

Chapter 11

Global Climate and the Evolution of Large Mammalian Carnivores during the Later Cenozoic in North America

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ABSTRACT

Taxon ranges of larger mammalian carnivores can be grouped into seven temporal intervals during the later Cenozoic. These intervals are of varied duration and seem to correspond to periodic faunal reorganizations that accompanied the progressive climatic deterioration occurring from the late Eocene to the Pleistocene. Recent oxygen isotope records from deep-sea cores serve as proxy for the pattern of global climate during the Cenozoic and compare reasonably well with the large carnivore intervals. Intervals A, B, and the early part of C characterize a time of cooler global climate ($\delta^{18}\text{O}$: +1.3 to +3.0‰) following the early Eocene climatic optimum. The later part of Interval C, following the mid-Miocene climatic optimum, and Intervals D through F record a gradual climatic deterioration ($\delta^{18}\text{O}$: +2.0 to +3.8‰) from the mid-Miocene to early Pliocene. Interval G ($\delta^{18}\text{O}$: +3.8 to +5.0‰) corresponds to the extreme global cooling of the later Pliocene and Pleistocene. Glacioeustatic decline in sea level during these intervals probably made possible the entrance of migrant Eurasian carnivores and other mammals into the New World via the Bering route. The periodic emergence of this land bridge and the effect of the climatic oscillations of the later Cenozoic on the mammalian fauna appear responsible for the faunal shifts.

INTRODUCTION

An improved record of Neogene and Quaternary fossil mammals has afforded a new perspective on faunal succession in North America during the last 40 million years. Well-constrained taxonomic ranges have resulted from (1) new discoveries of Neogene mammals from more refined lithostratigraphic contexts, and (2) continuing study of historic collections, most notably that of Childs Frick at the American Museum of Natural History. Taking advantage of these conditions, this study focuses on the evolutionary history of North American carnivores. In this case, range diagrams for large carnivores demonstrate distinct, episodic transformations at guild level: such reorganizations seem to have occurred at much greater frequency during the late Cenozoic, seemingly in step with climatic deterioration as charted by oxygen isotope curves.

Large carnivores, at the apex of the eco-

logical pyramid, influence the dynamic of prey populations (e.g., Schaller, 1972; Sinclair and Norton-Griffiths, 1979). The nature of social organization of a species, its body size, territorial extent, style of predation, and mode of locomotion, among other such factors, determine its interaction with various prey species. Thus, the identification of intervals characterized by stable, well-defined carnivore assemblages contributes to an improved understanding of mammalian faunal dynamics overall. Here I provide a summary of taxon ranges for North American large carnivores, calibrated against the Magnetic Polarity Time Scale (MPTS; Berggren et al., 1995). These taxa are arranged in faunal intervals from ~40 Ma to the Holocene (fig. 11.1, table 11.1). Seven intervals are recognized, each with its characterizing carnivore taxa, and defined by first appearances (FADs) and last occurrences (LADs). The implications of these intervals and their temporal spacing are discussed below. The usage fol-

