Dietary niches of creodonts and carnivorans of the late Eocene Cypress Hills Formation

Authors: Christison, Brigid E., Gaidies, Fred, Pineda-Munoz, Silvia, Evans, Alistair R., Gilbert, Marisa A., et al.

Source: Journal of Mammalogy, 103(1) : 2-17

Published By: American Society of Mammalogists

URL: https://doi.org/10.1093/jmammal/gyab123

Journal of Mammalogy, 103(1):2–17, 2022
https://doi.org/10.1093/jmammal/gyab123

Dietary niches of creodonts and carnivorans of the late Eocene Cypress Hills Formation

Brigid E. Christison,[1,*] Fred Gaidies,[2] Silvia Pineda-Munoz,[3,4] Alistair R. Evans,[5,6] Marisa A. Gilbert,[7] and Danielle Fraser[1,2,4,7]

[1]*Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada*
[2]*Department of Earth Sciences, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada*
[3]*Department of Earth and Atmospheric Sciences, Indiana University, 1001 E. 10th Street, Bloomington, IN 47401, USA*
[4]*Department of Paleobiology, Smithsonian National Museum of Natural History, Washington, District of Columbia 20560, USA*
[5]*School of Biological Sciences, Monash University, 25 Rainforest Walk, Melbourne, Victoria 3800, Australia*
[6]*Geosciences, Museums Victoria, P.O. Box 666, Melbourne, Victoria 3001, Australia*
[7]*Palaeobiology, Canadian Museum of Nature, P.O. Box 3443 Stn "D", Ottawa, Ontario K1P 6P4, Canada*

**To whom correspondence should be addressed: BrigidChristison@cmail.carleton.ca*

Modern North American carnivorous mammal assemblages consist of species from a single clade: the Carnivora. Carnivorans once coexisted with members of other meat-eating clades, including the creodonts (Hyaenodontida and Oxyaenida). Creodonts, however, went extinct in North America during the late Eocene and early Oligocene, potentially due to niche overlap and resource competition with contemporary carnivorans. In this study, we employ a community ecology approach to understand whether the dietary niches of coexisting creodonts and carnivorans overlapped during the late Eocene (Chadronian North American Land Mammal Age), a time when creodonts were dwindling and carnivorans were diversifying. We quantify niche overlap based on inferences of diet from carnassial tooth shape estimated using Orientation Patch Count, Dirichlet's Normal Surface Energy, and linear dental measurements as well as from body mass for all species in the Calf Creek Local Fauna of Cypress Hills, Saskatchewan (Treaty 4 land). Although creodonts and carnivorans shared characteristics of their carnassial tooth shape, suggesting similar chewing mechanics and feeding habits, we find that marked differences in body size likely facilitated niche partitioning, at least between the largest creodonts and carnivorans. Calculations of prey focus masses and prey mass spectra indicate that only the smallest creodont may have experienced significant competition for prey with the coeval carnivorans. We suggest that the ultimate extinction of creodonts from North America during the late Eocene and Oligocene was unlikely to have been driven by factors related to niche overlap with carnivorans.

Key words: body size, Carnivora, competition, Creodonta, Dirichlet's Normal Surface Energy, Hyaenodontida, niche overlap, Orientation Patch Count, Oxyaenida

During the Paleogene (66–23.03 million years ago [Ma]), the carnivorous mammal niche was filled by species from phylogenetically disparate groups, including the Hyaenodontida and Oxyaenida (collectively, "creodonts"), Mesonychia (carnivorous ungulate-like mammals), and Carnivoramorpha (Carnivora and closely related lineages; Van Valkenburgh 1999). Since the Oligocene (33.9–23 Ma), however, the carnivorans (members of the order Carnivora) have comprised the dominant clade of carnivorous mammals globally and have been the sole occupants of the North American carnivorous mammal niche (Janis et al. 1998). The origins of modern, carnivoran-dominated mammalian faunas, however, remain unclear: why are modern North American assemblages occupied by carnivorans and no other primarily carnivorous clades such as the creodonts? What drove noncarnivoran clades to extinction? The fossil record is the only source of direct information on species diversity, morphology, and ecology in the past. It holds the only key to understanding the circumstances surrounding the extinction of carnivorous mammals and the ecological processes leading to the formation of modern mammal assemblages

(Dietl and Flessa 2011; Dietl et al. 2015; Barnosky et al. 2017). Herein, we use a paleobiological and community ecology approach to explore dietary niche similarities among creodonts and carnivorans during the latest Eocene (~35 Ma) of Southern Saskatchewan (Treaty 4 land) as a means of investigating the drivers of extinction risk among creodonts.

"Creodonts" are an extinct, polyphyletic group of carnivorous mammals that appeared ~60 Ma (Polly 1993; Van Valkenburgh 1999; Solé et al. 2009; Friscia and Van Valkenburgh 2010) and are hypothesized to be a sister group to Carnivoramorpha (Gunnell 1998; Spaulding et al. 2009; O'Leary et al. 2013; Halliday et al. 2015). Carnivoramorpha consists of the entirely extinct Viverravidae and Miacoidea, as well as the crown group Carnivora (Wesley-Hunt and Flynn 2005; Goswami 2010). While carnivoramorphans emerged at approximately the same time as the creodonts, crown carnivorans did not emerge until the late Eocene (~37–34 Ma; Wesley-Hunt 2005; Wesley-Hunt and Flynn 2005; Goswami 2010). During the Paleocene through early Eocene (~60–50 Ma), North American creodonts became increasingly hypercarnivorous (>80% meat), some evolving massive body sizes (e.g., *Hemipsalodon grandis*, which was the size of a polar bear; Gunnell 1998; Wesley-Hunt 2005; Van Valkenburgh 2007). Thereafter, the North American creodonts experienced a long-term decline (Fig. 1); by the late Eocene, North American creodont species richness was only ~6% of what it was in the early Eocene (Fig. 1). By the Oligocene, creodonts survived only as species from a single genus (*Hyaenodon*; Van Valkenburgh 1999; Wesley-Hunt 2005). Subsequently, creodonts went extinct in North America during the Oligocene and globally during the Miocene (Gunnell 1998). Carnivorans, however, diversified quickly during the Eocene and adopted a wider variety of diets and ecologies (Van Valkenburgh 1999, 2007; Wesley-Hunt 2005), becoming the dominant carnivorous terrestrial mammals from the late Eocene through to today (Van Valkenburgh 1999).

The pattern of synchronous creodont decline and carnivoran diversification has been used to suggest that competition played a role in creodont extinction (Benton 1987; Flynn 1998; Van Valkenburgh 1999; Friscia and Van Valkenburgh 2010). Similarities in the dentition, such as the possession of carnassialized teeth (i.e., specialized slicing dentition), support the competition hypothesis because they indicate dietary similarity and a potential for resource competition (Van Valkenburgh 1999; Friscia and Van Valkenburgh 2010).

Deep-time studies suggest that resource competition can and does lead to extinction through either depressed rates of speciation, increased rates of local extinction, or both, for the less competitive clade (Gould and Calloway 1980; Benton 1987;

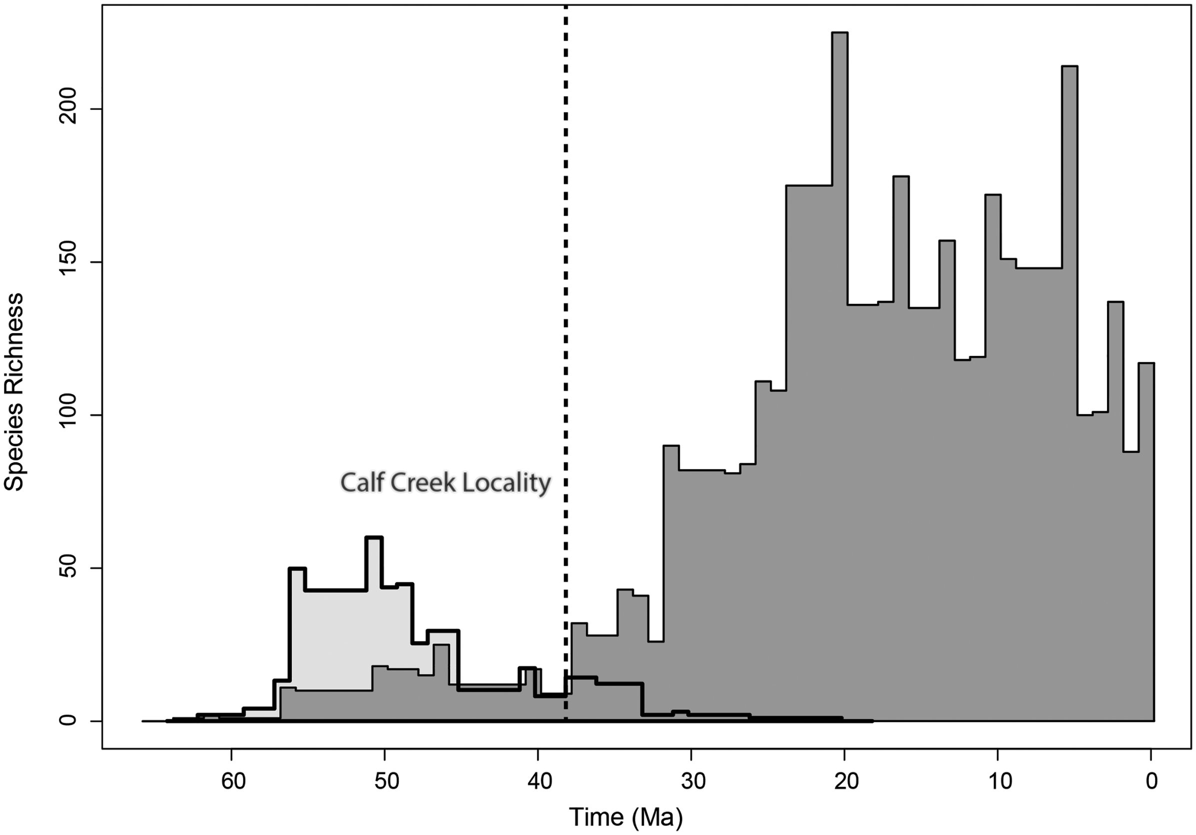

Fig. 1.—Creodont and carnivoran species richness during the Eocene. Time is millions of years ago (Ma). Vertical dashed line indicates the age of the Calf Creek Local Fauna. Light gray indicates creodont species richness. Dark gray indicates carnivoran species richness. The data were downloaded from the Paleobiology Database on March 2018, using the group name 'mammalia' and the following parameters: time intervals = Cenozoic, region = North America, paleoenvironment = terrestrial. Species richness plot was constructed using the paleotree R package (Bapst 2012).

Raia et al. 2006; Liow and Stenseth 2007; Liow et al. 2015; Žliobaitė et al. 2017; Fraser et al. 2020). Furthermore, resource competition is commonly observed in modern carnivoran assemblages (Dayan and Simberloff 1996; Werdelin 1996; Palomares and Caro 1999; Van Valkenburgh 2001; Hunter and Caro 2008; Monteserrero et al. 2020). In African savannah ecosystems, the large-bodied carnivorans *Panthera leo* (African lion), *Acinonyx jubatus* (cheetah), *Panthera pardus* (leopard), and *Crocuta crocuta* (spotted hyena) coexist (du Preez et al. 2017). These carnivorans are ecologically similar in many respects, including in dental morphology, indicating the potential for considerable overlap in dietary preference (Werdelin 1996). In particular, kleptoparasitism among spotted hyenas and other feliforms, a form of intraspecific resource competition, is frequently observed in the field (du Preez et al. 2017). Morphological differentiation, such as differences in body mass, however, facilitates coexistence among these large carnivores (Wilson 1975; Dayan and Simberloff 1996; Werdelin 1996). In African savannah ecosystems, lions are the largest felids (~160 kg) and they engage in pack hunting, expanding their range of prey and protecting their kills from kleptoparasites (du Preez et al. 2017). Cheetahs are comparatively small (~47 kg) and specialize in smaller prey that would not be sufficient to feed a large pride of lions (Durant 1998). They also exhibit avoidance behavior by inhabiting areas with low hyena and lion densities, a form of competitive exclusion (Durant 1998). Periods of drought or resource scarcity, however, bring carnivorous species into increasingly direct competitive contact (Pereira et al. 2014). Resource competition is therefore predicted to play an important role in species extinctions, particularly during periods of resource scarcity such as may occur during climate change (Wright 1983; Hortal et al. 2008; Jankowski et al. 2010; Sinervo et al. 2010; Urban et al. 2012).

