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## Trophic diversity in past and present guilds of large predatory mammals

Blaire Van Valkenburgh

**Abstract.**—Trophic diversity within guilds of terrestrial predators is explored in three modern and two ancient communities. The modern communities span a range of environments including savannah, rainforest, and temperate forest. The paleocommunities are North American, Orellan (31–29 Ma), and late Hemphillian (7–6 Ma), respectively. The predator guilds are compared in terms of: 1) species richness; 2) the array of feeding types; and 3) the extent of morphological divergence among sympatric species. Feeding type is determined from dental measurements that reflect the proportion of meat, bone, and non-vertebrate foods in the diet. Measurements include estimates of canine shape, tooth size, cutting blade length, and grinding molar area. Morphological divergence among sympatric predators is measured by calculating Euclidean distances among species in a six-dimensional morphospace. Results indicate that the number of predator and prey species are roughly correlated in both ancient and modern communities. Two of the predator guilds, the late Hemphillian and modern Yellowstone, contain relatively few species and appear to be the result of extinction without replacement. Despite differences in history, age, and environment, the extent of morphological divergence within guilds does not differ significantly for the sampled communities. It is clear that the basic pattern of adaptive diversity in dental morphology among coexisting carnivores was established at least 32 million years ago. It appears that interspecific competition for food has acted similarly to produce adaptive divergence among sympatric predators in communities that differ widely in time, space, and taxonomic composition.

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### Introduction

In the relatively recent past, numerous extinctions brought on by both Pleistocene and more recent events have radically altered the composition of many communities (cf. Olson and James 1984; McDonald 1984). Perhaps hardest hit were the large mammals; in North America, over seventy genera of mammals weighing more than 44 kg disappeared within the last 10,000 years (Kurtén and Anderson 1980; Martin 1984). Other continents suffered less, but in all cases, large species suffered relatively more extinctions than smaller species. As a consequence, many large mammals no longer coexist with taxa that could have profoundly affected their morphological and behavioral evolution (Guilday 1984; Graham and Lundelius 1984). For example, the wolf (*Canis lupus*) formerly coexisted with sabertooth cats (*Smilodon fatalis*) and dire wolves (*Canis dirus*), in addition to the coyotes, pumas, bears and bobcats with which it coexists today. Morphological and behavioral

features observed in modern grey wolves may represent adaptations to previous conditions of competition and coexistence. Such possibilities create a frustrating problem for those who study living species and their communities: how can the effects of past ecological conditions be recognized apart from those of the present?

One way to approach this problem is through the study of communities that existed prior to the Pleistocene. By comparing the structure of fossil and living communities, the influence of Recent perturbations, such as extinction and human interference, should become apparent. In effect, the fossil communities are used as pre-perturbation controls against which their modern counterparts are compared.

An additional advantage of fossil communities is that they represent a long timespan. The dynamics of living systems can only be studied for a limited number of seasons or years, usually less than twenty. During such short intervals, the effects of major environ-

mental catastrophes such as volcanic eruptions or large hurricanes are likely to be either missed or overestimated. (Woodley et al. 1981; Swanson 1987). By contrast, a fossil deposit will typically span a much greater time interval and records the community throughout a range of biotic and physical conditions. Admittedly, the resolution of paleontological studies is often less than that of neontological studies, but the fossil record can provide crucial evidence concerning ecological processes on a grand scale.

Of course, the fossils limit the kinds of data available. Due to the biases of preservation, it is difficult to estimate relative abundances of species (Behrensmeyer et al. 1979; Damuth 1982). However, the number of taxa and the morphological distance between taxa in a community can be quantified (Van Valkenburgh 1985). In the last 10 years, numerous studies of community structure have used these last two parameters to compare equivalent guilds in different localities, and the technique has been labeled the "ecomorphological approach" (e.g., Karr and James 1975; Findley 1976; Grant and Schluter 1984). The label reflects the use of morphology alone to infer significant aspects of a species niche, such as prey size from bill depth or jaw length.

In this paper, the ecomorphological approach is used to examine trophic diversity within the guild of large terrestrial predators in two ancient North American faunas of Orellan (Oligocene, 31.5–29 Ma) and late Hemphillian (Miocene, 7–6 Ma) age. The results are compared with those from a similar study of three modern guilds from different environments (Van Valkenburgh 1988). The Orellan paleoguild includes taxa that are phyletically distant from living Carnivora, early members of two extinct families of Carnivora (Amphicyonidae and Nimravidae) and terminal members of an extinct order of carnivorous mammals, the Creodonta. The late Hemphillian fauna includes representatives of the modern families of Carnivora, although several are from extinct subfamilies (e.g., Borophaginae, Machairodontinae).

The following questions are asked: 1) is species richness similar in modern and ancient guilds; 2) is the morphological distance

between sympatric species equivalent in all guilds; and 3) what does the fossil evidence suggest about the impact of extinction on diversity within predator guilds? The previous study of three extant guilds indicated that species richness within predator guilds is greater when the species richness of prey is high and that the average morphological distance between sympatric species is similar among guilds. This suggests that competition for food is an important structuring force in guilds of large predators, an idea with considerable empirical and theoretical support (Hairston et al. 1960; Schoener 1974; Van Valkenburgh 1985 and references therein).

### Materials and Methods

Fossil material of 17 extinct predators was measured in this study (Appendix 1). Numbers of specimens measured per species varied according to availability. When more than one specimen was measured, a species mean value was calculated.

Twelve functionally significant measures of cranial and dental anatomy were taken: skull length; length and width of the upper canine, largest lower premolar and all lower molars; and grinding area and cutting blade length of the lower molars (Fig. 1 and Appendix 2). As in the companion study of 47 living Carnivora (Van Valkenburgh 1988), these measurements were used to produce five morphometric ratios that describe canine shape, premolar shape and size, relative blade length, and grinding area of the lower molars (Appendix 2). Among living carnivores, these indices reflect the relative proportion of meat, bone, and non-vertebrate (e.g., fruits, insects) foods in the diet (Appendix 3).

Two of the indices, relative premolar size and relative blade length (RPS, RBL, Appendix 3), were able to clearly separate the extant Carnivora into four dietary groups on bivariate and multivariate plots. Fossil taxa were graphed on the same plots and placed in dietary categories according to their inclusion or proximity to one of the four dietary clusters. If the classification was uncertain, the values for other indices, such as canine shape and relative grinding area, were considered as well. The dietary categories are the same

ones used in Van Valkenburgh (1988): 1) meat—greater than 70 percent meat in diet; 2) meat/bone—greater than 70 percent meat with the addition of large bones; 3) meat/non-vertebrate—50–70 percent meat with the balance fruit and/or insects and 4) non-vertebrate/meat—less than 50 percent meat with fruit and/or insects predominating (Table 1). Although the meat/bone category is occupied by only three species at present (hyaenas), it is included because of its presumed ecological significance. Bone-crushing abilities give bone/meat species access to calories that are unavailable to other meat specialists.

In addition to these indices, an estimate of body size was made for each fossil predator using linear regressions of weight against skull length and/or head–body length for 47 living Carnivora (Van Valkenburgh 1985). Table 1 lists the values of the morphometric indices and estimated body weight for each extinct species.

As in the earlier study of locomotor diversity within predator guilds (Van Valkenburgh 1985), two of the morphometric indices and body weight are used as axes of a three-dimensional morphospace (Fig. 2). The two indices, relative premolar size and cutting blade length (RPS, RBL; Appendices 2 and 3), are among the best predictors of dietary type. Meat specialists like felids tend to have relatively long cutting blades and average size premolars; bone eaters have both long cutting blades for slicing meat and enlarged premolars for crushing bone; and more omnivorous taxa have relatively shorter blades and narrow premolars (Ewer 1973; Jaslow 1987; Van Valkenburgh 1988). Body size is used as an axis because of its demonstrated importance in determining prey size, as well as life history traits, foraging radius, metabolic requirements, and interspecific dominance (Rosenzweig 1966, 1968; McNab 1971; Eaton 1979; Eisenberg 1981; Lamprecht 1981; Gittleman and Harvey 1982; Gittleman 1986).

The diversity and packing of feeding types within guilds can be visually compared by plotting the members of each guild separately. In addition, Fig. 2A presents a morphospace that contains the entire sample of living Carnivora used in the analysis of diet-dental

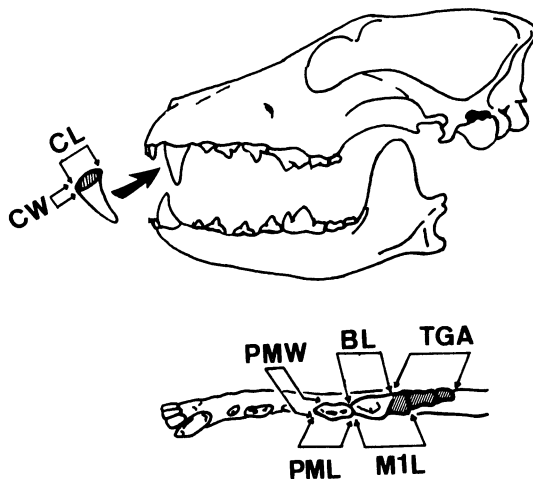


FIGURE 1. Dental measurements. CL, maximum anteroposterior length of canine. CW, maximum mediolateral width of canine. BL, blade length of carnassial tooth. PMW, maximum mediolateral width of premolar. PML, maximum anteroposterior length of premolar. M1L, maximum anteroposterior length of carnassial. TGA, total grinding area of lower molars (shaded area) measured from color slides by a polar planimeter. All other measurements were taken with dial calipers.

morphology correlations (Van Valkenburgh 1988). This graph displays the shape of the morphospace currently occupied by living Carnivora and serves as a framework for viewing each guild.

Because the 3-D plots can only display the morphological differences among sympatric predators in three characters, the Euclidean distances between pairs of guild members in six-dimensional space (one dimension per morphometric index plus body weight) are calculated. To compensate for differences in scale among the indices, the variables were transformed to standardized normal deviates (Sneath and Sokal 1973) before plotting or estimating distance values. The standardized deviates were calculated using data from predators of all the guilds.

Euclidean distance values are unaffected by correlations among variables and so can overlook the fact that some variables provide no new information (Van Valen 1974). To examine this possibility, correlations between the morphometric indices were tested with Spearman rank coefficients (Zar 1984). Of the 15 pairwise comparisons, only four differed significantly from zero ( $P < 0.05$ ). In two of

TABLE 1. Values of the morphometric indices and diet group assignments for the examined fossil species. All values are means; see Appendix 1 for list of measured specimens. Morphometric indices: LBW, log body weight; CS, canine shape; RPS, relative premolar size; PMD, premolar shape; RBL, relative blade length; RGA, relative grinding area. Diet groups: M, meat; M/B, meat/bone; M/N-V, meat/non-vertebrate. For details, see text and Appendix 2.