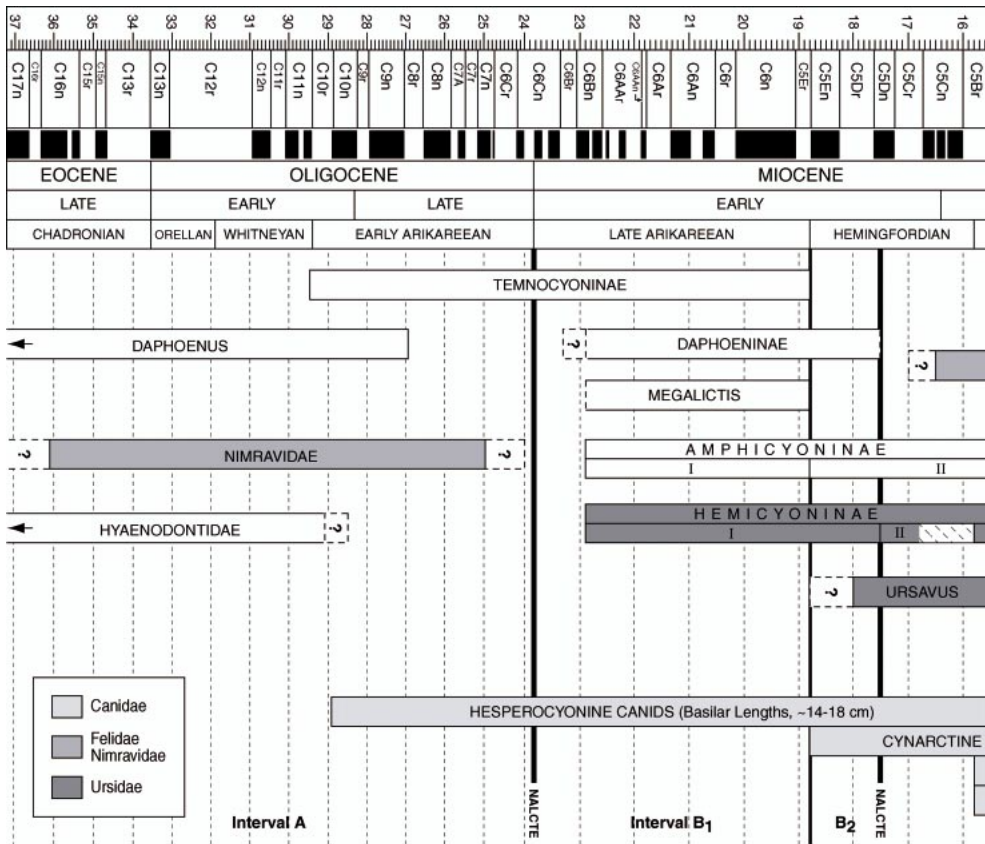


Fig. 11.1. Taxon range diagram of larger late Eocene to Pleistocene carnivores (carnivorans and creodonts) in relation to the North American Land Mammal “Ages” (NALMAs) and Lyellian epochs, calibrated against the Magnetic Polarity Time Scale of Berggren et al. (1995). North American Larger Carnivore Turnover Events (NALCTE) are indicated at ~37–36, 33.7, 23.8, 18.8, 17.5, 9.0, 6.0, 4.5, and 3.0 Ma (see text for discussion). Temporal intervals between the turnover events are designated Intervals A through G. Amphicyonine Group I, *Ysengrinia*, *Cynelos*; II, *Amphicyon*, *Cynelos*, *Pliocyon*; III, *Pseudocyon*, *Ischyrocyon*. Hemicyonine I, *Cephalogale*; II, *Phoberocyon*; III, *Plithocyon*; IV, new Clarendonian genus.

lowed here employs the term “carnivoran” for members of the Order Carnivora and “creodont” for members of the Hyaenodontidae and Oxyaenidae that currently comprise the Order Creodonta. The term “carnivore” refers to any flesh-consuming mammal.

FAUNAL ASSOCIATIONS OF LARGER NORTH AMERICAN CARNIVORES

INTERVALS A TO G (LATE EOCENE TO PLEISTOCENE)

Large (>10–20 kg) carnivorans take the stage with the advent of the White River car-

nivore fauna in the Chadronian North American Land Mammal Age (NALMA) (Hunt, 1996: fig. 2). Duchesnean and earlier associations of carnivores included only archaic early Tertiary groups placed in the miacoid Carnivora and the hyaenodont and oxyaenid Creodonta. Viverravid and miacid species comprise the miacoids (Matthew, 1909; Flynn, 1998), none larger than a modern coyote (*Canis latrans*). The largest of the miacoids was the viverravid *Didymictis vanclivei* from the early Eocene of the Huerfano basin, Colorado, with a basilar length of skull of ~15–16 cm; the very small viverravid