Climate (e.g., mean annual precipitation and temperature) strongly influences the biomass production of primary producers and, therefore, the metabolic energy available to consumers (Wright 1983; Currie 1991; Hawkins et al. 2003). The early Eocene Climatic Optimum (53–50 Ma) marked the highest global temperatures of the Cenozoic (Zachos et al. 2001, 2008; Woodburne et al. 2009). Global climates cooled slowly thereafter and, by the late Eocene (~38–34 Ma) and early Oligocene (~33 Ma), North American ecosystems had transitioned from near-tropical to less productive, comparatively temperate mixed tree and grass mosaics (Prothero 1994; Wing 1998). Competitive interactions may increase in these scenarios if individuals of different species with similar dietary niches are forced to rely on dwindling resources (Benton 1987; Van Valkenburgh and Hertel 1993; Urban et al. 2012; Van Valkenburgh et al. 2019). Resource competition may be particularly strong when inequalities in dispersal ability exist; failure of less competitive species to track their preferred climates and colonize new environments can lead to decreased abundance and inability to avoid resource competition with competitively dominant species, enhancing their extinction risk (Urban et al. 2012). The climate changes of the Eocene through Oligocene created considerable upheaval for mammals globally, resulting in major losses of herbivore biodiversity (Prothero 1994; Alroy et al. 2000; Zachos et al. 2001, 2008; Figueirido et al. 2011) and, potentially, enhanced resource competition among creodonts and carnivorans with similar dietary preferences (i.e., prey sizes and types). The degree to which late Eocene creodonts and carnivorans living in the same region shared dietary niche space and thus had the potential to compete for resources, however, remains understudied.

Inferring dietary niches and niche overlap of carnivorous mammals.—The dietary niche of carnivorous mammals depends in large part on their dental morphology and body mass (McNab 1989; Dayan and Simberloff 1996; Carbone et al. 1999; Holliday and Steppan 2004; Friscia et al. 2007). In the context of a community containing multiple types of prey, carnivore body mass is tightly linked to both the nutritional requirements and the types of prey they can reasonably access (McNab 1989; Carbone et al. 1999). Large-bodied species are, for example, capable of exploiting large prey and are less likely to expend energy on small prey (Carbone et al. 1999). Though large carnivorous mammals can and do exploit smaller prey (e.g., wolves are observed eating hares; Shave et al. 2020), large body size expands the range of accessible prey. Small-bodied carnivorous species are largely unable to access large-bodied prey (e.g., foxes are not observed to hunt moose). Significant overlap in body mass therefore indicates similarity in the range of prey available to individuals of two or more species. Conversely, differences in body mass indicate potential for reduced interspecific competition among coevol species (Hemmer 2004).

Mammalian teeth also vary widely in both form and function (Reilly et al. 2001; Wall and Smith 2001; Lucas 2004; Ungar 2010). Among carnivoramorphans, the carnassial teeth, comprised of the lower first molars (m1) and upper fourth premolars (P4), are distinctively large and buccolingually compressed, typically possessing an anteroposterior row of connected cusps. We use the notation "m" for molar and "p" for premolar, with lowercase letters indicating a lower tooth and uppercase indicating an upper tooth, followed by the number indicating the position in the mouth. Other clades such as carnivorous marsupials and creodonts evolved carnassialized molars independently (Ungar 2010). Hyaenodontid creodonts possessed multiple pairs of carnassialized teeth, with the primary pairs being the m3/M2 (Gunnell 1998).

Carnassialized teeth typically perform two functions, slicing and crushing (Mellett 1981; Evans and Fortelius 2008; Ungar 2010; Smits and Evans 2012; Evans and Pineda-Munoz 2018). The slicing function is performed by the opposing blades of the P4 and m1 in carnivoramorphans and M2 and m3 in hyaenodontid creodonts. As the proximal blade of the upper carnassial occludes with the distal blade of the lower carnassial, the teeth perform a shearing or scissor-like cutting action to slice food (Mellett 1981; Gunnell 1998; Ungar 2010). Blade functionality is crucial for muscle consumption because it concentrates force along a single edge, facilitating the separation of the muscle tissue on either side of the tooth (Evans and Fortelius 2008; Ungar 2010; Smits and Evans 2012). Carnassial teeth are also self-sharpening. As the blades occlude, they sharpen each other, maintaining slicing functionality throughout the animal's life (Mellett 1981). The crushing function is performed by the lower carnassial and the postcarnassial upper molar. Felid carnivorans, oxyaenids, and creodonts have lost their postcarnassial upper molars (Gunnell 1998; Martin 1998). Therefore, the bladed carnassial teeth perform the crushing function, if necessary (Ungar 2010). In nonfelid carnivorans, the protocone of the M1 occludes with the talonid of the m1, functioning as a mortar and pestle. Food caught between the two teeth is crushed by the protocone grinding into the talonid basin (Ungar 2010).

Among extant carnivorans, the shape of the carnassial teeth varies from the symmetrical single-bladed carnassials of hypercarnivorous (100–80% vertebrate flesh, i.e., muscle, ogans, bones of vertebrates) felids to the broad, flat carnassials of omnivorous or generalist (<80% plants and <60% vertebrate flesh or invertebrates) ursids (Evans and Fortelius 2008; Ungar 2010; Smits and Evans 2012). Overall, carnivorous species tend to have large carnassial blades that are mediolaterally compressed (Friscia et al. 2007). Generalist and herbivorous (>80% plants) species tend to de-emphasize the slicing efficacy of the carnassials through reduction or loss of the blade (e.g., bears; Ungar 2010). The carnassial and postcarnassial teeth of noncarnivorous species also tend to possess larger surfaces for grinding, particularly involving the upper fourth premolar (Friscia et al. 2007).

Both linear and topographic metrics are often used to capture tooth shape. The two topographic metrics we use are Orientation Patch Count (OPC) and Dirichlet's Normal Surface Energy (DNE). OPC is a quantification of the total number of "patches" on the digital surface mesh. "Patches" are composed of any points on the mesh that are in contact with each other and oriented in the same direction (Evans et al. 2007; Bunn et al. 2011; Wilson et al. 2012; Pineda-Munoz et al. 2016; Spradley et al. 2017). OPC estimates the complexity of the tooth surface, which has been shown to be high in herbivores and low in carnivores, corresponding with the degree of grinding during mastication (Evans et al. 2007; Wilson et al. 2012). DNE quantifies the average curvature of the tooth surface (Evans and Pineda-Munoz 2018). Insectivores, for example, have high DNE, while frugivores have low DNE (Bunn et al. 2011). The efficacy of both topographic methods for assessing mammal diets has been repeatedly demonstrated (Evans et al. 2007; Bunn et al. 2011; Wilson et al. 2012; Pineda-Munoz et al. 2016; Spradley et al. 2017). Furthermore, OPC and DNE categorize the diets of mammals most accurately when combined (Bunn et al. 2011; Spradley et al. 2017).

The dietary preferences of extant carnivorans are also captured by linear measurements of the cranium, mandible, and dentition (Van Valkenburgh 1988, 1991; Van Valkenburgh and Hertel 1993; Sacco and Van Valkenburgh 2004; Friscia et al. 2007; Meachen-Samuels and Van Valkenburgh 2009). Relevant to the present study, differences in the ratios of tooth width and blade length to total tooth length among species differentiate hypercarnivores (with buccolingually compressed carnassial teeth and long carnassial blades) from herbivorous species (with wide, short-bladed or bladeless carnassials; Friscia et al. 2007; Slater and Friscia 2019). Linear measures of the dentition have been repeatedly demonstrated to accurately reflect dietary preference in large and small extant carnivorans (Van Valkenburgh 1988, 1991; Van Valkenburgh and Koepfli 1993; Sacco and Van Valkenburgh 2004; Friscia et al. 2007; Meachen-Samuels and Van Valkenburgh 2009). We expect tooth shape to show a similar relationship to diet among extinct mammals. Thus, the probable diets of extinct taxa can be inferred using teeth (Evans et al. 2007; Pineda-Munoz et al. 2017), which are common in the fossil record (Behrensmeyer and Hill 1980).

The Calf Creek locality is situated on Treaty 4 land in southern Saskatchewan. This site preserves fossils of multiple species of carnivorans and creodonts from the late Eocene (Chadronian North American Land Mammal Age; Bryant 1993). Here we test for niche overlap (as a proxy for resource competition) among spatially and temporally contemporaneous creodonts and carnivorans using analyses of their dental shape and body mass estimates during the latest Eocene. We make morphological comparisons among individual species from a community ecology perspective, examining species that occurred at the same site at the same time, in contrast to previous studies (Friscia and Van Valkenburgh 2010). We interpret similarity in morphology among species within the same local fauna as support for resource competition among species and, thus, as a proximate contributor to the extinction of creodonts in North America.

Materials and Methods

The extinct species examined here are known from the Calf Creek Local Fauna, a late Eocene faunal assemblage of the Cypress Hills Formation. The Calf Creek locality is situated on the traditional lands of the Cree, Salteaux, Blackfoot, Dakota, Nakota, Lakota, and Métis nations on Treaty 4 land in southwestern Saskatchewan, ~25 km northwest of Eastend (Royal Saskatchewan Museum locality 72F1-0001; Bryant 1993). Detailed locality information is on file at the Royal Saskatchewan Museum. The Calf Creek Local Fauna is Chadronian (Latest Eocene; 38-33.9 Ma) in age and is the richest and most intensively sampled fossil site in the Cypress Hills Formation (Meyer 2007). The fossils come from unconsolidated sandy layers and are predominantly vertebrate microfossils, including mammal teeth (Bryant 1993; Storer and Bryant 1993). The fossils used in this study are housed at the Royal Saskatchewan Museum in Regina, Canada, the Canadian Museum of Nature in Ottawa, Canada, and the American Museum of Natural History (AMNH) in New York, United States. First, we reevaluated the taxonomy of the Calf Creek carnivorans and creodonts, with particular focus on *Parictis*, a genus with several similar member species (Clark and Guensburg 1972).

For the three-dimensional topographic estimates of tooth shape (described below), we sampled the carnassial teeth of six species of carnivoran and two species of creodont, both hyaenodontids (Table 1), from the Calf Creek Local Fauna

Table 1.—Body mass and prey focus mass estimates for all Calf Creek species. Body mass estimates are regressions by Smits (2015). Prey focus mass estimates are based on regressions by Volmer et al. (2016). "Prey focus mass F" designates regressions based on extant felids. "Prey focus mass C" designates regressions based on extant canids.

	Species	Code	Body mass (kg)	Prey focus mass F (kg)	Prey focus mass C (kg)	Mean prey focus mass (kg)
Carnivora	*Brachyrhynchocyon dodgei*	Bd	13.9	27.6	22.7	25.1
	Daphoneus lambei	Dl	7.4	14.6	12.1	13.4
	Daphoenus sp.	Dsp	13.2	26.2	21.6	23.9
	Dinictis sp.	Dinsp	18.5	36.7	30.2	33.5
	Hesperocyon gregarius	Hgreg	3.5	7	5.8	6.4
	Hoplophoneus sp.	Hsp	34.3	68.1	56.1	62.1
	Parictis cf. *P. gilpini*	Pg	1.9	3.8	3.1	3.4
	Parictis cf. *P. personi*	Pper	2.2	4.4	3.6	4
	Parictis parvus	Pp	1.6	3.2	2.6	2.9
Creodont	*Hemipsalodon grandis*	Hgrand	436.8	866.1	713.6	789.9
	Hyaenodon horridus	Hh	91.8	181.9	149.9	165.9
	Hyaenodon microdon	Hm	27.2	53.9	44.4	49.1

(Bryant 1993). Because not all specimens could be scanned, we also sampled eight species of carnivoran and three species of creodont, provisionally all of the creodont and carnivoran species occurring at Calf Creek (Table 1), using two-dimensional linear metrics (described below; Friscia et al. 2007; Meachen-Samuels and Van Valkenburgh 2009; Slater 2015).

