combined data set including both North American and western Eurasian records, 72.4% of omnivorous species, 66.9% of mesocarnivorous species, 61.6% of bone-breaking species, and 49.2% hypercarnivorous species occur only in 1 unit during any given time. Most widely distributed species (those that occur in more than 3 units) were most commonly bone breakers. All these differences are nonsignificant (*P* > 0.20).

Temporal duration of species is independent of all the variables (superfamily, size, diet) in North America (Tables 2 and 3), and in western Eurasia only the superfamily has a significant association with duration (Tables 2 and 3). Species of Feloidea, including the Nimravidae, Viverridae, Felidae, and Hyaenidae, in western Eurasia tended to span longer periods of time. Most of these longer duration species were felids and hyaenids. Some 36% of all the felid species and 31% of the hyaenid species occurred at least in 3 units. Both families included species that spanned 7 time units. Two of 4 nimravid species had long temporal spans.

Despite the observed lack of statistical relationship, some other trends in temporal range seem to exist. Hypercarnivorous species have the smallest proportion of short-duration species (39.7% occur only in 1 unit). Proportion of short-duration species increased from bone breakers (46.6%) to mesocarnivores (59.9%). Omnivorous species are less frequently short duration (50.5%) than mesocarnivorous species. Dif-
Table 4.—Species longevity of carnivore species as related to species maximum distribution. Geographic distribution is given as number of quadrants (western Eurasia) and provinces (North America—see text) occupied by the species. Longevity is shown in biochrons (approximately 1.4 million years—see text). $P$ is value for Pearson chi-square test for correlation between maximum distribution and longevity.

<table>
<thead>
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<th>North America</th>
<th>Western Eurasia</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\leq 2$</td>
<td>$&gt; 2$</td>
</tr>
<tr>
<td>provinces</td>
<td>provinces</td>
<td>quadrants</td>
</tr>
<tr>
<td>Biochrons</td>
<td></td>
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</tr>
<tr>
<td>$\leq 2$</td>
<td>72</td>
<td>175</td>
</tr>
<tr>
<td>$&gt; 2$</td>
<td>31</td>
<td>52</td>
</tr>
<tr>
<td>$P$</td>
<td>0.019</td>
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</tr>
</tbody>
</table>

Difference between hypercarnivores and mesocarnivores is significant ($P = 0.025$).

Very long duration species (occurring for at least 4 successive time units) are most commonly hypercarnivores. Some 22% of all hypercarnivores occur in at least 4 successive time units, whereas 13.7%, 11.3%, and 13.3% of bone breakers, mesocarnivores, and omnivores, respectively, occur for this extended period. Significant differences in duration of species between hypercarnivore and mesocarnivores were found ($P = 0.05$).

If the group of hypercarnivores and bone breakers is contrasted with the group of omnivores and mesocarnivores, a statistically significant interaction with the time range is found for western Eurasian data ($P = 0.038$) but not for North America ($P = 0.828$). Species with large distributions also tended to persist over longer time spans (Table 4). Modern North American fauna showed no significant interaction either between diet and distribution ($P = 0.884$) or size and distribution ($P = 0.749$).

**DISCUSSION**

*Temporal versus spatial distribution.*—Carnivore species have wide geographic ranges compared to other mammalian taxa (Pagel et al. 1991), probably because they often hunt in an opportunistic manner in various environments. Thus species distributions are somewhat independent of habitat type (Bothma and la Riche 1989; Emmons 1987; Sunquist and Sunquist 1989). A negative correlation between degree of habitat specialization and geographic range of a species has been observed for various groups (Brown 1984), including mammals (Eeley and Foley 1999).

Eeley and Foley (1999) also found a negative correlation between dietary specialization and geographic range in African primates. Carnivores rarely are dietary specialists. Although hypercarnivores have specialized in hunting, they rarely if ever specialize on particular prey (see Van Valkenburgh and Janis 1993 for discussion). Whether they cue on prey characters such as body size is not well known (see Jaksic 1989), but a correlation between prey size and predator size has been shown (Rosenzweig 1966).

In the Middle and Late Miocene, bone-breaking and hypercarnivorous species were more widely dispersed than more omnivorous carnivores. Mesocarnivorous and omnivorous carnivores may be more dependent on specific vegetation and thus display some degree of habitat specialization. They may, for example, require a supply of berries or fruit or an abundance of large insects. In modern ecosystems, species richness of omnivorous carnivores is highest in environments with thick vegetation and multiple canopy layers (Viranta and Andrews 1995).
Empirical and theoretical evidence argues that abundant species (in terms of population sizes) are also widespread (Brown 1984, and references therein). This prediction is an unlikely explanation for the observed tendency of hypercarnivores and bone breakers to be widespread. Hypercarnivores are at the upper end of the food chain and expected to have lower population densities than their prey and other less carnivorous guild members (Elton 1927). Consequently, fossils of hypercarnivores should be rarer than fossilized remains of their prey and other less carnivorous or omnivorous species. Thus, overrepresentation in the fossil record is not a likely cause of the pattern of wide distribution of hypercarnivores and bone breakers. However, overrepresentation could occur due to bias in preservation.

A statistically significant association was also found between large distribution and long species longevity. This finding is in concordance with observations made on marine invertebrate records (Jablonski et al. 1985). Geographically restricted species exhibit significantly higher extinction rates. They tend to have shorter longevity than species with larger distributions. For modern species, the area occupied is assumed to be inversely correlated with extinction probability (Boecklen and Simberloff 1986; MacArthur and Wilson 1967).