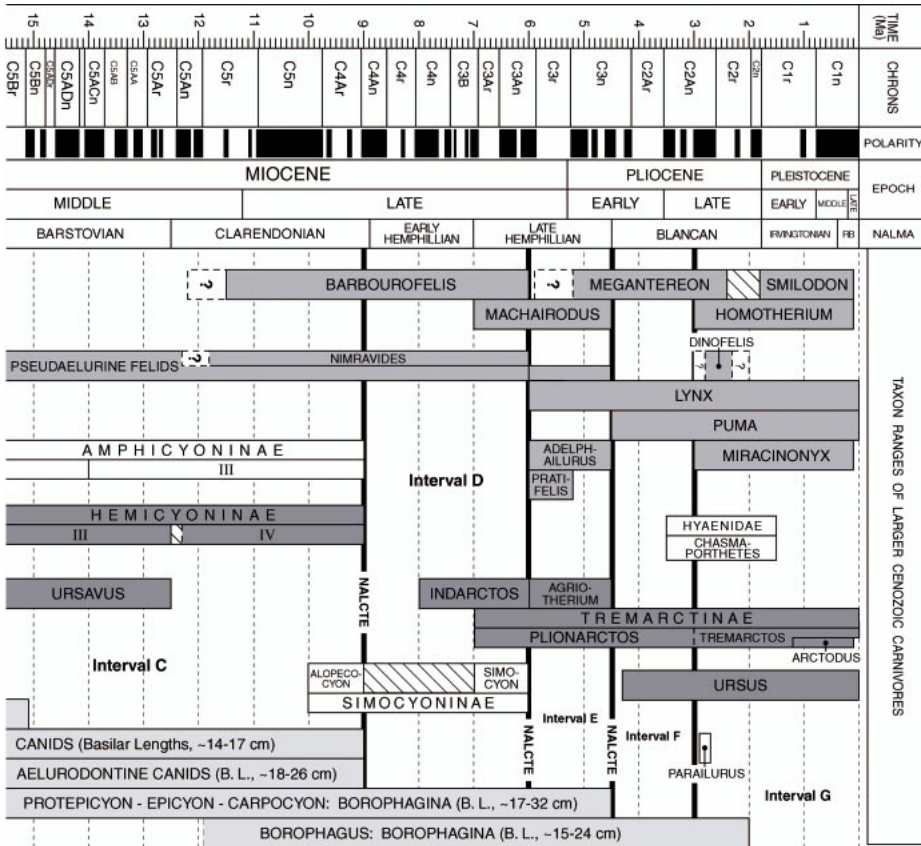


Fig. 11.1. Continued.

Viverravus minutus from the Bridger Basin, Wyoming, had a basilar length of ~4 cm, and most miacids measured <12 cm.

With the arrival of the Chadronian carnivoran-creodont fauna at ~37 Ma, there is an evident increase in the average body size of carnivores. The largest carnivorans in North America were nimravids cats and coyote-sized daphoenine beardedogs (*Daphoenus vetus*), accompanied by particularly large hyaenodont creodonts (*Hyaenodon megaloides*, *H. horridus*, *Hemipsalodon grandis*; Mellett, 1969, 1977). *Hyaenodon* attained its maximum species diversity in the Chadronian (Mellett, 1977). This hyaenodont-nimravid association was previously recognized as the first of four sequential mid- to late Cenozoic associations of large carnivorous mammals that characterized the last

40 million years in North America (Hunt and Tedford, 1993). Here I amplify our initial designations, extending and refining the definition of these associations, and describing their characterizing taxa in greater detail.

HYAENODONT-NIMRAVID ASSOCIATION (Interval A: ~37–23.7 Ma)

The hyaenodont-nimravine nimravid-daphoenine amphicyonid association is typical of Chadronian, Orellan, Whitneyan, and early Arikarean faunas of North America. Of the intervals recognized here, its 13.3 million year extent is by far the longest. Hyaenodont and nimravine nimravid diversity during this interval is remarkable, with nine species of hyaenodonts and ten of nimravids currently