When possible, we sampled carnassial teeth that had been collected from the Calf Creek locality. Tooth shape is a species-level trait that provides significant phylogenetic information (Kangas et al. 2004; Smits and Evans 2012; Pineda-Munoz et al. 2017; Evans and Pineda-Munoz 2018; Fraser et al. 2018), so we substituted the carnassials from specimens collected at other localities when necessary. Carnassial teeth of all six carnivorans and one hyaenodontid, *H. grandis*, were collected at the Calf Creek site itself. Since *Hyaenodon horridus* was collected from Calf Creek, but no carnassial teeth (M2 or m3) were found (Bryant 1993), we used the carnassials of AMNH F:AM 75728 from the Sheep Mountain locality in South Dakota, United States. *Hyaenodon microdon* also occurred at Calf Creek (represented by a broken lower first or second molar; Bryant 1993), but the taxon is rare in collections and, therefore, carnassial teeth were not available for three-dimensional tooth shape analysis.

Bryant (1993) identified several additional species that were questionably present at the site because they were represented only by incomplete and broken specimens that could not be identified confidently. These included *Daphoenus lambei*, *Hyaenodon* sp. (potentially, *H. raneyi*, *H. venturae*, or *H. crucians*), *Dinictis* sp., and *Hoplophoneus* sp. The specimen of *H. microdon* identified by Bryant (1993) could possibly belong to *H. venturae* (Mellett 1981), so we did not include additional specimens of *Hyaenodon*. Specimens of *Dinictis* and *Hoplophoneus* could not be scanned for three-dimensional tooth shape analysis but were included in the analysis of two-dimensional tooth shape. We treated all specimens separately in our analyses and utilized the identifications of Bryant (1993), except for instances (*Parictis*, as above) when we could reidentify specimens to species.

To create three-dimensional digital models of the fossil teeth, we used a SkyScan1173 (Bruker Corporation, Billerica, MA) to take X-ray absorption images of each specimen. These images were taken with a source voltage of 70–80 kV, and a source current of 100–114 µA. An Al 1.0-mm filter was used during image acquisition and each was taken with an exposure time of 1,300 ms. When space was limited (e.g., the tooth of interest was inset in a skull or jaw, as was the case for all creodonts), we made molds of the carnassial teeth using President Brand Putty Soft, a polyvinyl siloxane dental molding material. OPC and DNE do not require the internal structure of the tooth (these layers were removed), and each scan (whether it is of the tooth or the cast) was down sampled to a resolution of 10,000 polygons, so we assume no difference in OPC or DNE for using a cast instead of the actual tooth (Pampush et al. 2018). López-Torres et al. (2017) suggest that use of casts may lead to overestimation of OPC and DNE values because of a difference in surface "roughness" between specimens and casts. In their study, however, different specimens were used when scanning casts and fossils of the same species and, therefore, intraspecific differences and poor preservation cannot be ruled out. We therefore have no a priori reason to assume that casts and fossils should yield different results for OPC and DNE. If high-quality molding and casting materials are used, shape fidelity should be retained (Smith and Strait 2008). Casts were made using radio-opaque Epokwik epoxy resin both with and without black pigment, which is helpful when observing the casts directly but is not necessary for XR-CT scanning. For the casts, we used a source voltage of 70–80 kV, a source current of 160 µA, and an exposure time of 500 ms.

We created 3D surface meshes for each tooth from the XR-CT images in the open-access image processing program Fiji, which is a distribution of ImageJ (Schindelin et al. 2012). The meshes were then exported into stereolithography format (.stl) and edited in MeshLab, an open-access 3D mesh processing and editing program (Cignoni et al. 2008). Any part of the mesh that was not part of the tooth crown was removed. Each tooth was then oriented perpendicular to the z-axis to achieve results comparable to previous studies (Evans et al. 2007; Pineda-Munoz et al. 2017; Evans and Pineda-Munoz 2018). The models were down sampled to 10,000 polygons (Pampush et al. 2018) and exported to polygon file format (.ply) for OPC and DNE analysis in R. It is unknown if comparing tooth shape metrics between different software packages can lead to incomparable results, so we obtained OPC and DNE values using the R package "molaR" (Pampush et al. 2018).

Based on the analyses of Meachen-Samuels and Van Valkenburgh (2009), Slater (2015), and Slater and Friscia (2019), we analyzed tooth shape using two-dimensional linear measurements, which allowed us to include specimens that could not be scanned using XR-CT, either because the specimens were too damaged to be useful as 3D scans or because we could not obtain them. These measurements included height of the enamel crown, mediolateral width, and anteroposterior length of the upper and lower carnassial teeth. Because such two-dimensional metrics scale linearly with body mass (Van Valkenburgh 1990), we analyzed the ratio of enamel crown height and mediolateral width to anteroposterior length (similar to but a simplified version of the approach of Slater and Friscia 2019). When possible, we measured the same specimens as were analyzed for OPC and DNE. We supplemented these data using specimens from the collections at the Canadian Museum of Nature, AMNH, and the literature (Supplementary Data SD1 and SD2).

To make qualitative comparisons, we obtained OPC, DNE, and linear measurement data for the upper and lower carnassial teeth of 42 extant mammal species using existing tooth scans (Evans et al. 2007; Pineda-Munoz et al. 2017; Evans and Pineda-Munoz 2018). Specimens are from the Finnish Museum of Natural History (Helsinki, Finland), Smithsonian Institution (Washington, DC), Museum für Naturkunde (Berlin, Germany), and Naturhistoriska Rijkmuseet (Stockholm, Sweden; specimen numbers can be found in Supplementary Data SD2). The scans were made with surface laser scanners (Laser Design DS 2025 3D scanner with a RPS-120 probe [Laser Design Inc., Minneapolis, MN] or Nextec Hawk [Nextec Technologies, Israel]). Previous work shows that the exact nature of the machine used for three-dimensional scans does not affect morphological results, making all scans comparable (Wilson et al. 2012). Depending on the size of the tooth row, scanning resolution was set between 10 and 50 µm. We added scans of tooth casts from a further 10 species of extant carnivoran that occur near the Calf Creek locality (Banfield 1974) from the Canadian Museum of Nature collections. We have not included multiple specimens per species because we expect that tooth shape is relatively conserved within a species (an expectation that is supported by the fact that many species can be diagnosed using only dental remains and the use of tooth characters in phylogenetic analyses; Kangas et al. 2004; Smits and Evans 2012; Pineda-Munoz et al. 2016, 2017; Evans and Pineda-Munoz 2018). We also expect intraspecific variation to be much lower than interspecific variation in tooth shape, and so we opted to enhance the number of species we were able to include and, thus, to better represent dietary variability among carnivorans rather than repeatedly sample the same species. Furthermore, dental shape (based on two- and three-dimensional metrics) has been repeatedly demonstrated to correlate highly with dietary preference among carnivorous mammals (Van Valkenburgh 1988, 1991; Van Valkenburgh and Hertel 1993; Sacco and Van Valkenburgh 2004; Evans et al. 2007; Friscia et al. 2007; Meachen-Samuels and Van Valkenburgh 2009; Pineda-Munoz et al. 2017; Evans and Pineda-Munoz 2018).

In addition to tooth shape metrics, we compiled body mass estimates from Alroy (1998) and Smits (2015) for all species recorded at Calf Creek (Supplementary Data SD1), including those for which appropriate teeth for XR-CT scanning were unavailable. Smits (2015) and Alroy (1998) compiled fossil body mass estimates from published sources and reported species averages. In cases where estimates of body mass were unavailable at the species level, or identification to species was not possible (Bryant 1993), we used the average body mass for all the members of that genus, an accepted method of estimating a species' body mass (Smith et al. 2004; Smits 2015). Body masses for extant species were taken from Elton Traits 1.0, which are also species averages based on published measured body masses (Smith et al. 2003; Wilman et al. 2014; Supplementary Data SD2). Given that body mass is highly correlated with skeletal metrics (R^2 of 0.83–96; Van Valkenburgh 1990), combining skeletal estimates and direct measures of body mass likely does not introduce systematic bias but adds noise to the data that is proportional to the standard deviations associated with the regressions of skeletal metrics on body mass.

Multiple methods for estimating carnivore and creodont body masses are available in the published literature (e.g., Solé et al. 2009; Borths and Stevens 2017). Naturally, differences in body mass scaling among the skeletal components mean that different regressions may produce different estimates of body mass. As a test of the accuracy of the average body masses from Smits (2015) and Alroy (1998), we used additional methods of body mass estimation for *H. grandis*. We used femur and skull length regressions reported by Christiansen (1999) and Van Valkenburgh (1990) and calculated 441 and 345 kg, respectively. Because Christiansen (1999) reports a higher R^2 value (0.98) than Van Valkenburgh (1990) (0.95), we confidently used the estimate by Smits (2015), 436 kg, which is closer to the estimate based on the more accurate regression (Christiansen 1999) and within one standard deviation.

To compare the niches of carnivorans and hyaenodontids, we used principal component analyses (PCA) of extant carnivorous mammal tooth shape (m1 and P4 separately) and body masses in R. Our approach is methodologically similar to Friscia and Van Valkenburgh (2010). We then projected the extinct species into the same PCA space. We also compared the linear and topographic tooth shape metrics of creodonts and carnivores using biplots that excluded body mass estimates (Supplementary Data SD3). We use relative position in morphospace (the space represented by the PCA plots and biplots) as a proxy for niche similarity and thus potential for resource competition. The biplots do not provide more information than the PCAs, so we have included them only as Supplementary Data SD3.

We conducted a linear discriminant analysis (LDA) based on the OPC, DNE, and linear tooth measurements for both extant and extinct species. We classified the extant carnivorans into diet categories using Elton Traits (Wilman et al. 2014). The categories were as follows: hypercarnivore (diet 100–80% vertebrate flesh, i.e., muscle, ogans, bones of vertebrates), mesocarnivore (diet 80–60% vertebrate flesh), insectivore (diet >60% invertebrates), herbivore (>80% plants), and omnivore (<80% plants and <60% vertebrate flesh or invertebrates; Van Valkenburgh et al. 2004; Evans et al. 2007). Using the R package MASS (Vernables and Ripley 2002), we used the model derived from the LDA to infer the diets of the fossil species based on OPC, DNE, and linear tooth measurements in separate analyses of the upper and lower carnassials. Unfortunately, LDA of OPC and DNE among extant carnivorans yielded correct classification rates of only 64% and 54% for the lower and upper carnassials, respectively. OPC and DNE therefore classify carnivorans by diet with a success rate only slightly better than flipping a five-sided die. LDA of the two-dimensional linear metrics yielded slightly higher rates of correct classification of 72% and 69% for the lower and upper carnassials, respectively. These low rates most likely relate to our broad dietary categories as well as low sample sizes for insectivorous and herbivorous species. As the present study is focused on niche overlap, rather than precise inferences of diet, we opted not to use the LDA functions to classify the probably diets of Calf Creek species. We therefore only use the dietary categorizations of extant species to make qualitative comparisons with the extinct species.

We also calculated prey focus masses for all fossil species found at Calf Creek (Hemmer 2004; Hertler and Volmer 2008; Volmer et al. 2016). We first used the linear regressions from Volmer et al. (2016) to determine the prey focus mass for each taxon (i.e., the likely mean size of prey that comprise the majority of the diet). We calculated prey focus masses using the average of the regressions for both extant felids and canids, given that the Calf Creek taxa do not belong to either extant clade. We were not able to calculate the range of prey focus masses based on the maximum and minimum estimates from multiple individuals within a species, so we used a species average mass to estimate the likely mean size of the prey. Prey focus masses were then grouped into body mass categories as per Hemmer (2004), the intention being that carnivorous species will focus primarily on a single body mass category based on their own body mass, hunting strategy (e.g., group hunting, scavenging), and prey availability (Volmer et al. 2016). The prey mass categories are as follows: 0.5–1, 1–2, 2–5, 5–10, 10–20, 20–50, 50–100, 100–200, 200–500, 500–1,000, and 1,000–2,000 kg (Hemmer 2004). As did Hertler and Volmer (2008) and Volmer et al. (2016), we include the category within which the prey focus mass falls as well as the upper one and lower two body mass categories to derive prey mass spectra (i.e., the likely range of prey sizes that comprise the majority of the diet). In this way, prey mass spectra account for potential group hunting and scavenging.