Species	LBW	CS	RPS	PMD	RBL	RGA	Diet Group
<b>Creodonta</b>							
<i>Hyaenodon horridus</i>	1.97	0.68	2.28	0.56	1.00	0.00	M
<i>H. crucians</i>	1.30	0.75	2.23	0.54	1.00	0.00	M
<b>Nimravidae</b>							
<i>Hoplophoneus occidentalis</i>	1.87	0.54	1.76	0.47	1.00	0.00	M
<i>H. primaevus</i>	1.26	0.54	2.32	0.48	1.00	0.00	M
<i>Dinictis felina</i>	1.30	0.54	2.35	0.48	0.85	0.23	M
<i>Eusmilus dakotensis</i>	2.02	0.35	1.70	0.50	1.00	0.00	M
<b>Felidae</b>							
<i>Machairodus coloradensis</i>	2.21	0.42	2.14	0.42	1.00	0.00	M
<i>Pseudaeleurus hibbardi</i>	1.84	0.69	1.97	0.50	1.00	0.00	M
<i>Adelphailurus kansensis</i>	1.71	0.65	(2.00) <sup>1</sup>	(0.48) <sup>1</sup>	1.00	0.00	M
cf. <i>Felis proterolyncis</i>	1.19	0.77	2.05	0.49	1.00	0.00	M
<b>Canidae</b>							
<i>Mesocyon</i> sp.	1.11	0.64	1.91	0.48	0.68	0.88	M/N-V
<i>Osteoborus cyonoides</i>	1.62	0.70	3.11	0.66	0.74	0.73	M/B
<i>Canis davisii</i>	1.00	0.69	1.95	0.39	0.65	0.90	M/N-V
<i>Vulpes stenognathus</i>	0.84	(0.73) <sup>2</sup>	1.87	0.37	0.62	0.99	M/N-V
<b>Amphicyonidae</b>							
<i>Daphoenus vetus</i>	1.58	0.72	1.60	0.44	0.65	1.40	M/N-V
<i>D. hartshornianus</i>	1.41	0.72	1.56	0.46	0.67	1.24	M/N-V
<b>Ursidae</b>							
<i>Agriotherium schneideri</i>	2.54	0.73	2.02	0.55	0.60	1.39	M/N-V
<b>Mustelidae</b>							
<i>Plesiogulo marshalli</i>	1.53	0.77	2.50	0.61	0.64	0.57	M/B
<i>Pliotaxidea nevadensis</i>	0.36	(0.80) <sup>3</sup>	2.09	0.60	0.59	0.98	M/N-V

<sup>1</sup> There are no lower premolars known for *Adelphailurus kansensis*. These estimates are the mean value for PMS and PMD for six other sabertooth species (*Hoplophoneus occidentalis*, *H. primaevus*, *Dinictis felina*, *Eusmilus dakotensis*, *E. sicarius*, and *Machairodus coloradensis*).

<sup>2</sup> Because there are no upper canines known for *V. stenognathus*, their CD value was estimated by the mean value for 16 extant canids.

<sup>3</sup> Approximate (based on the alveolus of a single specimen figured in Hall [1946]).

these, the value of  $r$  fell below 0.5. The remaining two, CS versus RBL and RBL versus TGA, had  $r$  values of 0.63 and 0.84, respectively. Because the degree of independence among the variables was generally high, all six were retained in the distance analysis.

As in Van Valkenburgh (1985), three different estimates of dispersion were calculated based on the morphological distance between guild members: (1) the average link length of a minimum spanning tree connecting all guild members; (2) the average distance between each species and the guild centroid (determined as the mean value of each of the six characters); and (3) the average distance between any species and its nearest neighbor.

The species composition for each of the five guilds discussed in this paper is shown in Table 2. The guilds include all the non-aquat-

ic species within the community that capture and consume prey. The guild is confined to predators weighing 7 kg or more (i.e., jackal size and larger), because the evidence for strong competitive interactions among these animals is substantial, whereas that for competition between them and smaller carnivores is relatively weak (see Van Valkenburgh 1985). The three extant guilds, Yellowstone, Malaysia, and Serengeti, and the Orellan paleoguild were used in two previous studies and detailed references on their physical, biotic, and in the case of the Orellan, paleoecological, characteristics are in Van Valkenburgh (1985).

The late Hemphillian paleoguild is a new addition. Although the North American Late Miocene record is generally good, this particular time was chosen because the taxonomy

TABLE 2. Predator guild composition. The guild includes all the terrestrial mammals larger than 7 kg that take prey. Some carnivore taxa have been excluded because they eat almost no meat: the sloth bear (*Melursus ursinus*) from Chitawan; the aardwolf (*Proteles cristatus*) from Serengeti; and the sun bear (*Helarctos malayanus*) from Malaysia. Within each community there are several species which might be considered borderline members according to this definition (e.g., pigs and some primates). However, such animals have remained omnivorous or tended to herbivory throughout their history and have probably had only minor competitive interactions with predatory mammals; thus, they are excluded with caution. By contrast, most of the living omnivorous members of the order Carnivora have descended relatively recently from more predacious ancestors (e.g., ursids and viverrids; see Petter 1969, Crusafont-Pairo and Truyols Santonja 1956, 1957). Their tendency to eat fruit and insects can be viewed as a possible response to competition within the guild.

Serengeti	Yellowstone
Lion, <i>Panthera leo</i>	Puma, <i>Puma concolor</i>
Leopard, <i>P. pardus</i>	Lynx, <i>Lynx canadensis</i>
Cheetah, <i>Acinonyx jubatus</i>	Bobcat, <i>Lynx rufus</i>
Caracal, <i>Caracal caracal</i>	Wolf, <i>Canis lupus</i>
Serval, <i>Felis serval</i>	Coyote, <i>Canis latrans</i>
Wild dog, <i>Lycaon pictus</i>	Red fox, <i>Vulpes vulpes</i>
Blackbacked jackal, <i>Canis mesomelas</i>	Wolverine, <i>Gulo gulo</i>
Golden jackal, <i>C. aureus</i>	Badger, <i>Taxidea taxus</i>
Sidestriped jackal, <i>C. adustus</i>	Black bear, <i>Ursus americanus</i>
Spotted hyaena, <i>Crocota crocuta</i>	Grizzly bear, <i>Ursus arctos</i>
Striped hyaena, <i>Hyaena hyaena</i>	
Ratel, <i>Mellivora capensis</i>	
Civet, <i>Civettictis civetta</i>	
	Malaysia
	Tiger, <i>Panthera tigris</i>
	Leopard, <i>P. pardus</i>
	Clouded leopard, <i>Neofelis nebulosa</i>
	Temminck's cat, <i>Felis temminckii</i>
	Fishing cat, <i>F. viverrina</i>
	Dhole, <i>Cuon alpinus</i>
	Binturong, <i>Arctictis binturong</i>
	Civet, <i>Viverra megaspila</i>
	Orellan
Hemphillian	
<i>Machariodus coloradensis</i>	<i>Hoplophoneus occidentalis</i>
<i>Pseudaeleurus hibbardi</i>	<i>H. primaevus</i>
<i>Adelphailurus kansensis</i>	<i>Dinictis felina</i>
<i>Felis proterolyncis</i>	? <i>Eusmilus dakotensis</i>
<i>Canis davisi</i>	<i>Daphoenus vetus</i>
<i>Vulpes stenognathus</i>	<i>D. hartshornianus</i>
<i>Osteoborus cyonoides</i>	<i>Mesocyon</i> sp.
<i>Plesiogulo marshalli</i>	<i>Hyaenodon horridus</i>
<i>Agriotherium schneideri</i>	<i>H. crucians</i>
<i>Arctonasua fricki</i>	

of the carnivores appeared stable relative to that of earlier faunas. Thus, the possibility of either missing or adding guild members due to taxonomic errors of splitting or lumping were minimized. The late Hemphillian guild represents a composite of three discrete localities, separated by 50 to 200 miles: The Coffee Ranch of Texas; the Optima (Guymon) of Oklahoma; and the Edson Quarry of Kansas (Schultz 1977). Two of these, Coffee Ranch and Edson Quarry, are lenticular deposits which may represent seasonal lakes or bogs

(Dalquest 1969; Schultz 1977; Harrison 1983), whereas the Optima deposits are of stream channel origin (Savage 1941; Schultz 1977). Because fossil collections from each locality have numerous species in common, they are judged to have been roughly contemporaneous (Schultz 1977; Harrison 1983). However, no one locality has produced all ten species listed in Table 2, so the composite should be considered a probable maximum for late Hemphillian times. One omnivorous species, the badger (*Pliotaxidea nevadensis*), was

excluded from the guild due to its small size. One additional large cat, *Nimravides catacopis*, may be represented by a single tooth at Optima (Savage 1941; Martin and Schultz 1975), but its identity is questionable since the genus has been more recently listed as extinct by mid-Hemphillian times (Schultz 1977; Baskin 1981; Harrison 1983). It is excluded from the guild with caution.

For both paleoguilds, the possibility exists that species were present but not preserved or discovered, or species outside the order Carnivora that fulfilled the missing roles were overlooked. However, it appears unlikely that such artifacts of the record fully account for the great differences in species richness observed in the present paper (e.g., 9 versus 13 taxa). Taphonomic studies have shown that skeletons of species larger than 10 kg are subject to less post-mortem damage than those of smaller species and hence are more likely to be preserved in fossil deposits (Behrensmeyer et al. 1979). Skeletal and dental material from both the late Hemphillian and Orellan deposits described here is abundant, well-preserved, and probably provides a complete, or nearly complete, representation of the large predator community as it existed (cf. Dalquest 1969; Voorhies 1970; Damuth 1982; Harrison 1983).

The second possibility, that unexpected substitutes for the meat and meat/bone roles existed, such as large terrestrial reptiles or ground birds, can be largely ruled out since such potential surrogates are absent from Orellan and late Hemphillian faunas of North America (cf. Clark et al. 1967; Schultz 1977). However, as noted in the discussion of the Orellan guild below, there are some large artiodactyls (entelodonts) which may have scavenged occasionally.

## Results

The distribution of the sample of 47 modern Carnivora within the morphospace defined by log body weight, relative premolar size, and cutting blade length is shown in Fig. 2A. Position on the blade length axis (RBL) reflects the relative proportions of meat and non-vertebrate foods in the diet. The strictest meat species, the cats, all have similarly long

cutting blades (high RBL values) and cluster along the volume's left edge (RBL > 1, Fig. 2A). Slightly more omnivorous members of the meat group, such as the wolf and wild dog ("Cl," "Lp": Fig. 2A), have retained a talonid on their lower molar, have smaller blade length values than the felids, and are located near the center of the volume (RBL near 0). Adjacent to them, with still shorter shearing blades, are the members of the meat/non-vertebrate group (triangles). Members of the non-vertebrate/meat group have the relatively shortest cutting blades (low, negative RBL values) and form a clump near the right edge of the volume, although a few exist on the edge of the central cluster (squares: Fig. 2A). The premolar axis (RPS) distinguishes meat/bone specialists from all others and reveals species within other groups which tend toward bone-eating. Meat/bone eaters exhibit a combination of relatively wide premolars (high RPS) and long cutting blade (high RBL) and thus are positioned in the left, rear corner (stars: Fig. 2A).