TABLE 11.1

Late Eocene to Recent Faunal Associations of Large Carnivores in North America

Interval A (~37 to 23.7 Ma)	<p>Dominance of hyaenodont creodonts, nimravine "cats", and daphoenine amphicyonids.</p> <p>Appearance of temnocyonine amphicyonids in the later part of the interval at ~29.5 Ma.</p> <p>Canids are represented only by small fox-sized hesperocyonines and borophagines.</p>
Interval B (~23.7 to 17.5 Ma)	<p>Evolution of diverse species of large daphoenine and temnocyonine amphicyonids.</p> <p>Maximum diversity of hesperocyonine canids accompanied by small borophagines.</p> <p>First appearance of large Eurasian amphicyonine amphicyonids and hemicyonine ursids.</p> <p>Absence of hyaenodonts, nimravine "cats", and the daphoenine <i>Daphoenus</i>.</p> <p>Arrival of small to mid-sized ursine bears (<i>Ursavus</i>) from Eurasia (at ~18.0–18.8 Ma).</p>
Interval C (~17.5 to 9 Ma)	<p>Dominance of large amphicyonines and hemicyonines (with disappearance of <i>Amphicyon</i>, <i>Cynelos</i>, and <i>Pliocyon</i> by ~14 Ma, replaced by <i>Pseudocyon</i> and <i>Ischyrocyon</i>).</p> <p>Extinction of last hesperocyonine canids in early part of the interval (at ~15 Ma).</p> <p>Evolution of diverse lineages of large borophagine canids (aelurodontines and cynarctines, <i>Epicyon</i>, <i>Borophagus</i>).</p> <p>Arrival and initial dispersal of true felids (proailurines, <i>Pseudaelurus</i>), the first aeluroid carnivorans to migrate to North America.</p> <p>Arrival of barbourofelines (11.5–12.2 Ma) and simocyonines late in the interval (~10 Ma).</p>
Interval D (~9 to 6 Ma)	<p>Arrival of the first large ursine bears (Eurasian immigrant <i>Indarctos</i>).</p> <p>Absence of amphicyonids, hemicyonine ursids, aelurodentine and cynarctine canids.</p> <p>Presence of barbourofeline and large feline cats (<i>Nimravides</i>) and large hyaenoid borophagine canids (<i>Epicyon</i>).</p> <p>Appearance late in the interval at ~7 Ma of tremarctine ursids (<i>Plionarctos</i>), the machairodontine felid <i>Machairodus</i>, and the arctoid <i>Simocyon</i>.</p>
Interval E (~6 to 4.5 Ma)	<p>Presence of diverse species of Felidae in the interval (<i>Megantereon</i>, <i>Machairodus</i>, <i>Nimravides</i>, <i>Pseudaelurus</i>, <i>Lynx</i>, <i>Adelphailurus</i>, <i>Praifelis</i>).</p> <p>Arrival and persistence of the immigrant ursid <i>Agriotherium</i> and extinction of <i>Indarctos</i>.</p> <p>Absence and presumed extinction of barbourofelines and simocyonines.</p>
Interval F (~4.5 to ~3 Ma)	<p>Appearance of modern ursine bears (<i>Ursus</i>) and the felid <i>Puma</i>.</p> <p>Absence of the felids <i>Machairodus</i>, <i>Nimravides</i>, and <i>Pseudaelurus</i> (s.s.).</p> <p>Absence of the large agriotherine ursids and borophagine canids (except <i>Borophagus</i>).</p>
Interval G (~3 Ma to the Holocene)	<p>Appearance of the felids <i>Homotherium</i>, <i>Smilodon</i>, <i>Dinofelis</i>, and <i>Miracinonyx</i> and the hyaenid <i>Chasmaporthetes</i> (to ~1.5 Ma).</p> <p>Appearance of the tremarctine ursid <i>Tremarctos</i> and late in the interval <i>Arctodus</i> at ~1 Ma.</p> <p>Radiation of ursine bears; appearance of the ailurid <i>Parailurus</i> at ~2.9 Ma.</p> <p>Radiation of canine canids and feline felids (with arrival of <i>Panthera leo</i> at ~300–400ka).</p>

recognized (Mellett, 1977; Bryant, 1991, 1996). If size alone is considered, the dominant carnivores of this association are the large creodonts, *Hemiposalodon grandis* (basilar length, ~41 cm), *Hyaenodon megaloides* (skull length, ~40 cm), and *H. horridus* (skull lengths, 25–35 cm). The largest nimravids occur toward the end of the interval

in the Whitneyan and early Arikarean. Skull lengths of the larger nimravine genera range from ~13 to ~26 cm (Bryant, 1996; personal observations): *Dinictis*, ~13 to 18 cm; *Pogonodon*, ~20 cm; *Nimravus*, ~15 to 23 cm; *Hoplophoneus*, ~15 to 26 cm.

Daphoenine amphicyonids commonly accompany these groups and are represented by

four genera (*Daphoenus*, *Daphoenictis*, *Brachyrhynchocyon*, *Paradaphoenus*) and at least six species (Hunt, 1996). The largest is *Daphoenus vetus*, with males attaining basilar skull lengths of ~20 cm in the Orellan when the species is particularly well-represented in the White River Group of the Great Plains. *Daphoenus* achieves a maximum basilar length of ~23 cm by the time of its last occurrence in the early Arikareean.