Similarity in prey focus masses (i.e., overlap across most or the entire range of potential prey sizes) was interpreted as potential for resource competition. As an estimate of the degree of prey size overlap, we calculated the Competition Indices as did Hertler and Volmer (2008) and Volmer et al. (2016) among each of the creodont and carnivoran species. The index is calculated as the ratio of overlapping prey mass categories to nonoverlapping prey mass categories multiplied by 100. Each category that is within the prey mass spectrum but not the prey focus mass is counted once while the prey focus mass category is counted twice. For example, the prey mass spectrum of Species A includes the 5–10, 10–20, 20–50, and 50–100 kg prey mass categories with the prey focus mass falling in the 20–50 kg bin and the prey mass spectrum of Species B includes the 0.5–1.0, 1–2, 5–10, and 10–20 kg categories with their prey focus mass falling in the 5–10 kg category. In this scenario, Species A shows an overlap 40% in prey mass preference with Species B. We considered an overlap of >49% (the majority of the prey mass spectrum) to indicate a high probability of competition for prey. For comparison and to contextualize our findings, we assembled prey mass spectra for the modern Saskatchewan (Treaty 4) community of carnivorans. We sourced data on prey size from various sources (Bradley and Yousef 1975; Harestad and Bunnell 1979; Reimers et al. 1983; Swihart 1986; Djawdan and Garland Jr. 1988; Noguchi and Hesselberg 1991; Reid et al. 1994; Sovada et al. 1999; Blundell et al. 2000; Kelt and Van Vuren 2001; Palace et al. 2001; Christiansen and Adolfssen 2006; Carbone et al. 2007; Hartnoll et al. 2007; Tucker et al. 2016; Popp et al. 2018) and produced a comparable plot of prey focus masses and prey mass spectra for the modern assemblage. We have not employed a statistical comparison of creodont and carnivoran prey focus masses because they are categorical, and methods such as χ^2 are designed to test hypotheses relating to counts, which does not address the hypothesis proposed herein.

RESULTS

Taxonomic evaluation of the carnivoran specimens from Calf Creek locality suggests the presence of at least eight species (*Hesperocyon gregarius*, *Parictis* cf. *Parictis gilpini*, *Parictis parvus*, *Parictis* cf. *Parictis personi*, *Brachyrhynchocyon dodgei*, *Daphoenus* sp., *Dinictis* sp., and *Hoplophoneus* sp.). We agree with Bryant (1993) regarding the generic identification of carnassial specimens referred to the genus *Parictis*. As did Bryant (1993), we confirm that specimen P661.1512 (P4) resembles the type specimen PU 17795 (PU, Princeton University) in overall shape, being relatively short and possessing a short posterior blade (Clark and Guensburg 1972). We therefore suggest that P661.1512 be tentatively identified as *Parictis* cf. *P. personi*. Bryant (1993) identified specimen P661.1700 as *P. parvus* based on the relatively long trigonid and short talonid of the m1 (Clark and Guensburg 1972); however, we reidentified this specimen as *Parictis* cf. *P. gilpini*. We agree with the identifications of remaining specimens referred to the genus *Parictis* by Bryant (1993). The specimens referred to *Dinictis* sp. and *Hoplophoneus* sp. by Bryant (1993) are fragmentary and cannot be identified to species. Three creodonts were recorded at Calf Creek: *H. grandis*, *H. horridus*, and *H. microdon*, the latter of which is not represented by carnassial teeth.

We were able to XR-CT scan carnassial teeth from all taxa except *Dinictis* sp., *Hoplophoneus* sp., and *H. microdon*. Specimens of *H. microdon* are rare in collections, limiting our ability to access carnassial teeth of appropriate quality for scanning. Though specimens of *Dinictis* sp. and *Hoplophoneus* sp. are much more common, we were unable to access the XR-CT scanning facilities before submission of this manuscript due to covid-19. We did, however, include specimens of all three genera in our linear tooth shape analyses, substituting in *Dinictis felina* and *Hoplophoneus mentalis* as representatives of the Nimravidae.

All OPC, Dirichlet's DNE, linear measurement, and body mass data are summarized in Supplementary Data SD1 for extinct and Supplementary Data SD2 for extant species. Our cast specimens did not have uniformly higher OPC and DNE values than actual specimens, contra López-Torres et al. (2017; Supplementary Data SD1 and SD2).

The first and second axes from the PCA of lower carnassial shape (OPC and DNE) and $\log_{10}$ body mass combined explained 88.8% of the total variance. PC1 explained 61.4% of the variance and correlated positively with the tooth shape metrics, OPC and DNE. PC2 explained 27.5% of the variance and correlated negatively with OPC, DNE, and most strongly with $\log_{10}$ body mass (Fig. 2A). Similarly, the first and second axes from the PCA of upper carnassial shape and $\log_{10}$ body mass combined explained 86.5% of the total variance. PC1 explained 60.9% of the variance and correlated positively with both tooth shape metrics. PC2 explained 25.6% of the variance and correlated positively with $\log_{10}$ body mass (Fig. 2B).

The first and second axes from the PCA of lower carnassial shape (linear metrics) and $\log_{10}$ body mass combined explained 73.5% of the total variance. PC1 explained 42.0% of the variance negatively with $\log_{10}$ body mass and lower carnassial width (as a proportion of carnassial length), the latter of which was most highly correlated with PC1 (Fig. 2C; Supplementary Data SD4). Similarly, the first and second axes from the PCA of upper carnassial shape (linear metrics) and $\log_{10}$ body mass combined explained 85.3% of the total variance. PC1 explained 55.3% of the variance and was most strongly negatively correlated with lower carnassial width (as a proportion of carnassial length; Fig. 2D; Supplementary Data SD4).

The carnivorans and creodonts of Calf Creek fell within the range of variation in tooth shape and body mass present in extant carnivorans (Table 1; Fig. 2A–D), excepting *H. grandis*, whose body mass was estimated to be slightly greater than that of a polar bear (*Ursus maritimus*; Table 1; Supplementary Data SD2). For the lower carnassial, Calf Creek species showed slightly greater enamel crown height to carnassial tooth length ratios; the carnassial blades tended to be taller among the fossil species relative to their anteroposterior length (Fig. 2C). Overall, however, the extinct Carnivora and creodonts show less variable carnassial tooth shapes than extant carnivorans (i.e., morphological disparity is lower in the PCAs, having much simpler teeth than genera such as *Ailurus* [red panda]; Fig. 2A–D). The lower carnassials of the fossil species varied in OPC and DNE from similar to *Martes* (Mm) to *Puma concolor* (Pc) and *Canis lupus* (Cl; Fig. 2A). The upper carnassials of the fossil species were more variable in shape (i.e., they span a larger proportion of the PCA space), owing to the similarity of shape between the two sampled hyaenodontids and *Crocuta crocuta* (Cc; spotted hyena; Fig. 2B). The lower carnassials of the fossil species were more constrained in their linear proportions than the extant species, most closely resembling *Puma concolor* (Pc) and *Felis silvestris* (Fs; Fig. 2C). The linear proportions of the upper carnassials from the fossil species were more variable, bearing resemblance to an array of extant species including *Puma concolor* (Pc), *Vulpes lagopus* (Vl), and *Procyon lotor* (Pl; Fig. 2D). Overall, compared to the present-day assemblage of carnivorans from southwestern Saskatchewan (Treaty 4), the fossil forms showed a comparatively small degree of tooth shape variation (Fig. 2A–D).

Although the creodonts share some tooth shape characteristics with Calf Creek carnivorans (Fig. 2A–D), they are considerably larger in body mass (Table 1; Fig. 2A–D). At Calf Creek, *H. microdon* was the smallest creodont present and, in the absence of inferred pack hunting, the only species that was likely to have competed with the carnivorans for access to prey (Tables 1 and 2; Fig. 3). The prey focus masses of *H. grandis* and *H. horridus* were considerably larger than most of the carnivorans present at Calf Creek (Table 1; Fig. 3). The smallest carnivorans at Calf Creek may have preferentially hunted prey of ~3 kg, while the largest carnivorans preferentially hunted animals of ~26–68 kg (Fig. 3). The three hyaenodontid species were likely capable of killing animals of ~54–800 kg, with the largest two focusing on prey species of ~180–800 kg, well outside the range of the largest carnivoran (Fig. 3). Though pack hunting may have induced competition for prey between the largest carnivoran (*Hoplophoneus* sp.) and *H. horridus*, the latter was able to access much larger prey outside the most probable range of *Hoplophoneus* (Fig. 3).

The prey mass spectra for the two largest-bodied creodonts overlapped to the greatest degree with *Hoplophoneus* sp., while the smallest creodont may have shared prey preferences with several additional carnivorans (Fig. 3). Competition Indices, calculated based on overlap of prey mass spectra, suggest that *H. grandis* likely experienced little competition with coexisting carnivorans (Table 2). *Hyaenodon horridus* may have experienced greatest prey competition with *Hoplophoneus* sp., while *H. microdon* may have experienced greatest competition with *D. lambei* and, to some degree, the other carnivorans present at the Calf Creek (Table 2). In general, the creodonts share the majority of their prey mass spectra (>49%) with between zero and five species of carnivorans (two species, on average; Table 2). *Hemipsalodon grandis* and *H. horridus* share >49% of their prey mass spectra with zero and one species of carnivoran, respectively, though they may have competed with each other for prey (Table 2).

For comparison, we determined prey focus masses and prey mass spectra for modern Southern Saskatchewan (Treaty 4) carnivorans. Many of the extant carnivorans overlap entirely in prey size preference. The largest-bodied species also show