Each of the four diet groups is characterized by a limited range of premolar size and shear length values, and each tends to occupy a separate region of the volume floor. In general, the species in the center of the volume are more generalized in their diet than those near the edges. Moreover, this central clump includes a greater taxonomic variety than do the three satellite clusters (for details, see Van Valkenburgh 1988). There are intriguing gaps between the four clumps, indicating that there are combinations of premolar size, shear length and body weight which are not exhibited by any of the 47 species of extant Carnivora. For example, there is no species of large size (LBW > 1) in the meat/non-vertebrate group, nor is there a species with average or narrow width premolars (RPS near 0) that has retained a small grinding basin on the carnassial (RBL = 0 to 1). This suggests that such species with such morphologies might not be viable at present, but, as will become apparent, does not exclude their past existence.

*Results of guild comparisons.*—The three Recent guilds differ in the total number of species and the array of dietary types (Figs. 2, 3). The

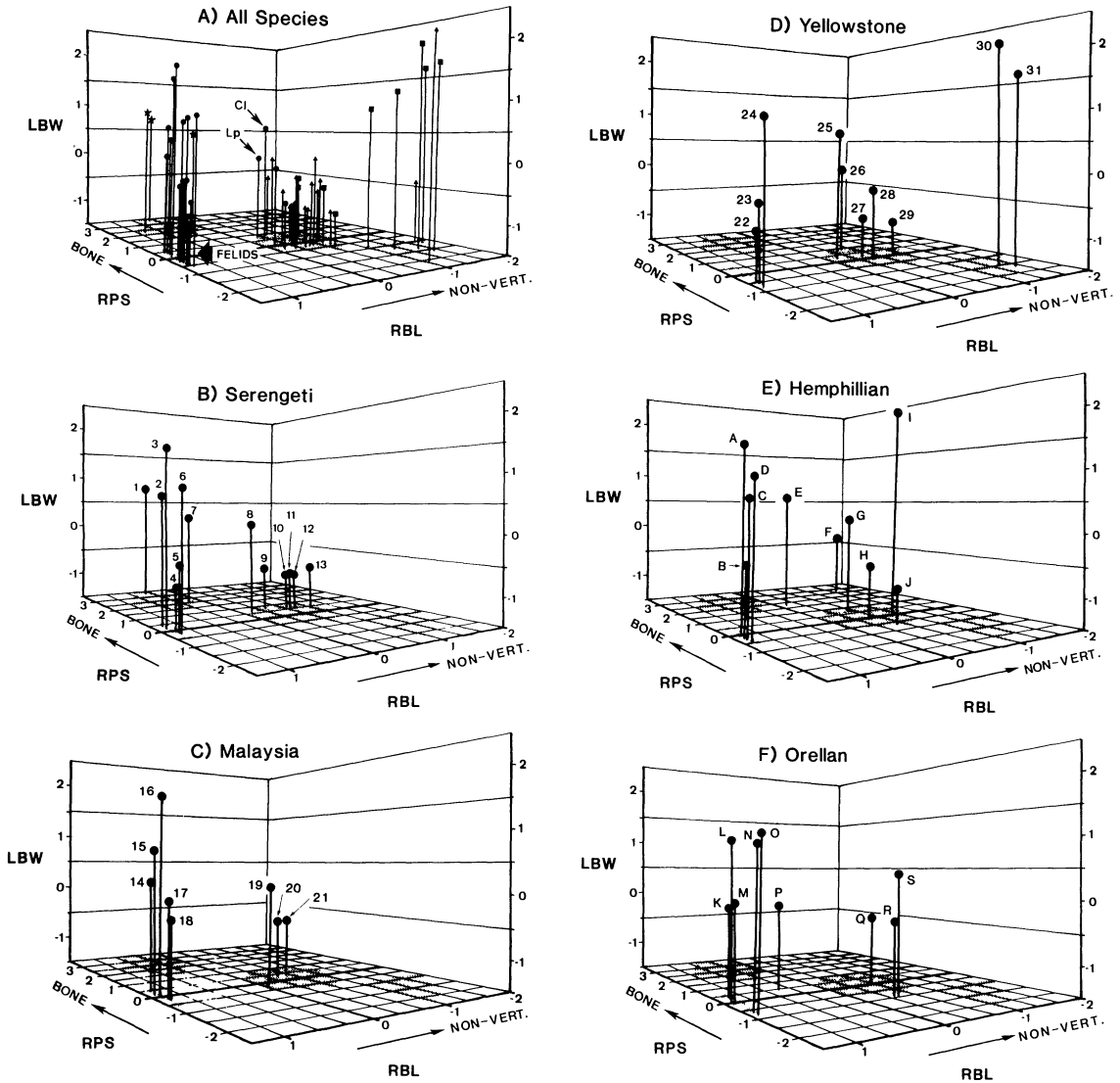


FIGURE 2. Guild morphospaces. For all plots, the axes are log body weight (LBW), relative premolar size (RPS), and relative blade length (RBL). Units are standardized normal deviates of values shown in Table 1. Shaded areas indicate the range of RPS and RBL values observed in (A), the sample of 47 Carnivora. (A) All species, includes 47 species described in Van Valkenburgh (1988). In (A), species are represented by symbols which indicate their dietary classification (Table 1). Meat, circles. Meat/non-vertebrate, triangles. Non-vertebrate/meat, squares. Abbreviations in (A) are as follows: Lp, *Lycaon pictus*; Cl, *Canis lupus*.

(B) the Serengeti predator guild, species as follows: 1, spotted hyaena; 2, leopard; 3, lion; 4, serval; 5, caracal; 6, cheetah; 7, striped hyaena; 8, wild dog; 9, ratel; 10, side-striped jackal; 11, blackbacked jackal; 12, golden jackal; 13, civet.

(C) the Malaysia guild, species as follows: 14, clouded leopard; 15, leopard; 16, tiger; 17, Temminck's cat; 18, fishing cat; 19, dhole; 20, civet; 21 binturong.

(D) Yellowstone guild, species as follows: 22, bobcat; 23, Canadian lynx; 24, puma; 25, wolf; 26, wolverine; 27, red fox; 28, coyote; 29, badger; 30, grizzly bear; 31, black bear.

(E) Late Hemphillian guild, species as follows: A, *Machairodus coloradensis*; B, *Felis proterolyncis*; C, *Pseudaeleurus hibbardii*; D, *Adelphailurus kansensis*; E, *Osteoborus cyonoides*; F, *Arctonasua fricki*; G, *Plesiogulo marshalli*; H, *Canis davisii*; I, *Agriotherium schneideri*; J, *Vulpes stenognathus*.

(F) Orellan guild, species as follows: K, *Hyaenodon crucians*; L, *Hyaenodon horridus*; M, *Hoplophoneus primaevus*; N, *Hoplophoneus occidentalis*; O, *Eusmilus dakotensis*; P, *Dinictis felina*; Q, *Mesocyon* sp.; R, *Daphoenus hartshornianus*; S, *Daphoenus vetus*.



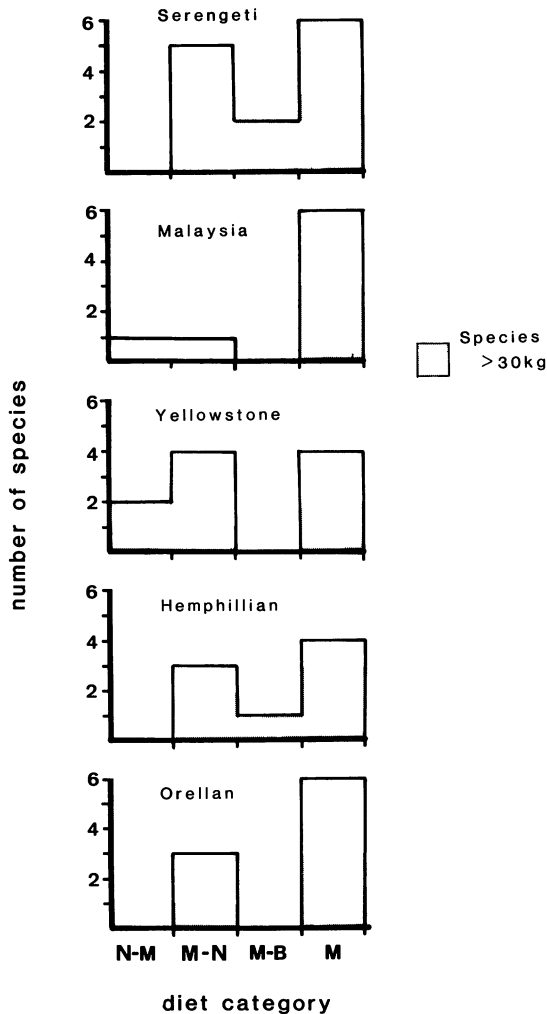


FIGURE 3. Species richness ( $n$ ) within dietary categories for each guild as labeled. Diet categories: N-V/M, non-vertebrate/meat; M/N-V, meat/non-vertebrate; M/B, meat/bone; M, meat.

Serengeti is the most species-rich, with thirteen carnivores, drawn from each of the four diet categories except non-vertebrate/meat. Yellowstone has ten predators, representing each diet group except meat/bone. Malaysia has the smallest number of species, eight, and like Yellowstone, is without a meat/bone specialist. Both tropical guilds, Malaysia and the Serengeti, contrast with Yellowstone in their greater number of meat specialists, six as opposed to four, and their lack of non-vertebrate/meat species.

Despite these differences, the morphological distance between species is similar in the

Serengeti and Malaysia, even when all six morphological characteristics are considered (Table 3). The greater average morphological distance between Yellowstone predators (average M.S.T. and D.F.C., Table 3) is due to the inclusion of bears in the guild. If the omnivorous bears are excluded, the dispersion among the remaining species is close to that shown in the two tropical guilds.

The three distance measures, M.S.T., N.N.D. and D.F.C., each contribute somewhat different information about the distribution of species within the volume. Of the three, the average link of the minimum spanning tree (M.S.T.) is probably the best indicator of overall morphological similarity among guild members. The mean distance from guild centroid (D.F.C.) increases with the addition of species, and nearest-neighbor distances (N.N.D.) are lowered by clumping within the volume. Unfortunately, neither M.S.T. or N.N.D. values can be compared statistically because their link lengths are not independent. Pairwise comparisons of D.F.C. values among the guilds (with or without bears included) showed no significant differences ( $P > 0.10$ , Mann-Whitney, two-tailed; Zar 1984).