Hyaenodonts, nimravine nimravid, and *Daphoenus* became extinct within the early Arikareean interval. The last records of hyaenodonts and *Daphoenus* in late Oligocene rocks of the lower Arikaree Group in the Great Plains are dated at ~28.0 Ma and ~28.6 Ma, respectively; *Daphoenus* survived to ~27 Ma in the Pacific Northwest in the John Day beds of Oregon. Nimravine cats persist only a short while longer to ~25–24 Ma. Hence these long-dominant groups appear to be extinct by ~27–24 Ma. Nimravines are represented by at least three genera (*Nimravus*, *Pogonodon*, *Eusmilus*) in lower Arikaree Group sediments, contemporaneous with the last occurrences of hyaenodonts and *Daphoenus*. Although creodonts became extinct in North America at ~28 Ma, they survived in southern Asia and Africa into the Miocene.

In the richly fossiliferous sediments of the central Great Plains in Nebraska, South Dakota, Wyoming, and Colorado, UNSM paleontologists have found no fossils of these groups above the lower Arikaree Group. Extensive explorations for fossil mammals in rocks of the upper Arikaree Group in Nebraska, Wyoming, and South Dakota have failed to produce a hyaenodont, nimravid, or *Daphoenus*. Thus the hyaenodont-nimravid association is apparently extinct by late Arikareean time (estimated to begin at ~23 Ma) in the North American midcontinent.

DOMINANCE OF AMPHICYONINES-HEMICYONINES (EXTENDING OVER INTERVALS B AND C)

Immigrant Eurasian amphicyonine bears and hemicyonine ursids characterize the large carnivoran assemblage in North America from the beginning of the Miocene to ~9 Ma at the end of the Clarendonian. During the late Hemingfordian, Barstovian, and

Clarendonian, the dominant large carnivorans are large amphicyonines and hemicyonines, joined in the later part of the period by a few borophagine canids. However, this era can be subdivided into two intervals. The first interval (Interval B), from ~23.7 to ~17.5 Ma (late Arikareean through early Hemingfordian), is characterized by temnocyonine and daphoenine amphicyonids that seem to be primarily if not entirely North American endemics, diluted by the arrival of the earliest species of amphicyonines and hemicyonines. The second interval (Interval C), from ~17.5 to 9 Ma (medial Hemingfordian through Clarendonian), sees the extinction of all temnocyonines and daphoenines; the larger carnivorans are amphicyonine, hemicyonine, and felid immigrants, and the endemic borophagine canids.

TEMNOCYONINE-DAPHOENINE-ENTELODONT ASSOCIATION (Interval B: ~23.7–17.5 Ma)

Beginning in the earliest Arikareean, the first temnocyonine amphicyonids are recorded in North America at Logan Butte in the John Day beds of Oregon (~29–29.5 Ma), in the Sharps Formation of the Wounded Knee area, South Dakota (LACM Locality 1872, estimated at ~28–29.5 Ma), and in pumice-bearing levels of the Gering Formation at Wildcat Ridge, Nebraska (~28.3 Ma). These early temnocyonines attained the size of coyotes or small wolves (~15–30 kg). Identified by a uniquely specialized dentition, temnocyonines are present throughout the Arikareean NALMA, and become extinct in the latest Arikareean. The last documented occurrences of temnocyonines are in Upper Harrison sediments in northwest Nebraska and southeastern Wyoming. Temnocyonines actually appear late in Interval A and extend into the early part of Interval B and are the only group of large carnivorans, other than the endemic hesperocyonine canids, spanning the Arikareean NALMA. Terminal species of large temnocyonines (~80 kg) in the latest Arikareean attained skull lengths of ~30 cm.

With the extinction of the hyaenodonts, nimravid, and *Daphoenus*, the mid-Arikareean interval (~25–23 Ma) displays a dearth of large carnivores. Remnocyonines diversity