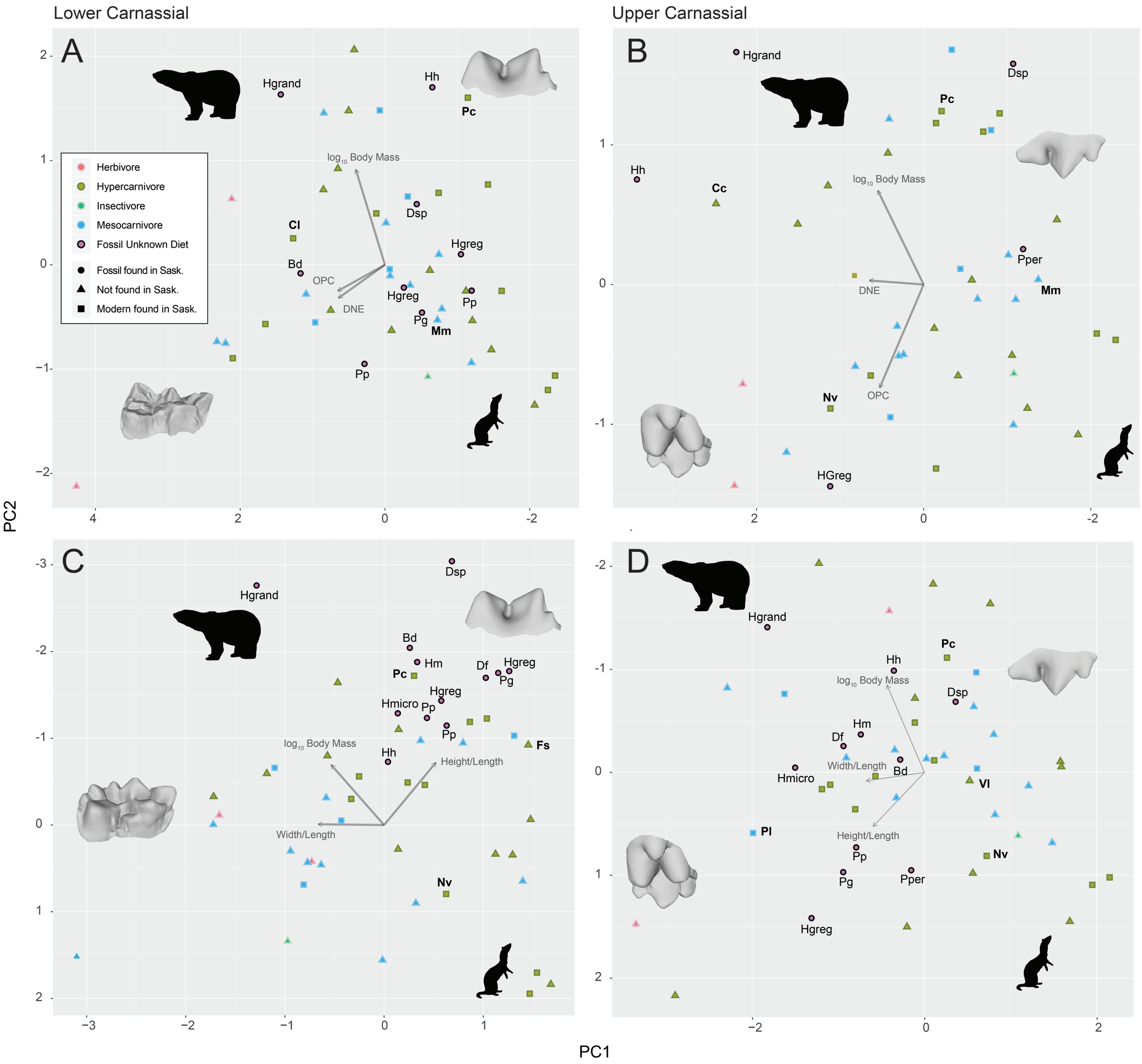

Fig. 2.—Principal component analyses of dental indicators of diet for fossil and extant carnivorous mammals. A) Orientation Patch Count (OPC), Dirichlet's Normal Surface Energy (DNE), and $\log_{10}$ body mass of lower carnassial teeth; B) OPC, DNE, and and $\log_{10}$ body mass of upper carnassial teeth; C) ratios of width divided by length and height divided by length, and $\log_{10}$ body mass of lower carnassial teeth; D) ratios of width divided by length and height divided by length, and $\log_{10}$ body mass of upper carnassial teeth. Arrows indicate direction and strength of loading of the variables onto the PCs. The polar bear (*Ursus maritimus*) silhouette indicates the area of the PCA space occupied by larger species, while the stoat silhouette (*Mustela erminea*) indicates the area of the PCA space occupied by smaller species. Species codes for the extinct taxa are *Brachyrhynchocyon dodgei* (Bd), *Daphoenus* sp. (Dsp), *Dinictis felina* (Df), *Hesperocyon gregarius* (Hgreg), *Hoplophoenus mentalis* (Hm), *Parictis* cf. *P. personi* (Pper), *Parictis* cf. *P. gilpini* (Pg), *Parictis parvus* (Pp), *Hemipsalodon grandis* (Hgrand), *Hyaenodon horridus* (Hh), and *Hyaenodon microdon* (Hmicro). Extant species are represented by bold text. Species codes for the extant species are *Crocuta crocuta* (Cc), *Felis silvestris* (Fs), *Martes martes* (Mm), *Neovison vison* (Nv), *Procyon lotor* (Pl), *Puma concolor* (Pc), and *Vulpes lagopus* (Vl).

considerable similarity in prey mass spectra (Supplementary Data SD5 and SD6). Modern Saskatchewan (Treaty 4) carnivorans overlap by >49% in prey mass spectra with three to seven other species in the same assemblage (Supplementary Data SD5 and SD6), thus overlapping to a higher degree that the Calf Creek species.

DISCUSSION

During the Paleogene and early parts of the Neogene, carnivoramorphans (i.e., Carnivora and closely related groups) shared the carnivorous mammal niche with creodonts (hyaenodontids and oxyaenids; Friscia and Van Valkenburgh

Table 2.—Competition indices among creodonts and carnivorans at the Calf Creek locality. Starred values are those >49% shared between a creodont species and carnivoran species. Species codes are found in Table 1.

	Hemipsalodon grandis	*Hyaenodon horridus*	*Hyaenodon microdon*	*Hoplophoneus* sp.	*Brachyrhynchocyon dodgei*	*Dinictis* sp.	*Daphoenus* sp.	*Daphoenus lambei*	*Hesperocyon gregarius*	*Parictis* cf. *P. personi*	*Parictis* cf. *P. gilpini*	*Parictis parvus*	*N* species >49% overlap
Hemipsalodon grandis	—	40	0	20	0	0	0	0	0	0	0	0	0
Hyaenodon horridus	60*	—	20	80*	40	40	40	20	0	0	0	0	2
Hyaenodon microdon	0	20	—	60*	60*	60*	60*	100*	40	40	40	40	5
Hoplophoneus sp.	20	80	40	—	80	80	80	40	20	0	0	0	4
Brachyrhynchocyon dodgei	0	60	80	80	—	100	100	80	40	20	20	20	6
Dinictis sp.	0	60	80	60	100	100	80	80	40	20	20	20	7
Daphoenus sp.	0	60	80	60	100	100	—	80	40	20	20	20	6
Daphoenus lambei	0	20	100	20	80	80	80	—	80	40	40	40	5
Hesperocyon gregarius	0	0	80	20	60	60	60	80	—	80	80	80	8
Parictis cf. *P. personi*	0	0	60	0	20	20	20	60	80	—	100	100	5
Parictis cf. *P. gilpini*	0	0	60	0	20	20	20	60	80	100	—	100	5
Parictis parvus	0	0	60	0	20	20	20	60	80	100	100	—	5

2010). During the middle and late Eocene, however, there was a steady decline in creodont diversity coincident with considerable diversification of carnivorans (Fig. 1; Van Valkenburgh 1999; Friscia and Van Valkenburgh 2010). By the end of the Eocene, creodont diversity was reduced to ~6% of their early Eocene diversity (Fig. 1). The combination of creodont diversity decline and probable dietary similarity among carnivoramorphans and creodonts suggests that creodonts were inferior competitors (Friscia and Van Valkenburgh 2010). Herein, we used tooth shape metrics and estimates of body mass to infer the potential for prey competition among carnivorans and hyaenodontids at Calf Creek (Chadronian; Latest Eocene) in Southwestern Saskatchewan (Treaty 4) similar to the work of Prufrock et al. 2016. Our study is novel because we use a community ecology approach, studying niche overlap only among species known to occur together.

Calf Creek carnivorous mammals (carnivorans and hyaenodontids) showed lower morphological disparity (i.e., body mass and tooth shape variability in PCA space) than the extant species (Fig. 2A–D). This is consistent with the fact that carnivorous mammal morphological disparity was relatively low during the late Eocene and increased greatly during the Oligo-Miocene (Slater 2015). Furthermore, members of the Calf Creek assemblage belonged to archaic groups (e.g., amphicyonids) that were comparatively morphologically unspecialized (Flynn 1998; Van Valkenburgh 1999). Our finding of lower morphological disparity for carnivorous mammals at the Calf Creek is therefore not unexpected. Furthermore, some of the dietary niches filled today by carnivorans may have been filled by other taxa not studied herein, including pantolestids and mesonychids (Van Valkenburgh 1999; Morlo et al. 2010; Hooker and Collinson 2012). To date, however, no other carnivorous mammal taxa have been collected at Calf Creek (Bryant 1993; Storer and Bryant 1993).

In our analyses of tooth morphology, low values of OPC and high Dirichlet's DNE (Fig. 2A and B), as well as high crown to carnassial tooth length ratios (Fig. 2C and D), were associated with species that ate primarily vertebrates. Species in these areas of the morphospace (e.g., *Puma concolor* [Pc]) possess tall, blade-like carnassial teeth, which facilitate cutting through vertebrate muscle (Evans and Fortelius 2008; Ungar 2010; Smits and Evans 2012). The extinct carnivorous mammals from the Calf Creek tended to possess carnassialized teeth typical of either specialist meat-eaters or those with mixed diets (i.e., mesocarnivores; Table 2; Fig. 2A–D); teeth of the Calf Creek carnivorans and creodonts showed low to intermediate OPC and high DNE values, most like hypercarnivorous taxa such as extant *Puma* and mesocarnivorous taxa such as *Martes* (Fig. 2A–D). The carnassial teeth of the creodonts, *H. grandis* and *H. horridus*, showed similar or slightly larger values of OPC, DNE, and enamel crown height to width ratios relative to the Calf Creek carnivorans (Fig. 2A–D). That is, the carnivorans and creodonts from the Calf Creek possessed similar carnassial morphologies, suggesting similarities in tooth function, mastication, and thus, diet (Table 2; Pineda-Munoz et al. 2017; Evans and Pineda-Munoz 2018). Where the hyaenodontids diverged in tooth shape from the carnivorans, they tended to resemble hypercarnivorous taxa such as *Crocuta crocuta* (spotted hyena; Fig. 2B).

Although analysis of tooth shape alone would support potential for resource competition among creodonts and carnivores at the Calf Creek, species from the two groups possessed divergent body masses (Fig. 2A–D). Body mass is a fundamental mammalian trait, being an important correlate of both diet and locomotor mode, among other characteristics (Peters 1983; Pineda-Munoz et al. 2016). Among modern carnivorans, body mass is one of the most important determinants of the resources available to individuals and, by extension, the entire species (Hemmer 2004; Carbone et al. 2007; Pineda-Munoz et al. 2016). Particularly for solitary hunters, the prey available to them is strongly limited by their body mass. Therefore, coexisting modern carnivore species frequently partition prey resources based on their respective body masses (Dayan and Simberloff 1996; Hertler and Volmer 2008; Volmer et al. 2016).

When we analyze both tooth shape and body mass, we find apparent niche separation among the carnivorans and the two largest creodonts at Calf Creek (Fig. 2A–D). *Hemipsalodon grandis* and *H. horridus* were much larger than the carnivorans present, resembling extant ursids in size (from *Ursus americanus* to *Ursus maritimus*). Most exceptionally, *H. grandis* was the size of an extant polar bear (*U. maritimus*), the largest extant ursid (Wilman et al. 2014). The Calf Creek carnivorans, on the other hand, range in body mass from marten (*Martes martes*) to coyote-sized (*Canis latrans*; Table 1; Fig. 2A–D).

Calculation of prey focus masses indicates that *H. grandis* was capable of killing large prey such as *Megacerops* (Brontotheriidae; *Megacerops* species vary greatly in size and herein we have used an estimate of 571 kg; Table 1; Fig. 3), which also occurred at Calf Creek (Bryant 1993; Storer and Bryant 1993). *Megacerops* was well outside the range of potential prey for Calf Creek carnivorans (Fig. 3). As such, *H. grandis* likely did not experience considerable prey competition from carnivorans (Table 2). The next largest creodont, *H. horridus*, may have at most experienced significant prey competition from the largest carnivoran,