The six-million-year-old late Hemphillian guild is similar to Malaysia and Yellowstone in low species-richness, but more like the Serengeti in the wide array of feeding types represented (Figs. 2E, 3). It differs from all the modern examples in the greater average morphological distance between species as measured by M.S.T. and N.N.D. (Table 3), even when the bear, *Agriotherium*, is removed. The values remain high even if the badger, *Pliotaxidea*, which was excluded from the analysis due to its small size, is added. The average D.F.C. is similar to that of the two larger guilds, Yellowstone and Serengeti, but greater than that of the similarly sized Malaysian guild (Table 3). However, the late Hemphillian D.F.C. value did not differ significantly from those of the other guilds ( $P > 0.20$ ; Mann-Whitney, two-tailed). In spite of this, I doubt the packing of late Hemphillian predator species within the morphospace is equivalent to that of the other guilds, all of which are similar to one another in all three distance

TABLE 3. Morphological distance characteristics of each guild. The mean link length of the minimum spanning tree (M.S.T.), the mean distance to nearest neighbor (N.N.D.), and the average distance between each species and its guild centroid (D.F.C.). SD is the standard deviation of each mean for each guild. Values for the Yellowstone are shown both with ( $N = 10$ ) and without ( $N = 8$ ) the bears included. For the late Hemphillian, values are shown for the guild with *Pliotaxidea* and *Arctonasua* included ( $N = 11$ ), excluded ( $N = 9$ ), and with the bear, *Agriotherium*, excluded as well ( $N = 8$ ). The fossil material of *Arctonasua fricki* is too incomplete for several of the dental measurements, so its values were estimated by those of its similarly sized relative, *A. eurybates*.

Guild	No. of species	Avg. link M.S.T.	Avg.		SD	Avg.	
			SD	N.N.D.		D.F.C.	SD
Serengeti	13	1.49	0.605	1.21	0.467	2.12	0.540
Malaysia	8	1.52	0.733	1.41	0.745	1.68	0.675
Yellowstone	10	1.67	1.06	1.11	0.695	2.33	0.784
	8	1.48	0.769	1.14	0.785	1.78	0.119
Late Hemphillian	11	1.95	0.934	1.97	0.930	2.61	0.796
	9	1.97	0.936	1.72	0.968	2.31	0.616
	8	1.84	0.922	1.57	0.917	2.20	0.684
Orellan	9	1.59	0.640	1.30	0.632	1.84	0.501

measures. Instead, it appears that D.F.C. values are relatively poor indicators of species packing when species tend to be distributed in clumps, as they are here. In such cases, the centroid lies far from either clump, and D.F.C. reflects the distance between clumps rather than between taxa. Thus, the distance between clumps is similar in the late Hemphillian and modern guilds, but that between taxa (as reflected by N.N.D. and M.S.T.) appears to be greater in the late Hemphillian.

There were ten predators in the late Hemphillian guild: four meat specialists (two sabertooth and two non-sabertooth felids), four meat/non-vertebrate species (an ursid, mustelid, and two canids), a meat/bone species (a canid), and a non-vertebrate/meat species (a procyonid). The meat/bone species, *Osteoborus cyonoides* (E in Fig. 2E), is a member of an extinct subfamily of canids, the Borophaginae, and represents a morphology (that is, combination of premolar size, shear length, and body weight) unknown within the sample of extant Carnivora (compare shaded area Figs. 2A, 2E). Note also that the meat/bone role was played by a canid in this instance, rather than a hyaenid as is true of the modern guilds. *Osteoborus* can be classified as a frequent consumer of bone with confidence, based on the measured characters (Table 1, Appendix 3) and previous descriptions of its dental morphology (Matthew and Stirton 1930; Dalquest 1969). The bear, *Agriotherium*, is unusual as well, both because it was much larger than any of the living members of the

meat/non-vertebrate group and because it had a highly carnivorous dentition relative to modern ursids. These two important examples of convergent evolution suggest that phyletic constraints may be readily circumvented to produce adaptive divergence within guilds.

The Orellan paleoguild, which existed from 31.5 to 29 Ma, is considerably older than the other four guilds and is composed almost entirely of representatives from extinct families of mammals (Table 2). For example, the meat group is made up of creodonts and nimravids cats, both of which have no living descendants. Despite these important historical differences, the general configuration and dispersion of species within the guild volume is remarkably similar to modern examples (compare Fig. 2B–D with 2F; Table 3). Considering the examples of convergence discussed above, and those of the Orellan paleoguild, it cannot be argued that similarity among guilds is simply due to similarities in phylogenetic background.

In the Orellan paleoguild, there were nine species, six in the meat and three in the meat/non-vertebrate group; meat/bone and non-vertebrate/meat species are absent (Fig. 3). As in the Miocene paleoguild, there are species which occur outside the bounds of the morphological space occupied by Recent taxa. *Dinictis felina* (Fig. 2F, "P") is a sabertooth cat (Family Nimravidae) which retains a small heel on its carnassial, much like extant hyaenas. The two bear-dogs, *Daphoenus vetus* and

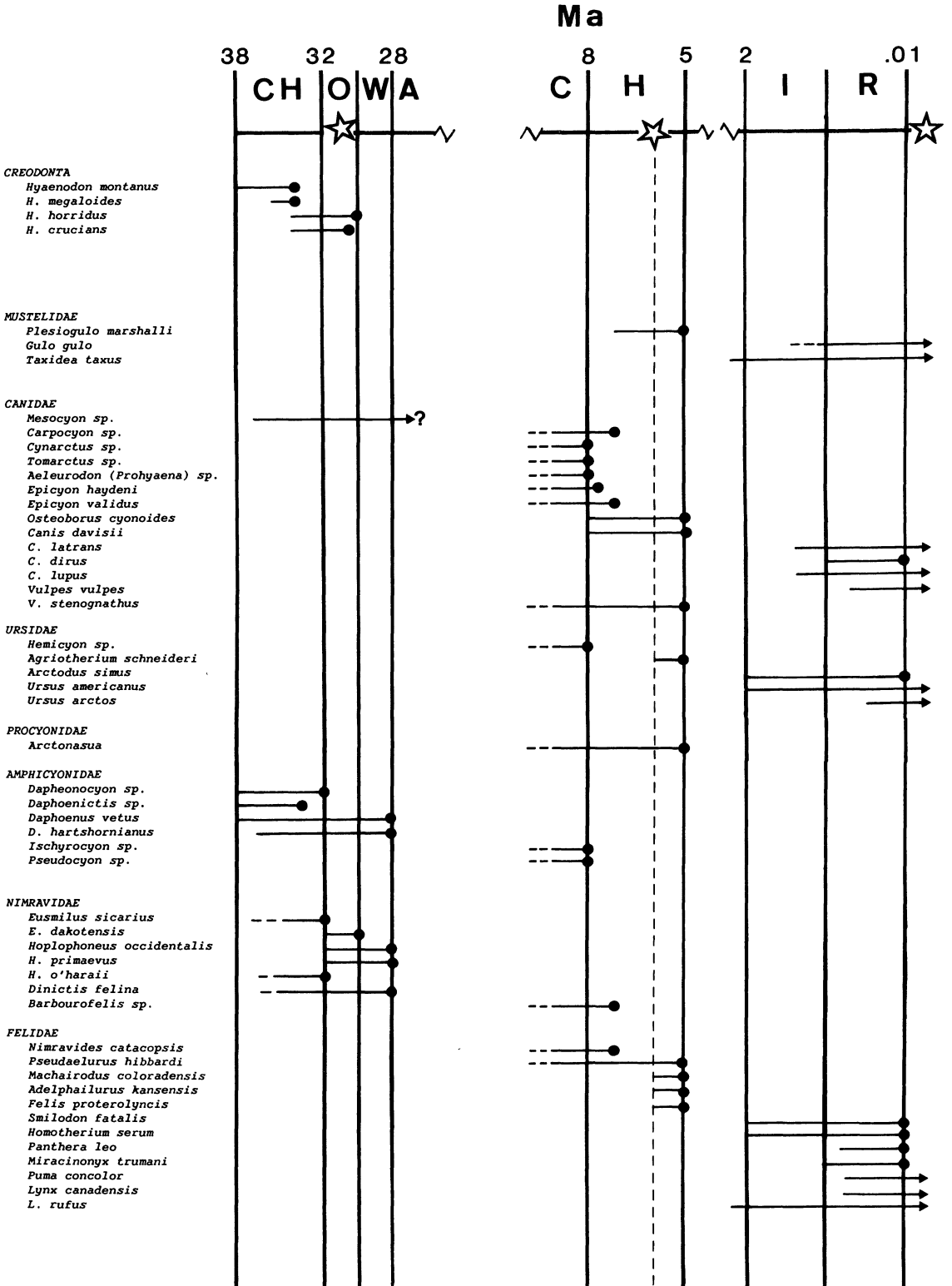


FIGURE 4. Stratigraphic ranges of predators within the North American guilds and the predators which preceded the guild members. The "?" for *Mesocyon sp.* is due to its uncertain taxonomic identity. The time scale is shown at

*D. hartshornianus* (Fig. 2F; "R" and "S"), lie close to the area occupied by extant meat/non-vertebrate species and might be included if the sample of extant species were larger.

The important differences among the guilds can be summarized as follows:

(1) the Serengeti guild contains 13 species whereas all four others contain eight to ten;

(2) the two tropical guilds, the Serengeti and Malaysia, and the Orellan, include six meat species, whereas the Yellowstone and late Hemphillian include but four;

(3) meat/bone specialists are found only in the Serengeti and late Hemphillian guilds; and

(4) the average morphological distance between sympatric species is similar in all guilds, except the late Hemphillian, where it appears somewhat large.

### Discussion

The results of the comparisons of the three Recent guilds are discussed in detail in Van Valkenburgh (1988) and are summarized here. In general, it appears that species richness within guilds, particularly of meat and meat/bone specialists, is greater in the environments where the biomass and species richness of prey are greater. The tropical guilds, Malaysia and Serengeti, have both a greater diversity and density of herbivore prey (arboreal and/or terrestrial) and meat eaters (including meat/bone specialists) than does the temperate environment of Yellowstone. In addition, the presence of scavengers (meat/bone species) in the Serengeti guild probably reflects the greater availability of carcasses in savannah as opposed to forest environments.

Although the distribution and biomass of prey in the tropical savannah and rainforest appear to reflect directly the abundance and availability of low-stature vegetation (Eisenberg and McKay 1974; Eisenberg and Seiden-

sticker 1976; Coe et al. 1976), the same cannot be said of Yellowstone. There, history has probably played a more prominent role than environment in setting diversity levels. In North America, the impact of the Pleistocene on the large mammal fauna was severe, and six large predators were eliminated from the continent (Fig. 4 and references therein). Of the six, four were meat specialists (felids), one was a meat/bone species (the dire wolf, *Canis dirus*), and one was a relatively carnivorous bear (*Arctodus simus*). Thus, species dependent on large herbivores were hit hardest by Pleistocene events. Not surprisingly, the species richness of large herbivores in western North America declined sharply over the same period, from about 14 to six (Kurtén and Anderson 1980).