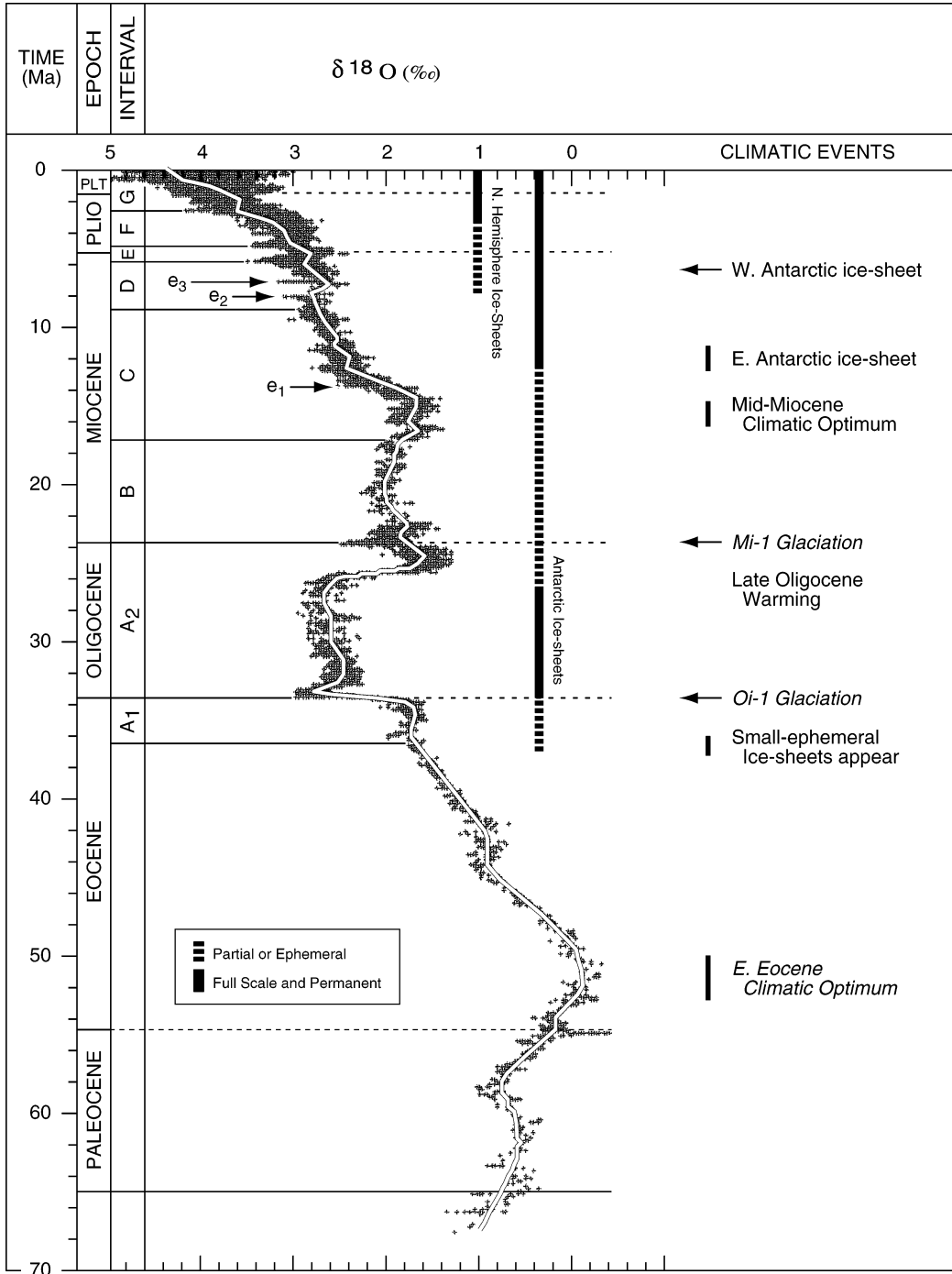


Fig. 11.2. The Cenozoic oxygen isotope curve of Zachos et al. (2001) and global climatic events relative to the guilds of larger carnivores designated by Intervals A through G. Subevents e_1 – e_3 within Intervals C and D are discussed in text (modified from Zachos et al., 2001).

at this time, seeming to fill this void.¹ However, the failure of other carnivores to increase in size and occupy the available meat-eating and carcass-consuming niches allows a group of artiodactyls, the Entelodontidae, to successfully enter this domain. Entelodonts increase in size from the late Oligocene into the early Miocene. By the time of their extinction at ~17.5 Ma, they were of enormous size, large males approaching ~800 kg. Documented evidence of scavenging by entelodonts is now known from a number of late Arikarean sites in North America (Joeckel, 1990; Hunt, 1990); it is likely that they were important carcass processors, able to crush bones of large ungulates. Both entelodonts and temnocyonines possess large, robust premolars suitable for durophagy. Their worn premolars commonly exhibit flattened tips with crimped enamel rims similar to the blunted premolars of living durophagous hyenas.