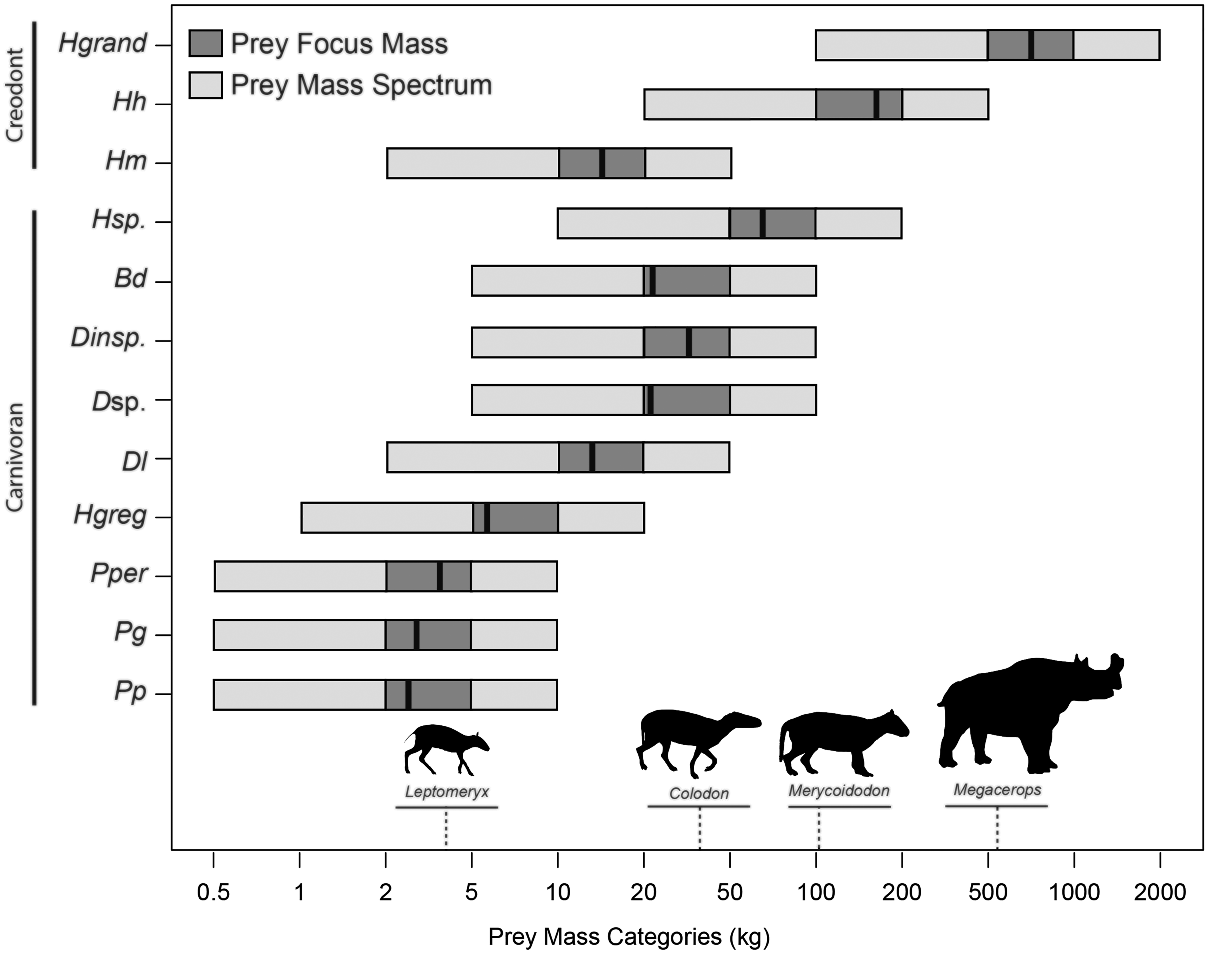

Fig. 3.—Prey focus masses and prey mass spectra are based on regressions by Volmer et al. (2016). Silhouettes represent an example of prey animal for some of the size categories, as indicated by the vertical dashed lines. Horizontal dark gray bars show the range of prey mass categories for each species, and light gray bars show how those categories would extend if the species exhibited group hunting or scavenging behavior. Species codes and data can be found in Table 1. Note that we have included examples of species that occurred at the Calf Creek as examples of prey species in various size classes that may have lived concurrently to the species in this study.

Hoplophoenus sp. (Table 2; Fig. 3). Group hunting, scavenging, and kleptoparastism can increase the potential prey size for carnivorous mammals by approximately one prey body size category (Volmer et al. 2016). Unfortunately, we cannot directly assess the degree to which such hunting behaviors influenced competitive dynamics in the fossil record. If we presume that every species in our dataset were group hunters or scavengers, it is not enough, for example, to increase our estimate of the potential prey size for *B. dodgei* to the extent that direct competition with *H. grandis* would have been commonplace (Fig. 3). Overall, the largest late Eocene creodonts likely ate prey much too large for the majority of carnivorans to exploit with regularity. Furthermore, the largest carnivorans did not reach body sizes comparable to the largest creodonts until the Miocene (Smith et al. 2010), further decreasing the probability that competition for prey was responsible for the ultimate demise of large-bodied creodonts like *H. grandis*. The smallest creodont, *H. microdon*, on the other hand, may have experienced significant competition with five species of coexisting carnivoran (Table 2; Fig. 3). We cannot, however, sufficiently address whether competition with one or even all five species of carnivoran would have been enough to drive creodonts toward their ultimate extinction in North America without comparison to modern assemblages.

Our compilation of prey focus masses and prey mass spectra for modern Saskatchewan (Treaty 4) carnivorans shows overall greater potential for competition than for the late Eocene Calf Creek species (Supplementary Data SD1; Supplementary Data SD5 and SD6). On average, Saskatchewan carnivorans share the majority (>49%) of their prey mass spectra with another five species (Supplementary Data SD5 and SD6). In contrast, the creodonts from Calf Creek may have experienced significant prey competition with two other species in the assemblage, on average (Table 2). We therefore cannot definitively state that there was sufficient competition for prey between the late Eocene creodonts and carnivorans in Southern Saskatchewan (Treaty 4) to have been the major driving force of the loss of all genera except *Hyaenodon* by the early Oligocene.

Our comparisons of tooth shape and body mass suggest that there was little apparent niche overlap among carnivoran and creodont species during the late Eocene (Chadronian North American Land Mammal Age) of southwestern Saskatchewan (Treaty 4). We cannot, however, reject the possibility of competition-driven extinction among early and middle Eocene creodonts (Friscia and Van Valkenburgh 2010), or that competitive interactions drove creodonts toward more extreme niches (e.g., specializing on large-bodied prey), indirectly increasing their risk of extinction. By the late Eocene, the largest hyaenodontids occupied unique ecospaces enabled by their massive body sizes, which may very well have been driven by resource competition in the early and mid-Eocene (Friscia and Van Valkenburgh 2010; Raia et al. 2016). Our findings at Calf Creek suggest, however, that competition may not have been the proximate driver of the loss of most of the remaining North American creodont diversity at the end of the Eocene. What then may have driven most genera of creodont to extinction by the end of the Eocene? We hypothesize that the evolution of highly specialized niches among late Eocene creodonts enhanced their extinction risk during the climate changes that followed.

The earliest Oligocene (~34–33 Ma) is marked by a rapid period of global cooling (Zachos et al. 2001, 2008) that resulted in the loss of large browsing herbivores such as the brontotheres. Ecosystems became drier and more open, resulting in considerable turnover among herbivorous species (Prothero 1998a). Preferences for large-bodied prey that ultimately went extinct may therefore have disadvantaged creodonts during the considerable ecological upheaval of the earliest Oligocene (Janis 1993; Prothero 1994; Gunnell 1998; Van Valkenburgh 1999; Badgley and Fox 2000; Liow and Stenseth 2007; Morlo et al. 2010; Lovegrove and Mowoe 2013; Kort 2019). Large browsers such as brontotheres became extinct, giving way to smaller, grass-eating mammals like equids and rhinoceroses, which were better suited to the new environment (Prothero 1994; Figueirido et al. 2011; Secord et al. 2012; Huang et al. 2017). Rhinoceroses appeared in North America in the middle Eocene, but North American rhinoceroses did not approach modern sizes until the Miocene, leaving a gap in the availability of large, accessible herbivores that may have affected the large-bodied, hypercarnivorous creodonts (Prothero 1998b; Smith et al. 2010). Furthermore, hyaenodontid creodonts differed markedly from carnivorans in the proportions of their postcranial skeleton, having relatively short legs, which may have been a disadvantage in increasingly open ecosystems (Janis 1993; Gunnell 1998; Van Valkenburgh 1999; Kort 2019). Hypotheses based on postcranial proportions, however, remain to be tested. Furthermore, our results may not be generalizable to other North American localities. We hypothesize, based on our present analysis, that modern carnivorans owe their current success to late Eocene and early Oligocene climate change rather than competitive superiority. Future works should expand the geographic scope of the present study and incorporate additional morphological niche proxies (e.g., limb proportions).

ACKNOWLEDGMENTS

The majority of the research and work that went into the preparation of this manuscript took place on the traditional and unceded territories of the Algonquin-Anishnaabeg Nation. The fossils examined in this study were collected predominantly from the traditional lands of the Cree, Salteaux, Blackfoot, Dakota, Nakota, Lakota, and Métis nations on Treaty 4 land. We would like to thank Margaret Currie, and Ryan McKellar, as well as the curators and administrators at the Canadian Museum of Nature, the Royal Saskatchewan Museum, and the AMNH for their assistance in obtaining the specimens used in this study. We would also like to thank all members of the Palaeobiology and Evolution Ottawa group, in particular Jade Atkins, Alanna Cantelon, Dana Korneisel, and Mike Thompson, and lab members Matthew Brenning and Zoe Landry for their ongoing support. Thanks goes to the anonymous reviewers who made insightful comments during the completion of this manuscript.

Supplementary Material

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Orientation Patch Count (OPC), Dirichlet's Normal Surface Energy (DNE), and dental measurements (in mm) for the upper and lower carnassial teeth of fossil carnivoran and creodont specimens used in (Christison et al. 2021). H = height; L = length; W = width. CMN = Canadian Museum of Nature; CIT-LACM = California Institute of Technology at the Los Angeles County Museum of Natural History; F:AM = Frick American Mammals, American Museum of Natural History; F-PM = Field Museum; RSM = Royal Saskatchewan Museum (Clark and Guensburg 1972; Mellett 1981; Bryant 1993).

Supplementary Data SD2.—Orientation Patch Count (OPC), Dirichlet's Normal Surface Energy (DNE), and dental measurements (in mm) for the upper and lower carnassial teeth of extant carnivoran specimens used in (Christison et al. 2021). Body mass and diet categories were determined from Elton Traits 1.0 (Wilman et al. 2014). H = height; L = length; W = width. CMN = Canadian Museum of Nature; MZH = Finish Museum of Natural History; NRM = Naturhistoriska Rijkmuseet; USNM = Smithsonian National Museum of Natural History; ZMB = Museum für Naturkunde.

Supplementary Data SD3.—A) Orientation Patch Count (OPC) and Dirichlet's Normal Surface Energy (DNE) of lower carnassial teeth; B) OPC and DNE of upper carnassial teeth; C) Ratios of width divided by length and height divided by length of lower carnassial teeth; D) Ratios of width divided by length and height divided by length of upper carnassial teeth. Species are coded by genus and species (e.g., Cc (*Crocuta crocuta*), Cl (*Canis lupus*), and Nv (*Neofelis vison*)), with extant species represented by bold text. Species codes and data can be found in Table 1 for fossil specimens and Supplementary Data SD2 for extant carnivorans.

Supplementary Data SD4.—Loadings from Principal Component Analyses of dental measurements used in (Fig. 2A–D; Christison et al., 2021). PC = principal component.

Supplementary Data SD5.—Competition indices among carnivorans from modern Southern Saskatchewan (Treaty 4 land) discussed in Christison et al., 2021.

Supplementary Data SD6.—Prey focus masses and prey mass spectra for extant Southern Saskatchewan carnivorans. Horizontal dark gray bars show the range of prey mass categories for each species, and light gray bars show how those categories would extend if the species exhibited group hunting or scavenging behavior. Species codes for extant carnivorans can be found in Supplementary Data SD2.

Funding

This research was funded by a Canadian Museum of Nature Research Activity Grants and a Natural Sciences and Engineering Research Council of Canada Discovery Grant (RGPIN-2018-05305) awarded to D.F.

Literature Cited

Alroy J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. Science (New York, N.Y.). 280:731–734.

Alroy J., Koch P.L., Zachos J.C. 2000. Global climate change and North American mammalian evolution. Paleobiology 26:259–288.

Badgley C., Fox D.L. 2000. Ecological biogeography of North American Mammals: species density and ecological structure in relation to environmental gradients. Journal of Biogeography 27:1437–1467.

Banfield A. 1974. The mammals of Canada. Toronto (Canada): University of Toronto Press.

Bapst D.W. 2012. Paleotree: an R package for paleontological and phylogenetic analyses of evolution. Methods in Ecology and Evolution 3:803–807.

Barnosky A.D., Hadly E.A., Gonzalez P., Head J., Polly D., Lawing M., Eronen J.T., Ackerly D.D., Alex K., Biber E., et al. 2017. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. Science 355:488–491.

Behrensmeyer A.K., Hill A. 1980. Fossils in the making: vertebrate taphonomy and paleoecology. Chicago (IL): University of Chicago Press.

Benton M.J. 1987. Progress and competition in macroevolution. Biological Reviews 62:305–338.

Blundell G., Bowyer R.T., Ben-David M., Dean T.A., Jewett S.C. 2000. Effects of food resources on spacing behavior of river otters: does forage abundance control home-range size? Biotelemetry 15:325–333.