By contrast, the East African guild has undergone little change for close to two million years (Fig. 5 and references therein). Unfortunately, the fossil record of Malaysian carnivores is poor, but the evidence from the herbivores suggests that the rainforest community persisted throughout the Pleistocene, although its boundaries fluctuated (Verstappen 1975).

The similarity among the guilds in the average morphologic distance between sympatric predators is somewhat surprising. In the earlier study of locomotor diversity within predator guilds, predators were more similar to one another in the measured skeletal characters in the Serengeti, where terrestrial herbivore diversity and biomass levels are highest (Van Valkenburgh 1985). The difference in results between the locomotor and dietary analysis probably reflects the greater influence of environment on locomotor than dental anatomy. The Serengeti environment is predominantly grassland and the predators may have converged on an appropriate attack behavior (long-distance pursuit) and associ-

←

the top. The stars mark, from left to right, the times of the Orellan, Hemphillian and Yellowstone guilds, respectively. Abbreviations as follows: CH, Chadron; O, Orellan; W, Whitneyan; A, Arikarean; C, Clarendonian; H, Hemphillian; I, Irvingtonian; R, Rancholabrean. References: Jepsen 1933; Simpson 1941; Savage 1941; Scott and Jepsen 1941; Hough 1948, 1949; Mellett 1977; Hunt 1974; Munthe 1979; Kurtén and Anderson 1980; Baskin 1980, 1981; Harrison 1981, 1983; Savage and Russell 1983; Tedford et al. 1988.

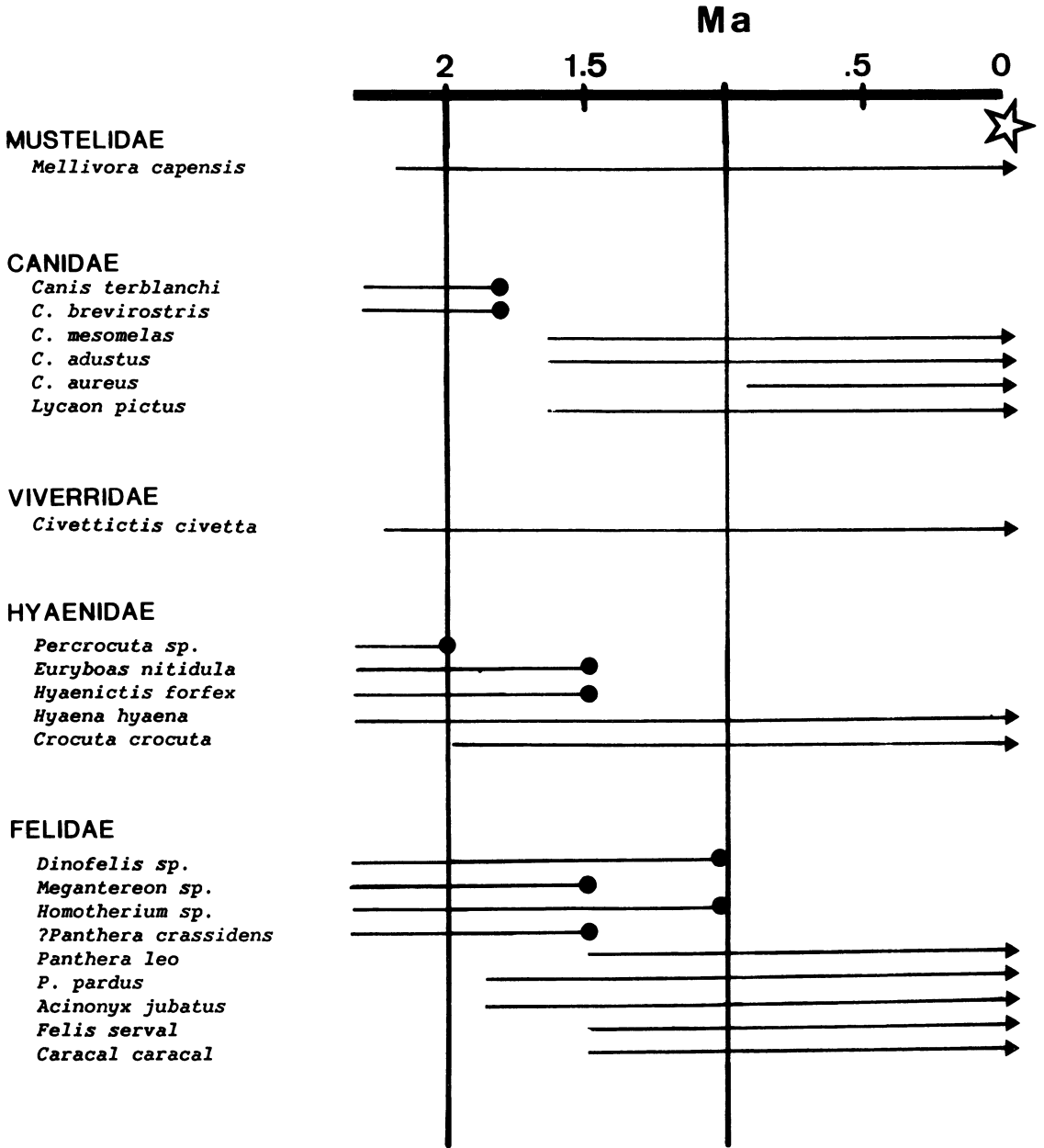


FIGURE 5. Stratigraphic ranges of the Serengeti predators and the predators that preceded them in Africa. The time scale is shown at the top; the star indicates the time of the studied guild (the present). References: Hendeby 1974a, b, c; Savage 1978; Brain 1981; Walker 1984.

ated morphology. By contrast, the character of meat does not change with location and predators in very different environments are likely to have similarly adapted dental morphologies.

Nevertheless, it is remarkable that the impact of extinction on the Yellowstone guild

is not apparent in the packing of species within the morphospace. The loss of six large predators might be expected to produce a guild that appears overdispersed relative to other, less disturbed guilds. Although this is not the case for the guilds examined here, it may be that the Yellowstone guild is over-

dispersed relative to the pre-Pleistocene paleoguild of the same area. I was unable to test this for the Wyoming area, but work in progress on the predators of southern California indicates that a 27 percent drop in the number of predators since the Rancholabrean was accompanied by nine percent and 25 percent rises in M.S.T. and N.N.D. values, respectively. Thus, it appears that extinction can result in greater morphological spacing within predator guilds.

*The late Hemphillian paleoguild.*—Paleobotanical evidence suggests that the dominant plant community in central North America during the Hemphillian was savannah-woodland mosaic with gallery forests (Leopold 1969; Wolfe 1978). Given this environment, the diversity of large herbivores is unexpectedly low, 13 species as opposed to the Serengeti's 24. As in the Recent examples, predator diversity is correspondingly low, ten species as opposed to 13. The presence of a bone-eater, *Osteoborus cyonoides*, suggest a relatively high predictability of carcasses, perhaps reflecting high ungulate biomass and/or the savannah environment.

As at Yellowstone, the low numbers of large herbivore and carnivore species in the late Hemphillian of North America appear to be the result of extinction without replacement. Six million years before, ungulate species richness was comparable to that of modern East Africa (Webb 1983). Two successive waves of extinction in the late Clarendonian (circa 9 Ma) and the early Hemphillian (circa 7 Ma) eliminated many herbivore and carnivore taxa. The causes of the decline are thought to be increased aridity and climatic cooling, both of which might lower plant productivity as savannah progressed toward steppe (Wolfe 1978; Webb 1983, 1984). As herbivore diversity dropped, competition for food among predators might have intensified, resulting in some extinctions.

The late Clarendonian guild included 14 predators, seven of which were lost by the early Hemphillian (Table 4). All seven were canids, amphicyonids or ursids; the sole nimravid and two felids persisted across the Mio-Pliocene boundary (Fig. 4). Two new canids appeared as replacements, *Osteoborus* and *Canis*

TABLE 4. Species richness of predators and prey in North America in the Late Miocene and Early Pliocene. For the late Clarendonian and early Hemphillian faunas, species richness is based on surveys of the collections of the American Museum of Natural History in New York and data in Tedford et al. (1988) and Webb (1983).

North American Land Mammal Age	Ma.	No. of large predators	No. of large herbivores
Lt. Clarendonian	9	14	18
E. Hemphillian	7	8	8
Lt. Hemphillian	6	10	13

*davissii*, bringing the total number of guild members to eight in the early Hemphillian. The mid-Hemphillian event eliminated three more species, two cats and a canid, but was followed by the immigration of five new predators, three felids, an ursid and a mustelid. Thus there was a net gain in species richness within the guild during Hemphillian time, from eight to ten (Table 4). This appears to have been associated with similar changes in the numbers of large herbivores throughout this interval, suggesting that predator species richness tracked that of the prey. This is to be expected if competition for food at all affects the structure of predator guilds. A smaller array of prey morphologies can support a more limited range of predator morphologies.

The role of competition in guild evolution is further supported by an examination of the sequence of extinctions and replacements during the Hemphillian. The loss of several dog-like predators in the late Clarendonian is partially filled by the subsequent appearance of two canids. Similarly, the extinction of two cat-like ambush predators precedes the immigration of three new felids.

The late Hemphillian paleoguild differs from the three modern examples in the greater average morphological distance between species, even when the bear, *Agriotherium*, is excluded (M.S.T., N.N.D.: Table 3). The apparent overdispersion of the late Hemphillian guild is probably due to the preceding extinction events. As mentioned above, extinctions might occur randomly with respect to morphological spacing within the guild and produce a relatively dispersed guild. Over time, given favorable conditions of prey richness and abundance, these gaps could be filled

by new species and dispersion within the guild would decrease. Substantiation of this idea will require more comparisons of guilds before and after extinction events.

*The Orellan paleoguild.*—Unlike the late Hemphillian, the Orellan was not immediately preceded by a severe extinction event. There were extinctions of carnivore taxa at or near the Chadron–Orellan boundary, but all were replaced by similar species so that overall paleoguild diversity levels remained stable for 6–8 m.y. (Fig. 4).

Because the Carnivora (creodonts excluded) of the Orellan are closer, in a temporal sense, to the earliest representatives of their order than are extant carnivores, it might be expected that the Orellan carnivores would appear more similar to one another, and less dentally specialized, than extant sympatric predators. However, a glance at Fig. 2 shows this not to be true. Although only two of the four feeding categories are represented, the difference in dental morphology between the meat and meat/non-vertebrate species is almost always as great or greater than that observed between the two types today (compare Fig. 2F with 2B and 2D). The one exception is the sabertooth nimravid cat, *Dinictis felina* (Fig. 2F, "P"), which, unlike any extant and most extinct cats, did not devote its entire carnassial to a cutting blade.