In the mid- to late Arikarean, bearded dogs of the genus *Daphoenodon* appear together with temnocyonines at many localities in the Great Plains and in Florida. At the carnivore den site at Agate National Monument a large temnocyonine was found in a burrow only a meter from dens with individuals of *Daphoenodon superbis* (Hunt et al., 1983; Hunt, 1990). The genus *Daphoenodon* includes several lineages, all probably descended from the earliest species, *D. notionastes*, known only from Florida (Frailey, 1979) and the Gulf Coast (Albright, 1996). Some species maintain a short-legged subdigitigrade stance, but one lineage evolves a long-legged digitigrade predator, *Borocyon*,

¹ Nonmarine rocks in North America dating from ~25 to 23 Ma have been difficult to confidently identify. In the John Day Formation of north-central Oregon, recent dating of tuffs (Fremd et al., 1994) has established that the interval between the Tin Roof Tuff (~25.1–25.3 Ma) and the ATR Tuff (22.6 ± 0.13 Ma) falls within this time interval. However, no large carnivores have been recently collected from this interval nor can fossils from the older 19th-century collections be placed with certainty in these beds. The Arikaree Group of the Great Plains and Rocky Mountain basins may include sediments of this age, but reliable radiometric dates have not been obtained because of the scarcity of datable tuffs. In intervals within the Arikaree Group that may fall within the ~25 to 23 Ma window, temnocyonine bearded dogs are the only large carnivores that have been found.

that survives to the end of Interval B and attains great size (basilar skull lengths, 28–30 cm). *Borocyon* last occurs in the early Hemingfordian Runningwater Formation of Nebraska, and with its demise, daphoenine amphicyonids become extinct and are replaced by immigrant amphicyonines.

Endemic New World daphoenines (*Daphoenodon*, *Borocyon*) and temnocyonines coexist with Old World amphicyonines (*Ysengrinia*, *Amphicyon*, *Cynelos*) within Interval B. These are the largest terrestrial carnivores (~50–100 kg) evolved on the continent up to this time (Hunt, 1998b). The immigrant amphicyonines *Ysengrinia*, *Cynelos*, and *Amphicyon* appear at ~23.0, ~19.2, and ~18.8 Ma, respectively, and herald the beginning of a Eurasian amphicyonine migration into North America that continues into the mid-Miocene.

Accompanying the amphicyonines are immigrant hemicyonine ursids. The oldest North American records of hemicyonines are referable to *Cephalogale*, discovered in late Arikarean sediments of western Nebraska and southeastern Wyoming (Hunt, 1998a). New World species of *Cephalogale* range from ~23 to ~17.5 Ma. The youngest records of the genus are found in early Hemingfordian sites in western Nebraska and Florida where they are as large as a small *Ursus americanus*.

An enormous predatory mustelid, *Megalictis ferox*, also is confined to Interval B. Characterized by a robust, short-limbed postcranial skeleton indicative of powerful musculature, coupled with a short-faced cranium, shearing carnassials, strong canines, and well-developed crushing premolars, *Megalictis* apparently functioned as a giant wolf-verine-like predator (Hunt and Skolnick, 1996).

Canids are endemics in Intervals A–C, restricted to North America. Throughout Interval B, canids are relatively small animals, the hesperocyonines and borophagines reaching skull lengths of ~14–18 cm in only a few species (Wang, 1994; Wang et al., 1999).

AMPHICYONINE-HEMICYONINE-BOROPHAGINE ASSOCIATION (Interval C: ~17.5–9 Ma)

With the disappearance of endemic daphoenines at the end of Interval B (~17.5

Ma), the Old World amphicyonines (*Amphicyon*, *Cynelos*) became the largest carnivorans of the Hemingfordian NALMA. By the late Hemingfordian Sheep Creek fauna of western Nebraska, these two genera reached skull lengths of 33–34 cm (*Cynelos idoneus*) and 37–39 cm (*Amphicyon frendens*). These amphicyonine lineages eventually attained maximum size in the early Barstovian (*Cynelos sinapius*, 39–44 cm; *Amphicyon ingens*, 42–52 cm; *Pliocyon*, 29–30 cm), immediately prior to their apparent extinction by ~14 Ma. With the disappearance of the large scavenging entelodonts, it is likely that these amphicyonines processed carcasses in addition to active hunting. The appearance of hyaenoid borophagines at this time also suggests a response to the availability of the durophagous niche, climaxing with the huge bone-crushing canid *Epicyon haydeni* (basilar skull lengths, late Clarendonian–early Hemphillian, 28–32 cm) in the Ogallala Formation of the Great Plains.