Borths M.R., Stevens N.J. 2017. The first hyaenodont from the late Oligocene Nsungwe Formation of Tanzania: paleoecological insights into the Paleogene-Neogene carnivore transition. PLoS ONE 12:e0185301.

Bradley W., Yousef M. 1975. Thermoregulatory responses in the plains pocket gopher, *Geomys bursarius*. Comparative Biochemistry and Physiology Part A: Physiology 52:35–38.

Bryant H.N. 1993. Carnivora and Creodonta of the Calf Creek. Journal of Paleontology 67:1032–1046.

Bunn J.M., Boyer D.M., Lipman Y., St Clair E.M., Jernvall J., Daubechies I. 2011. Comparing Dirichlet normal surface energy of tooth crowns, a new technique of molar shape quantification for dietary inference, with previous methods in isolation and in combination. American Journal of Physical Anthropology 145:247–261.

Carbone C., Mace G.M., Roberts S.C., Macdonald D.W. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402:286–288.

Carbone C., Teacher A., Rowcliffe J.M. 2007. The costs of carnivory. PLoS Biology 5:e22.

Christiansen P. 1999. Scaling of the limb long bones to body mass in terrestrial mammals. Journal of Morphology 239:167–190.

Christiansen P., Adolfssen J.S. 2006. Bite forces, canine strength, and skull allometry in carnivores. Journal of Zoology 266:133–151.

Cignoni P., Callieri M., Corsini M., Dellepiane M., Ganovelli F., Ranzuglia G. 2008. MeshLab: an open-source mesh processing tool. In: Proceedings of the 6th Eurographics Italian Chapter Conference 2008; 2 to 4 July, 2008 Salerno, Italy. Geneva, Switzerland: Eurographics Association; p. 129–136.

Clark J., Guensburg T.E. 1972. Arctoid genetic characters as related to the genus *Parictis*. Field Museum of Natural History 1150:1–71.

Currie D.J. 1991. Energy and large-scale patterns of animal and plant species richness. American Naturalist 137:27–49.

Dayan T., Simberloff D. 1996. Patterns of size separation in carnivore communities. Carnivore Behavior, Ecology, and Evolution 1:243–266.

Dietl G.P., Kidwell S.M., Brenner M., Burney D.A., Flessa K.W., Jackson S.T., Koch P.K. 2015. Conservation paleobiology: leveraging knowledge of the past to inform conservation and restoration. Annual Review of Earth and Planetary Sciences 43:79–103.

Dietl G.P., Flessa K.W. 2011. Conservation paleobiology: putting the dead to work. Trends in Ecology & Evolution 26:30–37.

Djawdan M., Garland T. Jr. 1988. Maximal running speeds of bipedal and quadrupedal rodents. Journal of Mammalogy 69:765–772.

Durant S.M. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. Journal of Animal Ecology 67:370–386.

Evans A.R., Fortelius M. 2008. Three-dimensional reconstruction of tooth relationships during carnivoran chewing. Palaeontologia Electronica 11:1–11.

Evans A.R., Pineda-Munoz S. 2018. Inferring mammal dietary ecology from dental morphology. In: Croft D.A., Su D.F., Editors S.W.S., editors. Methods in paleoecology: reconstructing Cenozoic terrestrial environments and ecological communities. Cham (Switzerland): Springer Nature Switzerland AG; p. 37–52.

Evans A.R., Wilson G.P., Fortelius M., Jernvall J. 2007. High-level similarity of dentitions in carnivorans and rodents. Nature 445:78–81.

Figueirido B., Janis C.M., Pérez-Claros J.A., De Renzi M., Palmqvist P. 2011. Cenozoic climate change influences mammalian evolutionary dynamics. Proceedings of the National Academy of Sciences of the United States of America 109:722–727.

Flynn J.J. 1998. Early Cenozoic Carnivora (“Miacoidea”). In: Janis C.M., Scott K.M., Jacobs L.L., editors. Evolution of tertiary mammals of North America. Cambridge: Cambridge University Press; p. 112–123.

Fraser D., Soul L.C., Tóth A.B., Balk M.A., Eronen J.T., Pineda-Munoz S., Shupinski A.B., Villaseñor A., Barr W.A., Behrensmeyer A.K., et al. 2020. Investigating biotic interactions in deep time. Trends in Ecology and Evolution 36:61–75.

Fraser D., Haupt R.J., Andrew Barr W. 2018. Phylogenetic signal in tooth wear dietary niche proxies: what it means for those in the field. Ecology and Evolution 8:11363–11367.

Friscia A.R., Van Valkenburgh B., Biknevicius A.R. 2007. An ecomorphological analysis of extant small carnivorans. Journal of Zoology 272:82–100.

Friscia A., Van Valkenburgh B. 2010. Ecomorphology of North American Eocene carnivores; evidence for competition between carnivorans and creodonts. In: Goswami A., Friscia A., editors. Carnivoran evolution. Cambridge: Cambridge University Press; p. 311–341.

Goswami A. 2010. Introduction to Carnivora. In: Goswami A., Friscia A., editors. Carnivoran evolution. Cambridge: Cambridge University Press; p. 1–24.

Gould S.J., Calloway C. 1980. Clams and brachiopods—ships that pass in the night. Paleobiology 6:383–396.

Gunnell G.G. 1998. Creodonta. In: Janis C.M., Scott K.M., Jacobs L.L., editors. Evolution of tertiary mammals of North America. Cambridge: Cambridge University Press; p. 91–109.

Halliday T.J.D., Upchurch P., Goswami A. 2015. Resolving the relationships of Paleocene placental mammals. Biological Reviews 92:521–550.

Harestad A.S., Bunnell F.L. 1979. Home range and body weight—a re-evaluation. Ecology 60:389–402.

Hartnoll R.G., Baine M.S.P., Britton A., Grandas Y., James J., Velasco A., Richmond M.G. 2007. Reproduction of the black land crab, *Gecarcinus ruricola*, in the San Andres Archipelago, Western Caribbean. Journal of Crustacean Biology 27:425–436.

Hawkins B.A., Field R., Cornell H.V., Currie D.J., Guégan J., Kaufman D.M., Kerr J.T., Mittelbach G.G., Oberdorff T., O’Brien E.M., et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117.

Hemmer H. 2004. Notes of the ecological role of European cats (Mammalia: Felidae) of the last two million years. In: Baquedano E., Rubio Jara S., editors. Iscelanea en homenaje a Emiliano Aguirre, Paleontología. Alcalá de Henares (Spain): Museo Arqueológico Regional; p. 214–232.

Hertler C., and Volmer R. 2008. Assessing prey competition in fossil carnivore communities—a scenario for prey competition and its evolutionary consequences for tigers in Pleistocene Java. Palaeogeography, Palaeoclimatology, Palaeoecology 257:67–80.

Holliday J.A., Steppan S.J. 2004. Evolution of hypercarnivory: the effect of specialization on morphological and taxonomic diversity. Paleobiology 30:108–128.

Hooker J.J., Collinson M.E. 2012. Mammalian faunal turnover across the Paleocene-Eocene boundary in NW Europe: the roles of displacement, community evolution and environment. Austrian Journal of Earth Sciences 105:17–28.

Hortal J., Rodríguez J., Nieto-Díaz M., Lobo J.M. 2008. Regional and environmental effects on the species richness of mammal assemblages. Journal of Biogeography 35:1202–1214.

Huang S., Eronen J.T., Janis C.M., Saarinen J.J., Silvestro D., Fritz S.A. 2017. Mammal body size evolution in North America and Europe over 20 myr: similar trends generated by different processes. Proceedings of the Royal Society B: Biological Sciences 284:20162361.

Hunter J., Caro T. 2008. Interspecific competition and predation in American carnivore families. Ethology, Ecology & Evolution 20:295–324.

Janis C.M. 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. Annual Review of Ecology and Systematics 24:467–500.

Janis K.M. 1998. Carnivorous mammals. In: Janis C.M., Scott K.M., Jacobs L.L., editors. Evolution of tertiary mammals of North America. Cambridge: Cambridge University Press; p. 73–90.

Jankowski J.E., Robinson S.K., Levey D.J. 2010. Squeezed at the top: interspecific aggression may constrain elevational ranges in tropical birds. Ecology 91:1877–1884.

Kangas A.T., Evans A.R., Thesleff I., Jernvall J. 2004. Nonindependence of mammalian dental characters. Nature 432:211–214.

Kelt D.A., Van Vuren D.H. 2001. The ecology and macroecology of mammalian home range area. American Naturalist 157:637–645.

Kort A.E. 2019. The paleoecology of *Patriofelis ulta* and implications for oxyaenid extinction. Bloomington, IN, USA: Indiana University.

Liow L.H., Reitan T., Harnik P.G. 2015. Ecological interactions on macroevolutionary time scales: clams and brachiopods are more than ships that pass in the night. Ecology Letters 18:1030–1039.

Liow L.H., Stenseth N.C. 2007. The rise and fall of species: implications for macroevolutionary and macroecological studies. Proceedings of the Royal Society B: Biological Sciences 274:2745–2752.

López-Torres S., Selig K.R., Prufrock K.A., Lin D., Silcox M.T. 2017. Dental topographic analysis of paromomyid (Plesiadapiformes, Primates) cheek teeth: more than 15 million years of changing surfaces and shifting ecologies. Historical Biology 30:76–88.

Lovegrove B.G., Mowoe M.O. 2013. The evolution of mammal body sizes: responses to Cenozoic climate change in North American mammals. Journal of Evolutionary Biology 26:1317–1329.

Lucas P.W. 2004. Dental morphology: how teeth work. Cambridge: Cambridge University Press.

Martin L.D. 1998. Felidae. In: Janis C.M., Scott K.M., Jacobs L.L., editors. Evolution of tertiary mammals of North America. Cambridge: Cambridge University Press; p. 236–242.

McNab B.K. 1989. Basal rate of metabolism, body size, and food habits in the order Carnivora. In: Gittleman J.L., editor. Carnivore behavior, ecology, and evolution. Boston, MA: Springer.; p. 335–354.

Meachen J., Van Valkenburgh B. 2009. Craniodental indicators of prey-size preference in the Felidae. Biological Journal 96:784–799.

Mellett J.S. 1981. Mammalian carnassial function and the "Every Effect". Journal of Mammalogy 62:164–166.

Meyer T. 2007. Chadronian "insectivores" of the Cypress Hills, Saskatchewan. Saskatoon, Saskatchewan, Canada: University of Saskatchewan.

Monteserrero P., Díaz-Ruiz F., Lukacs P.M., Alves P.C., Ferreras P. 2020. Ecological traits and the spatial structure of competitive coexistence among carnivores. Ecology 101:e03059.

Morlo M., Gunnell G.F., Nagel D. 2010. Ecomorphology of North American Eocene carnivores: evidence for competition between carnivores and creodonts. In: Goswami A., Friscia A., editors. Carnivoran evolution. Cambridge: Cambridge University Press; p. 269–310.

Noguchi G.E., Hesselberg R.J. 1991. Parental transfer of organic contaminants to young-of-the-year spottail shiners, *Notropis hudsonis*. Bulletin of Environmental Contamination and Toxicology 46:745–750.

O'Leary M.A., Bloch J.I., Flynn J.J., Gaudin T.J., Giallombardo A., Giannini N.P., Goldberg S.L., Kraatz B.P., Luo Z.X., Meng J., ET AL. 2013. The placental mammal ancestor and the post-K-Pg radiation of placentals. Science (New York, N.Y.) 339:662–667.

Palace V.P., Allen-Gil S.M., Brown S.B., Evans R.E., Metner D.A., Landers D.H., Curtis L.R., Klaverkamp J.F., Baron C.L., Lockhart W.L. 2001. Vitamin and thyroid status in arctic grayling (*Thymallus arcticus*) exposed to doses of 3,3',4,4'-tetrachlorobiphenyl that induce the phase I enzyme system. Chemosphere 45:185–193.

Palomares F., Caro T.M. 1999. Interspecific killing among mammalian carnivores. American Naturalist 153:492–508.