These results contrast with those of the study of locomotor diversity within the same guilds (Van Valkenburgh 1985). In that study, all the predators of the Orellan appear to have been slower and more forceful than their modern counterparts. Apparently, there has been a tendency towards greater speed in both predator and prey over the Cenozoic (Bakker 1983), probably in response to a global increase in the amount of grassland and open woodland habitats (Webb 1977, 1978; Wolfe 1985). The texture of meat and bone is unlikely to have changed over the same timespan and so adaptations for consuming these substances evolved early and remained stable. This is not true of the dental adaptations of herbivores; a progressive increase in tooth height and resistance to wear has been documented for several groups (Scott 1913; Gregory 1971; Webb 1977). In this case, the quality

of the food did appear to change over time as grasses became more resistant to grazing.

The strong divergence in dentition among the Orellan fissipeds seems not to have been accompanied by a similar divergence in cranial morphology. In a study of cranial shape characteristics of fissipeds, Radinsky (1982) showed that differences that distinguish modern families of carnivores were less pronounced in the Oligocene. The disparities in our results are surprising, in view of the close functional relationship between skull and dentition. However, the skull is undoubtedly subject to a wider variety of selection pressures than teeth since it serves many complex functions, such as housing the brain and sense organs, in addition to its role in feeding behavior. Consequently, teeth and skulls might be expected to evolve at different rates.

Given that the 31-million-year-old paleoguild is composed almost entirely of extinct families and orders of carnivores, it is remarkable that the array of feeding types is so similar to that of the modern guilds (Fig. 3). Like Malaysia, it includes six meat species (three over 30 kg), no meat/bone or non-vertebrate/meat species, and a small number of meat/non-vertebrate species. This suggests a rainforest environment with low ungulate diversity and density, but numerous folivores and frugivores. This is the environment first predicted by the locomotor adaptations of the Orellan predators, but contradicted by a lack of arboreal animals, the presence of a few open-habitat ungulates, and the paleobotanical data (Webb 1977; Retallack 1983; Van Valkenburgh 1985). A mixture of woodland, gallery forest, and some grassland seems most consistent with all the evidence.

In such an environment, terrestrial herbivore diversity should be lower than that of the Serengeti, since grasslands are less extensive. In addition, browsing, rather than grazing, ungulates should predominate. Bone/meat species might be present since carcass predictability should be higher than in a continuous forest, especially if the climate is dry or cool. The Orellan herbivore fauna is less diverse than the Serengeti (11 species versus 24), and browsing ungulates are more common than grazers (Gregory 1971; Webb 1977).

However, there are no bone/meat species, despite the fact that the Orellan appears to have been seasonally arid (Clark et al. 1967; Singler and Picard 1981; Retallack 1983).

It should be noted that there is an unusual group of Oligocene taxa, neither creodonts or carnivores, that may have been fulfilling the hyaena role in part: the entelodonts. The entelodonts were giant pig-like artiodactyls with relatively pointed premolars and large canines, two features which are reminiscent of carnivores (Matthew 1901; Scott and Jepsen 1941). As shown by the extant polar bear, meat-eating can be accomplished with teeth more typical of non-vertebrate/meat species (Van Valkenburgh 1988). A detailed examination of dental function and microwear in entelodonts might reveal if they were the hyaenas of the Orellan. If they were not, it appears that a potentially profitable mode of life remained unexploited within the Orellan community (see Stanley et al. 1983).

Despite its unique taxonomic composition, the Orellan paleoguild is remarkably similar in morphological diversity to the late Hemphillian and Recent guilds (Fig. 2). In part, this reflects the characters that were chosen to describe the morphology. For example, if I had used the shape of the lower second molar, then the creodonts, which have narrow, carnassial-shaped molars, would stand out as a unique morphology. However, the functional interpretation of the creodonts would not change; their diets would still be considered to have been 70–100 percent meat. So although the design and phylogeny of the Orellan animals differ markedly from their modern counterparts in some cases (e.g., creodonts, nimravid cats), the trophic structure within the paleoguild is similar to the Recent guilds. This tendency toward the evolution of convergent feeding adaptations in distantly related carnivores suggests that similarities in trophic structure among the guilds cannot be explained as a simple consequence of heritage constraints (i.e., all guilds look alike because they are composed of canids, felids, and hyaenids). Instead, the similarities in guild structure strongly suggest that guilds of large predators are shaped, at least loosely, by interspecific competition for food. As a

result, predator guild structure ultimately reflects the resource base.

### Summary and Conclusions

(1) Body weight and five dental indices are used to examine the diversity of dietary types within three Recent and two fossil guilds of large predators.

(2) Results show that guilds differ primarily in the number of member species and the relative representation of the four dietary types: meat, meat/bone, meat/non-vertebrate, and non-vertebrate/meat.

(3) The diversity of meat and meat/bone species within guilds is correlated with prey diversity in both ancient and modern guilds.

(4) Historical evidence suggests that the apparently depauperate Yellowstone and late Hemphillian guilds are the result of extinction without replacement.

(5) Predators have existed in the past with dental morphologies that are unique and possibly suboptimal relative to modern taxa, although these unique, extinct taxa coexisted with species of modern aspect.

(6) Despite the fact that the 31-million-year-old paleoguild is composed of members of extinct families and orders of predators, the array of dietary types is very similar to that of the Recent guilds, especially Malaysia.

(7) The basic pattern of adaptive divergence in dental morphology among sympatric carnivores was established at least 32 million years ago.

(8) The correlations between resource availability and dietary diversity in guilds, documented in the Recent and confirmed by the fossil communities, suggest that interspecific competition for food plays an important role in the evolution of predator guilds.

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### Literature Cited

- BAKKER, R. T. 1983. The deer flees, the wolf pursues: incongruencies in predator-prey coevolution. Pp. 350-383. *In* Futuyma, D. J. and M. Slatkin (eds.), *Coevolution*. Sinauer Associates; Sunderland, Massachusetts.
- BASKIN, J. A. 1980. The generic status of *Aeleurodon* and *Epicyon* (Carnivora, Canidae). *Journal of Paleontology* 54:1349-1351.
- BASKIN, J. A. 1981. *Barbourofelis* (Nimravidae) and *Nimravides* (Felidae) with a description of two new species from the late Miocene of Florida. *Journal of Mammalogy* 62:122-139.
- BASKIN, J. A. 1982. Tertiary Procyoninae (Mammalia:Carnivora) of North America. *Journal of Vertebrate Paleontology* 2:71-93.
- BEHRENSMEYER, A. K., D. WESTERN, AND D. D. BOAZ. 1979. New perspectives in vertebrate paleoecology from a recent bone assemblage. *Paleobiology* 5:12-21.
- BRAIN, C. K. 1981. *The Hunters or the Hunted*. University of Chicago Press; Chicago, Illinois. 365 pp.
- BURT, W. H. 1931. *Machaerodus catocopsis* Cope from the Pliocene of Texas. University of California Publications in Geological Sciences 20:261-293.
- BUTTERWORTH, E. M. 1916. A new mustelid from the Thousand Creek Pliocene of Nevada. University of California Publications, *Bulletin of the Department of the Geological Sciences* 10:21-24.
- CLARK, J., J. R. BEERBOWER, AND K. K. KIETZKE. 1967. Oligocene sedimentation, stratigraphy, paleoecology and paleoclimatology in the Big Badlands of South Dakota. *Fieldiana: Geological Memoirs* 5:1-158.
- COE, M. J., D. H. CUMMINGS, AND J. PHILLIPSON. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* 22:341-354.
- CRUSAFONT-PAIRO, M. AND J. TRUYOLS-SANTONJA. 1956. A biometric study of the evolution of fissioned carnivores. *Evolution* 10:314-332.
- CRUSAFONT-PAIRO, M. AND J. TRUYOLS-SANTONJA. 1957. Estudios masterométricos en la evolución de los fissionados. *Boletín del Instituto de Geológico y Minero España* 68:83-224.
- DALQUEST, W. W. 1969. Pliocene carnivores of the Coffee Ranch (type Hemphill) local fauna. *Bulletin of the Texas Memorial Museum* 15:1-44.
- DAMUTH, J. 1982. Analysis of the preservation of community structure in assemblages of fossil mammals. *Paleobiology* 8: 434-446.
- EATON, R. L. 1979. Interference competition among carnivores: a model for the evolution of social behavior. *Carnivore* 2:9-16.
- EISENBERG, J. F. 1981. *The Mammalian Radiations*. University of Chicago Press; Chicago, Illinois. 610 pp.
- EISENBERG, J. F. AND G. M. MCKAY. 1974. Comparison of ungulate adaptations in the New World and Old World tropical rainforests with special reference to Ceylon and the rainforests of Central America. Pp. 585-602. *In* Geist, V. and F. Walther (eds.), *The Behavior of Ungulates and its Relation to Management*. IUCN Publications, new series 24; Morges, Switzerland.
- EISENBERG, J. F. AND J. SEIDENSTICKER. 1976. Ungulates in Southern Asia: a consideration of biomass estimates for selected habitats. *Biological Conservation* 10:293-308.
- EWER, R. F. 1973. *The Carnivores*. Cornell University Press; Ithaca, New York. 494 pp.
- FINDLEY, J. S. 1976. The structure of bat communities. *American Naturalist* 110:129-139.
- GITTLEMAN, J. L. AND P. H. HARVEY. 1982. Carnivore home-range size, metabolic needs and ecology. *Behavior, Ecology and Sociobiology* 10:57-63.
- GITTLEMAN, J. L. 1986. Carnivore life history patterns: allometric, phylogenetic and ecological associations. *American Naturalist* 127:744-771.
- GRAHAM, R. W. AND E. L. LUNDELIUS, JR. 1984. Coevolutionary disequilibrium and Pleistocene extinctions. Pp. 223-249. *In* Martin, P. S. and R. G. Klein (eds.), *Quaternary Extinctions*. University of Arizona Press; Tucson, Arizona.
- GRANT, P. AND D. SCHLUTER. 1984. Interspecific competition inferred from patterns of guild structure. Pp. 201-233. *In* Strong, D. R., Jr., D. Simberloff, L. G. Abele, and A. B. Thistle (eds.), *Ecological Communities: Conceptual Issues and the Evidence*. Princeton University Press; Princeton, New Jersey.
- GREGORY, J. T. 1971. Speculations on the significance of fossil vertebrates for the antiquity of the Great Plains of North America. *Abhandlungen der Hessischen Landesamtes für Bodenforschung* 60:64-72.
- GUILDAY, J. E. 1984. Pleistocene extinction and environmental change: case study of the Appalachians. Pp. 250-258. *In* Martin, P. S. and R. G. Klein (eds.), *Quaternary Extinctions*. University of Arizona Press; Tucson, Arizona.
- HAIRSTON, N. G., F. E. SMITH, AND L. B. SLOBODKIN. 1960. Community structure, population control and competition. *American Naturalist* 94:421-425.
- HALL, E. R. 1946. A new genus of American Pliocene badger with remarks on the relationships of badgers of the Northern Hemisphere. *Carnegie Institution of Washington Publications, Contributions to Paleontology* 551:9-23.
- HARRISON, J. A. 1981. A review of the extinct wolverine *Plesiogulo* (Carnivora: Mustelidae) from North America. *Smithsonian Contributions to Paleobiology* 46:1-27.
- HARRISON, J. A. 1983. The Carnivora of the Edson local fauna (late Hemphillian), Kansas. *Smithsonian Contributions to Paleobiology* 54:1-42.
- HATCHER, J. B. 1895. Discovery in the Oligocene of South Dakota of *Eusmilus*, a genus of sabre-toothed cats new to North America. *American Naturalist* 29:1091-1093.
- HENDEY, Q. B. 1974a. Faunal dating of the late Cenozoic of Southern Africa, with special reference to the Carnivora. *Quaternary Research* 4:149-161.
- HENDEY, Q. B. 1974b. New fossil carnivores from the Swartkrans Australopithecine site (Mammalia: Carnivora). *Annals of the Transvaal Museum* 29:27-47.
- HENDEY, Q. B. 1974c. The late Cenozoic Carnivora of the southwestern Cape province. *Annals of the South African Museum* 63:1-369.
- HIBBARD, C. W. 1934. Two new genera of Felidae from the middle Pliocene of Kansas. *Transactions of the Kansas Academy of Sciences* 37:239-255.
- HOUGH, J. 1948. A systematic revision of *Daphoenus* and some allied genera. *Journal of Paleontology* 22:573-600.
- HOUGH, J. 1949. The subspecies of *Hoplophoneus*. *Journal of Paleontology* 23:536-555.
- HUNT, R. M. 1974. *Daphoenictis*, a cat-like carnivore (Mammalia, Amphicyonidae) from the Oligocene of North America. *Journal of Paleontology* 48:1030-1047.
- JASLOW, C. R. 1987. Morphology and digestive efficiency of red foxes (*Vulpes vulpes*) and grey foxes (*Urocyon cinereoargenteus*) in relation to diet. *Canadian Journal of Zoology* 65:72-79.
- JEPSEN, G. L. 1933. American eusmiloid sabre tooth cats of the Oligocene epoch. *Proceedings of the American Philosophical Society* 72:355-369.
- KARR, J. G. AND F. C. JAMES. 1975. Ecomorphological configu-