Although my analyses of the 4 diet categories did not reveal significant differences in species longevity, when categories were grouped, western Eurasian data showed a relationship with longevity ($P = 0.038$). Species that were categorized as meat dependant (hypercarnivores and bone breakers) spanned longer periods of time than less meat dependant species.

Disparity between Eurasian and North American data.—My results were largely concordant between regions, although some disparity exists. Sample size (number of species) for North America was smaller ($n = 122$, compared to $n = 249$ for western Eurasia), suggesting that North American carnivore fauna was either locally (alpha diversity) less diverse than western Eurasian fauna, or North American species had wider distributions causing a low continental (gamma) diversity. Eurasian faunas displayed a higher degree of endemism as Janis (1993) suggested for the Miocene. The geography of western Eurasia was broken up with remnants of the Paratethys Sea, and western Eurasia probably remained patchy with abundant forests and some woodland until the end of the Miocene, while savanna-type open habitats dominated North America in the Miocene.

Faunal exchange between North America and Eurasia took place during the Middle and Late Miocene. Both regions also experienced immigration from the south, and several marked faunal turnovers occurred in both regions.

Taxonomically, North American and western Eurasian carnivore faunas share many elements but also differ to some extent. Many common genera of ursids and amphicyonids occurred in both regions. Interestingly, it seems that European amphicyonids and ursids repeatedly immigrated to North America during the Miocene (Hunt 1996). Canids as a family were endemic to North America and did not reach western Eurasia until the Late Miocene, while the hyaenids flourished in western Eurasia. Only 1 hyaenid species migrated to the New World (Hunt 1996). Both hyaenids and canids exhibited an array of dietary adaptations from omnivory to hypercarnivory, and convergent evolution appears to have taken place between the 2 families (Werdelin and Solounias 1991). Hunt (1996) suggests that in the Old World ursids and amphicyonids along with hyaenids filled niches occupied by canids in North America.

Felids evolved in Eurasia but soon migrated to North America where an independent radiation of felids was initiated during the Late Miocene (Hunt 1996). Nimravids, which were already vanishing in the Middle
Miocene, shared 1 genus (Barbouroufelis) between the continents.

Families consisting of smaller bodied forms such as Mustelidae, Procyonidae, and Viverridae tended to be more endemic. No viverrids occurred in North America, and Procyonidae was largely North American with an Early Miocene radiation in Europe. Mustelidae is a diverse family, with radiations both in western Eurasia and North America. Two modern mustelid genera, Martes and Mustela, occurred in both North America and Eurasia.

**Implications for modern fauna.**—Modern holarctic fauna lacks most of the specialized hypercarnivore ecomorphs present in the Miocene communities due to the Late Quaternary extinctions. Some of these survived in Africa or in the southernmost parts of Asia, while others such as sabertooth felids became globally extinct.

Sabertooth cats (machairodontine felids and nimravids in the Miocene) are now completely absent. Large bearlike ambush hunters (some amphicyonids and ursids in the Miocene) are represented by only polar bears (Ursus maritimus). Pantherine felids, common at the end of the Miocene through most of the Quaternary, are now completely absent in North America (with an exception of the jaguar, P. onca, observed occasionally in southernmost regions) and Europe.

Devoted bone breakers are also rare in modern faunas. Bone crackers with specialized conical-shaped premolars are now present mainly in Africa in the family of hyaenas. In the Eurasian Miocene, the Hyaenidae and Percrocutidae included many forms evolving in different lineages with bone cracking P3, p4, and p3. In North America some of the borophagine canids used P4, m1, and p4 for cracking bones (Werdelin 1989).

My data set of modern North American carnivores showed no interactions between diet, body mass, and distribution. Because of the depauparate nature of carnivore faunas after the Quaternary extinction, it is not surprising that no trends were found. To test whether hypercarnivores generally tend to be more widely distributed, data from different geological time periods should be studied. The Quaternary period is of special interest, because the faunas are well known and because of the close affinity to living carnivores.

**Hypercarnivores.**—The tendency for a widespread distribution with no obvious lengthening of temporal longevity of hypercarnivores lends support to the idea that competition among large predators is very high (Hairston et al. 1960). Extinction risk is high, and new species from different lineages evolve rapidly to fill any vacant niches. Van Valkenburgh (1991) proposed that intraspecific competition, even that between littermates, may be a significant selection factor for increased hypercarnivory. In addition, inter-specific competition must play a role.

Carnivore guild members compete not only indirectly for prey, but also directly via intraguild predation. In the modern mammalian communities, intraguild predation is fairly common and may be significant to coexistence of carnivore species (Palomares and Caro 1999). In many cases, large hypercarnivores hunt smaller and often more omnivorous carnivores. Small carnivores that hunt in groups may also successfully kill larger predators. Also, solitary small carnivores may hunt the young of their larger guild members. However, data compiled by Palomares and Caro (1999) show that in most cases killer species are hypercarnivorous (18 in total of 27 killer species), whereas hypercarnivores themselves are victims less often (17 in total of 54 victim species).

In conclusion, hypercarnivores seem to have evolved quickly as a result of intense selection, and they have become widely distributed because they require wider home ranges than more generalized feeders (Schoener 1969). Hypercarnivores are commonly present in various ecosystems, and distributions of individual species are typically large. Population densities are low,
causing high risk of extinction. Longevity may be further shortened by intense competition within the guild.

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LITERATURE CITED


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