Pampush D., Winchester J.M., Morse P.E., Vining A.Q. 2018. Package 'molaR'. https://CRAN.R-project.org/package=molaR

Pereira L.M., Owen-Smith N., Moléon M. 2014. Facultative predation and scavenging by mammalian carnivores: seasonal, regional, and intra-guild comparisons. Mammal Review 44:44–55.

Peters R.H. 1983. The ecological implications of body size. New York: Cambridge University Press.

Pineda-Munoz S., Evans A.R., Alroy J. 2016. The relationship between diet and body mass in terrestrial mammals. Paleobiology 42:659–669.

Pineda-Munoz S., Lazagabaster I.A., Alroy J., Evans A.R. 2017. Inferring diet from dental morphology in terrestrial mammals. Methods in Ecology and Evolution 8:481–491.

Polly P.D. 1993. Hyaenodontidae (Creodonta, Mammalia) and the position of systematics in evolutionary biology. Berkeley (CA): University of California at Berkeley.

Popp N.J., Hamr J., Larkin J., Mallory F. 2018. Black bear (*Ursus americanus* and wolf (*Canis* spp.) Summer Diet Selectivity in Ontario, Canada. Mammal Research 63:1–9.

du Preez B., Purdon J., Trethowan P., Macdonald D.W., Loveridge A.J. 2017. Dietary niche differentiation facilitates coexistence of two large carnivores. Journal of Zoology 302:149–156.

Prothero D.R. 1994. The late Eocene-Oligocene extinctions. Annual Review of Earth and Planetary Sciences 22:145–65.

Prothero D.R. 1998a. The chronological, climatic, and paleogeographic background to North American Mammalian evolution. In: Janis C.M., Scott K.M., Jacobs L.L., editors. Evolution of tertiary mammals of North America. Cambridge: Cambridge University Press; p. 9–15

Prothero D.R. 1998b. Rhinocerotidae. In Janis C.M., Scott K.M., Jacobs L.L., editors. Evolution of tertiary mammals of North America. Cambridge: Cambridge University Press; p. 595–605.

Prufrock K.A., López-Torres S., Silcox M.T., Boyer D.M. 2016. Surfaces and spaces: troubleshooting the study of dietary niche space overlap between North American stem primates and rodents. Surface Topography: Metrology and Properties 4:024005.

Raia P., Carotenuto F., Mondanaro A., Castiglione S., Passaro F., Saggese F., Melchionna M., Serio C., Alessio L., Silvestro D., ET AL. 2016. Progress to extinction: increased specialisation causes the demise of animal clades. Scientific Reports 6:30965.

Raia P., Meloro C., Loy A., Barbera C. 2006. Species occupancy and its course in the past: macroecological patterns in extinct communities. Evolutionary Ecology Research 8:181–194.

Reid D.G., Code T.E., Reid A.C.H., Herrero S.M. 1994. Spacing, movements, and habitat selection of the river otter in boreal Alberta. Canadian Journal of Zoology 72:1314–1324.

Reilly S.M., McBrayer L.D., White T.D. 2001. Prey processing in amniotes: biomechanical and behavioral patterns of food reduction. Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology 128:397–415.

Reimers E., Klein D.R., Sørumgård R. 1983. Calving time, growth rate, and body size of Norwegian reindeer on different ranges. Arctic and Alpine Research 15:107–118.

Sacco T., Van Valkenburgh B. 2004. Ecomorphological indicators of feeding behaviour in the bears (Carnivora: Ursidae). Journal of Zoology 263:41–54.

Schindelin J., Arganda-Carreras I., Frise E., Kaynig V., Longair M., Pietzsch T., Preibisch S., Rueden C., Saalfeld S., Schmid B., ET AL. 2012. Fiji: an open-source platform for biological-image analysis. Nature Methods 9:676–682.

Secord R., Bloch J.I., Chester S.G., Boyer D.M., Wood A.R., Wing S.L., Kraus M.J., McInerney F.A., Krigbaum J. 2012. Evolution of the earliest horses driven by climate change in the Paleocene-Eocene Thermal Maximum. Science (New York, N.Y.) 335:959–962.

Shave J.R., Cherry S.G., Derocher A.E., Fortin D. 2020. Seasonal and inter-annual variation in diet for grey wolves *Canis lupus* in Prince Albert National Park, Saskatchewan. Wildlife Biology 3.

Sinervo B., Méndez-de-la-Cruz F., Miles D.B., Heulin B., Bastiaans E., Villagrán-Santa Cruz M., Lara-Resendiz R., Martínez-Méndez N., Calderón-Espinosa M.L., Meza-Lázaro R.N., ET AL. 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science (New York, N.Y.) 328:894–899.

Slater G.J. 2015. Iterative adaptive radiations of fossil canids show no evidence for diversity-dependent trait evolution. Proceedings of the National Academy of Sciences of the United States of America 112:4897–4902.

Slater G.J., Friscia A.R. 2019. Hierarchy in adaptive radiation: a case study using the Carnivora (Mammalia). Evolution 73:524–539.

Smith F.A., Lyons S.K., Ernest S.K.M., Jones K.E., Kaufman D.M., Dayan T., Marquet P.A., Brown J.H., Haskell J.P. 2003. Body mass of late quaternary mammals. Ecology 84:3403.

Smith F.A., Brown J.H., Haskell J.P., Lyons S.K., Alroy J., Charnov E.L., Dayan T., Enquist B.J., Ernest S.K.M., Hadly E.A., et al. 2004. Similarity of mammalian body size across the taxonomic hierarchy and across space and time. American Naturalist 163:672–691.

Smith F.A., Boyer A.G., Brown J.H., Costa D.P., Dayan T., Ernest S.K., Evans A.R., Fortelius M., Gittleman J.L., Hamilton M.J., ET AL. 2010. The evolution of maximum body size of terrestrial mammals. Science (New York, N.Y.) 330:1216–1219.

Smith N.E., Strait S.G. 2008. PaleoView3D: from specimen to online digital model. Palaeontologia Electronica 11(11A):17p.

Smits P.D. 2015. Expected time-invariant effects of biological traits on mammal species duration. Proceedings of the National Academy of Sciences of the United States of America 112:13015–13020.

Smits P.D., Evans A.R. 2012. Functional constraints on tooth morphology in carnivorous mammals. BMC Evolutionary Biology 12:146.

Solé, F., Gheerbrant E., Amaghzaz M., Bouya B. 2009. Further evidence of the African antiquity of hyaenodontid (“Creodonta”, Mammalia) evolution. Zoological Journal of the Linnean Society 156:827–846.

Sovada M.A., Roaldson J.M., Sargeant A.B. 1999. Foods of American badgers in west-central Minnesota and southeastern North Dakota during the duck nesting season. The American Midland Naturalist 142:410–414.

Spaulding M., O’Leary M.A., Gatesy J. 2009. Relationships of Cetacea (Artiodactyla) among mammals: increased taxon sampling alters interpretations of key fossils and character evolution. PLoS ONE 4:e7062.

Spradley J.P., Pampush J.D., Morse P.E., Kay R.F. 2017. Smooth operator: The effects of different 3D mesh retriangulation protocols on the computation of Dirichlet normal energy. American Journal of Physical Anthropology 163:94–109.

Storer J.E., Bryant H.N. 1993. Biostratigraphy of the Cypress Hills Formation (Eocene to Miocene), Saskatchewan: equid types (Mammalia: Perissodactyla) and associated faunal assemblages. Journal of Paleontology 67:660–669.

Swihart R.K. 1986. Home range-body mass allometry in rabbits and hares (Leporidae). Acta Theriologica 31:139–148.

Tucker M.A., Ord T.J., Rogers T.L. 2016. Revisiting the cost of carnivory in mammals. Journal of Evolutionary Biology 29:2181–2190.

Ungar P.S. 2010. Mammalian teeth: origin, evolution, and diversity. Baltimore (MD): John Hopkins University Press.

Urban M.C., Tewksbury J.J., Sheldon K.S. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proceedings of the Royal Society B: Biological Sciences 279:2072–2080.

Van Valkenburgh B. 1988. Trophic diversity in past and present guilds of large predatory mammals. Paleobiology 14:155–173.

Van Valkenburgh B. 1990. Skeletal predictors of body mass in carnivores. In: Damuth J., MacFadden B.J., editors. Body size in mammalian paleobiology. Cambridge: Cambridge University Press; p. 181–205.

Van Valkenburgh B. 1991. Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): evolutionary interactions among sympatric predators. Paleobiology 17:340–362.

Van Valkenburgh B. 1999. Major patterns in the history of carnivorous mammals. Annual Review of Earth and Planetary Sciences 27:463–493.

Van Valkenburgh B. 2001. The dog-eat-dog world of carnivores. In Stanford C.B., Bunn H.T., editors. Meat-eating & human evolution. New York: Oxford University Press; p. 101–121.

Van Valkenburgh B. 2007. Deja vu: the evolution of feeding morphologies in the Carnivora. Integrative and Comparative Biology 47:147–163.

Van Valkenburgh B., Hertel F. 1993. Tough times at La Brea: Tooth Breakage in Large Carnivores of the Late Pleistocene. Science 261:456–459.

Van Valkenburgh B., Koepfli K. 1993. Cranial and dental adaptations to predation in canids. Symposium of the Zoological Society of London 65:15–37.

Van Valkenburgh B., Peterson R.O., Smith D.W., Stahler D.R., Vucetich J.A. 2019. Tooth fracture frequency in gray wolves reflects prey availability. eLife 8:1–15.

Van Valkenburgh B., Wang X., Damuth J. 2004. Cope’s rule, hypercarnivory, and extinction in North American canids. Science (New York, N.Y.) 306:101–104.

Vernables W.N., Ripley B.D. 2002. Modern applied statistics with S. 4th ed. New York: Springer.

Volmer R., Hertler C., van der Geer A. 2016. Niche overlap and competition potential among tigers (*Panthera tigris*), sabertoothed cats (*Homotherium ultimum, Hemimachairodus zwierzyckii*) and Merriam’s dog (*Megacyon merriami*) in the Pleistocene of Java. Palaeogeography, Palaeoclimatology, Palaeoecology 441:901–911.

Wall C.E., Smith K.K. 2001. Ingestion in mammals. In: Encyclopedia of life sciences. New York, NY, USA: Macmillan Publishers Ltd, Nature Publishing Group; p. 1–6.

Werdelin L. 1996. Community-wide character displacement in Miocene hyaenas. Lethaia 29:97–106.

Wesley-Hunt G.D. 2005. The morphological diversification of carnivores in North America. Paleobiology 31:35–55.

Wesley-Hunt G.D., Flynn J.J. 2005. Phylogeny of the Carnivora: basal relationships among the carnivoramorphans, and assessment of the position of ‘Miacoidea’ relative to Carnivora. Journal of Systematic Palaeontology 3:1–28.

Wilman H., Belmaker J., Simpson J., de La Rosa C., Rivadeneira M., Jetz W. 2014. EltonTraits 1.0: species-level foraging attributes of the world’s birds and mammals. Ecology 95:2027.

Wilson D.S. 1975. The adequacy of body size as a niche difference. American Naturalist 109:769–784.

Wilson G.P., Evans A.R., Corfe I.J., Smits P.D., Fortelius M., Jernvall J. 2012. Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. Nature 483:457–460.

Wing S.L. 1998. Tertiary vegetation of North America as a context for mammalian evolution. In: Janis C.M., Scott K.M., Jacobs L.L., editors. Evolution of tertiary mammals of North America. Cambridge: Cambridge University Press; p. 37–65.

Woodburne M.O., Gunnell G.F., Stucky R.K. 2009. Climate directly influences Eocene mammal faunal dynamics in North America. Proceedings of the National Academy of Sciences of the United States of America 106:13399–13403.

Wright D.H. 1983. Species-energy theory: an extension of species-area theory. Oikos 41:496.

Zachos J.C., Dickens G.R., Zeebe R.E. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451:279–283.

Zachos J., Pagani M., Sloan L., Thomas E., Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science (New York, N.Y.) 292:686–693.

Žliobaitė I., Fortelius M., Stenseth N.C. 2017. Reconciling taxon senescence with the Red Queen’s hypothesis. Nature 552:92–95.

Submitted 26 June 2019. Accepted 09 October 2021.

Associate Editor was Roger Powell.