- rations and convergent evolution. Pp. 258-291. *In* Cody, M. L. and J. M. Diamond (eds.), *Ecology and Evolution of Communities*. Belknap Press; Cambridge, Massachusetts.
- KAY, R. F. 1975. The functional adaptations of primate molar teeth. *American Journal of Physical Anthropology* 43:195-216.
- KITTS, D. B. 1958. *Nimravides*, a new genus of Felidae from the Pliocene of California, Texas and Oklahoma. *Journal of Mammalogy* 39:368-375.
- KURTÉN, B. AND E. ANDERSON. 1980. Pleistocene Mammals of North America. Columbia University Press; New York, New York. 442 pp.
- LAMPRECHT, J. 1981. The function of social hunting in larger terrestrial carnivores. *Mammal Reviews* 11:169-179.
- LEOPOLD, E. B. 1969. Late Cenozoic palynology. Pp. 377-438. *In* Tschudy, R. H. and R. A. Scott (eds.), *Aspects of Palynology*. Wiley-Interscience; New York, New York.
- MARTIN, L. D. AND C. B. SCHULTZ. 1975. Scimitar-toothed cats, *Machairodus* and *Nimravides*, from the Pliocene of Kansas and Nebraska. *Bulletin of the University of Nebraska State Museum* 10:55-63.
- MARTIN, P. S. 1984. Prehistoric overkill: the global model. Pp. 354-403. *In* Martin, P. S. and R. G. Klein (eds.), *Quaternary Extinctions*. University of Arizona; Tucson, Arizona.
- MATTHEW, W. D. 1901. Tertiary mammals of northeastern Colorado. *Memoirs of the American Museum of Natural History* 1:353-447.
- MATTHEW, W. D. AND R. A. STIRTON. 1930. Osteology and affinities of *Borophagus*. University of California Publications in Geological Sciences 19:171-217.
- MCDONALD, J. N. 1984. The reordered North American selection regime and late Quaternary megafaunal extinctions. Pp. 404-439. *In* Martin, P. S. and R. G. Klein (eds.), *Quaternary Extinctions*. University of Arizona; Tucson, Arizona.
- MCNAB, B. K. 1971. On the ecological significance of Bergmann's rule. *Ecology* 52:845-854.
- MELLETT, J. S. 1977. Paleobiology of North American *Hyaenodon* (Mammalia: Creodonta). *Contributions to Vertebrate Evolution* 1:1-134. S. Karger; New York, New York.
- MUNTHE, L. K. 1979. The skeleton of the Borophaginae: morphology and function. Unpublished Ph.D. thesis, University of California, Berkeley. 226 pp.
- OLSON, S. L. AND H. F. JAMES. 1984. The role of Polynesians in the extinction of the avifauna of the Hawaiian Islands. Pp. 768-784. *In* Martin, P. S. and R. G. Klein (eds.), *Quaternary Extinctions*. University of Arizona; Tucson, Arizona.
- PETTER, G. 1969. Interpretation evolutive caractères de la denture des viverrides Africains. *Mammalia* 33:607-625.
- RADINSKY, L. B. 1982. Evolution of skull shape in carnivores. 3. The origin and early radiation of the modern carnivore families. *Paleobiology* 8:177-195.
- RETALLACK, G. 1983. Late Eocene and Oligocene paleosols from Badlands National Park, South Dakota. *Geological Society of America Special Papers* 193:1-82.
- RIGGS, E. S. 1896. A new species of *Dinictis* from the White River Miocene of Wyoming. *Kansas University Quarterly* 4:237-241.
- ROSENZWEIG, M. L. 1966. Community structure in sympatric Carnivora. *Journal of Mammalogy* 47:602-612.
- ROSENZWEIG, M. L. 1968. The strategy of body size in mammalian carnivores. *American Midland Naturalist* 80:299-315.
- SAVAGE, D. E. 1941. Two new middle Pliocene carnivores from Oklahoma with notes on the Optima fauna. *American Midland Naturalist* 25:692-710.
- SAVAGE, D. E. AND D. E. RUSSELL. 1983. *Mammalian Paleofaunas of the World*. Addison-Wesley; Reading, Massachusetts. 432 pp.
- SAVAGE, R. J. G. 1978. Carnivora. Pp. 249-267. *In* Maglio, V. J. and H. B. S. Cooke (eds.), *Evolution of African Mammals*. Harvard University Press; Cambridge, Massachusetts.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27-39.
- SCHULTZ, C. B. AND L. D. MARTIN. 1975. Bears (Ursidae) from the late Cenozoic of Nebraska. *Bulletin of the University of Nebraska State Museum* 10:47-54.
- SCHULTZ, G. B. 1977. The Ogallala formation and its vertebrate faunas in the Texas and Oklahoma panhandles. Pp. 5-105. *In* Schultz, G. E. (ed.), *Guidebook, Field Conference on Late Cenozoic Biostratigraphy of the Texas Panhandle and Adjacent Oklahoma*, August 4-6, 1977. Kilgore Research Center Special Publication 1. West Texas State University; Canyon, Texas.
- SCOTT, W. B. 1889. Notes on the osteology and systematic position of *Dinictis felina*, Leidy. *Proceedings of the Academy of Natural Sciences in Philadelphia* 41:211-245.
- SCOTT, W. B. 1913. *A History of Land Mammals in the Western Hemisphere*. Macmillan Press; New York. 786 pp.
- SCOTT, W. B. AND G. JEPSEN. 1941. The mammalian fauna of the White River Oligocene. *Transactions of the American Philosophical Society* 28:747-980.
- SIMPSON, G. G. 1941. The species of *Hoplophoneus*. *American Museum Novitates* 1123:1-21.
- SINGLER, C. R. AND M. D. PICARD. 1981. Paleosols in the Oligocene of Northwest Nebraska. *University of Wyoming Contributions to Geology* 20:57-68.
- SNEATH, P. H. A. AND R. R. SOKAL. 1973. *Numerical Taxonomy*. W.H. Freeman; San Francisco, California. 573 pp.
- STANLEY, S. M., B. VAN VALKENBURGH, AND R. S. STENECK. 1983. Coevolution and the fossil record. Pp. 328-349. *In* Futuyma, D. J., and M. L. Slatkin (eds.), *Coevolution*. Sinauer Associates; Sunderland, Massachusetts.
- SWANSON, F. J. 1987. Ecological effects of the eruption of Mount St. Helens. Pp. 1-2. *In* Bilderback, D. E. (ed.), *Mount St. Helens 1980: Botanical Consequences of the Explosive Eruptions*. University of California Press; Berkeley, California.
- TEDFORD, R. H., T. GALUSHA, M. F. SKINNER, B. E. TAYLOR, R. W. FIELDS, J. R. MACDONALD, J. M. RENSBERGER, S. D. WEBB, AND D. P. WHISTLER. 1988. Faunal succession and biochronology of the Arikarean through Hemphillian interval (Late Oligocene through earliest Pliocene epochs), North America. Pp. 153-210. *In* Woodburne, M. O. (ed.), *Cenozoic mammals of North America*. University of California Press; Berkeley, California.
- VAN VALEN, L. 1974. Multivariate structural statistics in natural history. *Journal of Theoretical Biology* 45:235-247.
- VAN VALKENBURGH, B. 1985. Locomotor diversity within past and present guilds of large predatory mammals. *Paleobiology* 11:406-428.
- VAN VALKENBURGH, B. 1988. Carnivore dental adaptations and diet: a study of trophic diversity within guilds. *In press* *In* Gittleman, J. L. (ed.), *Carnivore Behavior, Ecology and Evolution*. Cornell University Press; Ithaca, New York.
- VAN VALKENBURGH, B. AND C. B. RUFF. 1987. Canine tooth strength and killing behaviour in large carnivores. *Journal of Zoology* 212:1-19.
- VERSTAPPEN, H. T. 1975. On palaeoclimates and landform development in Malesia. Pp. 3-36. *In* Bartsira, G. and W. A. Casparie (eds.), *Modern Quaternary Research in Southeast Asia*. A. A. Balkema; Rotterdam, Netherlands.
- VOORHIES, M. R. 1970. Sampling difficulties in reconstructing late Tertiary mammalian communities. *Proceedings of the North American Paleontology Convention* 1:454-468.
- WALKER, A. 1984. Extinction in hominid evolution. Pp. 119-152. *In* Nitecki, M. H. (ed.), *Extinction*. University of Chicago Press; Chicago, Illinois.

- WEBB, S. D. 1977. A history of savannah vertebrates in the New World. Part 1: North America. *Annual Review of Ecology and Systematics* 8:355-380.
- WEBB, S. D. 1978. A history of savannah vertebrates in the New World. Part 2: South America and the Great Interchange. *Annual Review of Ecology and Systematics* 9:393-426.
- WEBB, S. D. 1983. The rise and fall of the late Miocene ungulate fauna in North America. Pp. 267-306. In Nitecki, M. H. (ed.), *Coevolution*. University of Chicago Press; Chicago, Illinois.
- WEBB, S. D. 1984. Ten million years of mammal extinction in North America. Pp. 189-210. In Martin, P. S. and R. G. Klein (eds.), *Quaternary Extinctions*. University of Arizona Press; Tucson, Arizona.
- WOLFE, J. A. 1978. A paleobotanical interpretation of Tertiary climates in the northern hemisphere. *American Scientist* 66: 694-703.
- WOLFE, J. A. 1985. Distribution of major vegetational types in the Tertiary. *Geophysical Monographs* 32:357-375.
- WOODLEY, J. D., E. A. CHORNESKY, P. A. CLIFFORD, J. B. C. JACKSON, L. S. KAUFMAN, N. B. KNOWLTON, J. C. LANG, M. P. PEARSON, J. W. PORTER, M. C. ROONEY, K. W. RYLAARSDAM, V. J. TUNNICLIFFE, C. M. WAHLE, J. L. WULFF, A. S. G. CURTIS, M. D. DALLMEYER, B. P. JUPP, M. A. R. KOEHL, J. NEIGEL, AND E. M. SIDES. 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749-755.
- ZAR, J. H. 1984. *Biostatistical Analysis*, Second Edition. Prentice-Hall; Englewood Cliffs, New Jersey. 718 pp.

#### Appendix 1: Fossil Specimens

Institution abbreviations: AM, American Museum of Natural History, New York; FAM, Frick Collection, The American Museum of Natural History; FM, Field Museum, Chicago; KU, University of Kansas, Lawrence; MSU, Midwestern State University; PU, Princeton University Museum, Princeton; TMM, Texas Memorial Museum, Austin; UC, University of California, Berkeley; UNSM, University of Nebraska State Museum, Lincoln; USNM, United States National Museum, Washington, D.C.; WT, West Texas State College, Panhandle Plains Museum, Canyon.

#### Creodonta

*Hyaenodon horridus*. FAM 7567, 75279, 75692, 75622, 75732; Mellett (1977).  
*H. crucians*. FAM 75609, 75657, 75658, 75596, 75571, 75596; AM 647, 648, 1372; Mellett (1977).

#### Canidae

*Mesocyon* sp. FAM 63382, 63367, 63386, 63379, 27557, 54110.  
*Canis davisii*. Harrison (1981).  
*Osteoborus cyonoides*. FM UM310, 681, 682, 27161, 27162, 23626; WT 2175; and 37 specimens at MSU.  
*Vulpes stenognathus*. Savage (1941).

#### Mustelidae

*Plesiogulo marshalli*. Harrison (1981).  
*Pliotaxidea nevadensis*. MU 1334; Butterworth (1916); Hall (1946).

#### Procyonidae

*Arctonasia fricki*. Baskin (1982).

#### Ursidae

*Agrotherium schneideri*. WT 2137; MSU 41261-1, 41261-2; UNSM 76011; FM P27163; Savage (1941); Harrison (1983); Schultz and Martin (1975).

#### Amphicyonidae

*Daphoenus vetus*. KU 138, 8205, 8207, 9870, 2562, 5002; PU 11423, 13600, 13580, 13584, 63339, 12635; UNSM 26151, 25785; AM 38812, 39111, 63341, 12451, 11857, 39098, 9759; and 24 specimens from the Frick Collection.  
*D. hartshornianus*. PU 10546; KU 165, 122, 8205; AM 6811; Scott and Jepsen (1941).

#### Nimravidae

*Hoplophoenus occidentalis*. AM 1407; FAM 62025, 62015.  
*H. prmaevus*. AM 38980, 38982, 38927, 62014, 62007, 69370, 38981, 62021, 62103, 62017, 62012; USNM 18191, 18189; Scott and Jepsen (1941).  
*Dmuctis felina*. FM 62031, 62032, 62051, 62040, 62053, 62058, 62030, 69375, 62055, 62049, 62045, 62052, 62035; AM 1393, 38805, SD230-4152, SD44-928, SD5-146; Riggs (1896); Scott (1889); Scott and Jepsen (1941).  
*Eusmilus dakotensis*. USNM 12820; Jepsen (1933); Hatcher (1895).

#### Felidae

*Pseudaeleurus hbbardi*. MSU 11483; TMM 41261-3, 41261-5, 41261-6; UC 50664  
*Adelphalurus kansensis*. Hibbard (1934); Harrison (1983).  
*Machairodus coloradenis*. MSU 3527; TMM 41261-8, 41261-9, 41261-11, 5658; Dalquest (1969); Schultz and Martin (1975); Burt (1931).  
*Nimravides catacopis*. AM HIG227-1790, KAN41-7-271, 104044, HIG35-558; Kitts (1958).  
 cf. *Felis proterolyncus*. Savage (1941).

#### Appendix 2: Morphometric Indices of Dietary Type

*Upper canine shape* (CS).—The cross-sectional shape of the upper canine tooth was estimated as the ratio of its mediolateral width to its anteroposterior length at the dentine-enamel junction (CMW over CAL, Fig. 1). Canine shape appears to reflect prey-killing behavior as much or more than it reflects diet. Modern felids have relatively round canines and kill prey with a single strong bite. By contrast, canids use their narrow canines to produce more shallow, slashing wounds. Most sabertooth cats had canines shaped more like living canids than felids, and thus their killing behavior probably differed from that of living felids (see Van Valkenburgh and Ruff [1987] for details).

*Premolar shape and size* (PMD, RPS).—The shape of the largest lower premolar (the fourth in all sampled species except the hyaenas where the third is largest) was measured as the ratio of maximum mediolateral width to maximum anteroposterior length (PMW over PML, Fig. 1). To gauge relative premolar size (RPS), the maximum width of the largest lower premolar (PMW, Fig. 1) was divided by the cube root of body weight. The premolars of meat/bone species tend to be relatively larger and more round in cross-section than those of species in other dietary groups (Appendix 3).

*Relative blade length* (RBL).—The relative proportion of the first lower molar devoted to slicing as opposed to grinding is estimated by the ratio of the anteroposterior length of the trigonid measured along the buccal margin (BL) divided by maximum M1 length (M1L, Fig. 1). This ratio proved to be a good indicator of the relative proportion of meat in the diet: both meat and meat/bone species have relatively longer blades than species within the two omnivorous groups (Appendix 3).

*Relative grinding area* (RGA).—The relative proportion of the molar area devoted to grinding as opposed to slicing is estimated by dividing the square root of the total grinding area of the molars (TGA, Fig. 1) by the total blade length of the carnassial (BL, Fig. 1). The entire occlusal area of the lower second and third (if present) molars, as well as that of the talonid of the lower M1 was measured with a polar planimeter. The area estimates were made from color transparencies of the lower molars, taken with the occlusal surface parallel to the plane of focus of the camera. This estimate of grinding area differs from that of Kay (1975), who measured individual wear facet areas, but is suitable for carnivores because they tend to wear the entire occlusal surface as a flat plane. Relative grinding area is greater among species in the two omnivorous groups as opposed to those in the meat and meat/bone groups (Appendix 3).

Appendix 3

Mean value ( $\bar{x}$ ) and standard deviation (sd) of each morphometric variable for the four diet groups. The diet categories are defined in the text. Species included in each group are listed below the table. For references to behavioral data used to classify each species, see Van Valkenburgh (1988). LBW, log body weight; CS, canine shape; RPS, relative premolar size; PMD, premolar shape; RBL, relative blade length; RGA, relative grinding area. A superscript indicates that the mean is significantly different at the 0.05 level or better (Student's *t*, two-tailed test) from that of another group: 1, significantly different from the meat group; 2, meat/bone; 3, meat/non-vertebrate; 4, non-vertebrate/meat.

Group		LBW	CS	RPS	PMD	RBL	RGA
(1) Meat (N = 20)	$\bar{x}$	1.39	73.9 <sup>3,4</sup>	2.14 <sup>2,4</sup>	0.48 <sup>2</sup>	0.94 <sup>3,4</sup>	0.07 <sup>3,4</sup>
	SD	0.403	7.98	0.216	0.032	0.115	0.15
(2) Meat/Bone (N = 3)	$\bar{x}$	1.60	71.1	3.79 <sup>1,3,4</sup>	0.65 <sup>1,3</sup>	0.85 <sup>3,4</sup>	0.03 <sup>4</sup>
	SD	0.127	0.354	0.391	0.062	0.067	0.0
(3) Meat/Non-vert. (N = 17)	$\bar{x}$	1.09 <sup>4</sup>	69.6 <sup>1</sup>	2.18 <sup>2,4</sup>	0.53 <sup>2,4</sup>	0.61 <sup>1,2</sup>	0.48 <sup>1,2,4</sup>
	SD	0.409	10.3	0.430	0.076	0.080	0.237
(4) Non-vert./Meat (N = 7)	$\bar{x}$	1.65 <sup>3</sup>	66.2 <sup>1</sup>	1.57 <sup>1,2,3</sup>	0.60 <sup>3</sup>	0.55 <sup>1,2</sup>	0.87 <sup>1,2,3</sup>
	SD	0.666	4.32	0.540	0.071	0.064	0.247

Meat group: *Lynx rufus*, *L. canadensis*, *Felis yagourundi*, *F. aurata*, *F. temmincki*, *F. viverrina*, *F. serval*, *Neofelis nebulosa*, *Caracal caracal*, *Uncia uncia*, *Puma concolor*, *Acinonyx jubatus*, *Panthera onca*, *P. pardus*, *P. leo*, *P. tigris*, *Canis lupus*, *Cuon alpinus*, *Lycan pictus*, *Speothos venaticus*.

Meat/bone group: *Crocota crocuta*, *Hyaena hyaena*, *H. brunnea*.

Meat/non-vertebrate group: *Viverra megaspila*, *Viverra zibetha*, *Civettictis civetta*, *Duscycyon culpaeus*, *Cerdocyon thous*, *Chrysocyon brachyurus*, *Canis aureus*, *C. adustus*, *C. mesomelas*, *C. latrans*, *Vulpes vulpes*, *Mellivora capensis*, *Gulo gulo*, *Taxidea taxus*, *Meles meles*, *Nasua nasua*, *Ursus maritimus*.

Non-vertebrate/meat group: *Arctictis binturong*, *Procyon lotor*, *Nyctereutes procyonoides*, *Selenarctos thibetanus*, *Trenarctos ornatus*, *Ursus americanus*, *Ursus arctos*.