There is a major shift in the large amphicyonines at ~14 Ma, the boundary between early Barstovian and early late Barstovian faunas in the Great Plains. *Amphicyon*, *Cynelos*, and *Pliocyon* are replaced by new lineages of large *Pseudocyon* and mid-sized *Ischyrocyon*, which then dominate the later Barstovian and Clarendonian of North America. The only known skull of *Pseudocyon* from the late Barstovian of Nebraska has a basilar length of 37 cm, and several mandibles also indicate its great size. *Ischyrocyon*, known from a number of skulls from 36 to 47 cm, attains enormous size in the Clarendonian. The earliest populations of *Ischyrocyon* from the Barstow syncline, California, are somewhat smaller (basilar skull lengths, 28–34 cm, N = 7).

Early Barstovian canids contemporaneous with the *Amphicyon-Cynelos-Pliocyon* group remain of modest size: the largest are the borophagines *Tomarctus* (basilar lengths, ~19–19.5 cm), *Paracynarctus* (~14–16 cm), *Aelurodon* (~20 cm), and the hesperocyonine *Osbornodon* (~20 cm). Coincident with the appearance of the *Pseudocyon-Ischyrocyon* group at ~14 Ma, borophagine canids begin a steady and conspicuous size increase, documented by larger species of *Aelurodon*, *Carpocyon*, *Protepicyon*, and cynarctines in

the later Barstovian. With the extinction of the great amphicyonids near the end of the Clarendonian, the late Clarendonian and Hemphillian are typified by large species of the borophagine canids *Epicyon* and *Borophagus*.

In the later Hemingfordian, near the beginning of Interval C, the carnivorous Eurasian hemicyonine *Phoberocyon* appears in eastern North America, represented by dental and postcranial remains at Thomas Farm in Florida (Tedford and Frailey, 1976) and possibly in Delaware (Emry and Eshelman, 1998:158). During the early Barstovian, *Phoberocyon* is succeeded by the Old World hemicyonine *Plithocyon*, known from a large sample from the Barstow syncline, California, and from rare remains from New Mexico and Nebraska. These hemicyonine ursids differed from the living ursine bears in their less specialized, hypercarnivorous dentitions (relative to ancestral amphicyonodont ursids; Hunt, 1998a) and their long-footed, digitigrade stance, suggesting that they were active pursuit predators.

Early in Interval C, at ~16.5–17 Ma, the first felids enter North America from Eurasia and persist as relatively small lynx- to leopard-sized cats until the appearance of the large lion-sized felid *Nimravides* in the Clarendonian. Also, true ursine bears (*Ursavus*), although never very large at this time (<50 kg), become evident in Hemingfordian and Barstovian (but not Clarendonian) faunas, probably inhabiting well-vegetated environments as isolated individuals.

BOROPHAGINE CANID-URSID *INDARCTOS*-FELID ASSOCIATION (Interval D: ~9–6 Ma)

During the early Hemphillian (~9–7 Ma), the large canids *Epicyon*, *Borophagus*, and the smaller *Carpocyon* are joined by the great immigrant ursavine bear *Indarctos*. Apparently *Indarctos oregonensis*, the large borophagine dogs (*Epicyon haydeni*), the large long-limbed felid *Nimravides*, and the barbourifeline nimravid *Barbourifelis* have replaced the great amphicyonines and hemicyonines, marking a radical alteration in the large carnivore assemblage. The “cats” and borophagines are species that have continued to increase in size from the Clarendonian

faunas into the Hemphillian. At ~7 Ma, later in the Hemphillian interval, appear additional Eurasian immigrant species: the machairodont felid *Machairodus*, the arctoid “dog” *Simocyon*, and the mustelid *Eomellivora* (Tedford et al., 1987). The earliest tremarctine ursid *Plionarctos* also appears at this time (~7 Ma; Tedford and Martin, 2001; Hunt, 1998a). Intervals D and E have been commented on by others (Tedford et al., 1987; Webb and Opdyke, 1995) as a time of renewed immigration from the Eurasian mainland across the Bering route into North America, and a number of species of smaller carnivores and mammals also participate in this migration.

BOROPHAGINE CANID-URSID *AGRIOTHERIUM*-FELID ASSOCIATION (Interval E: ~6–4.5 Ma)

The late Hemphillian is populated by new faunal elements, recording a continuing dilution of the North American carnivoran fauna by Old World species. At ~6 Ma the migrant ursid *Agriotherium* and mustelid *Plesiogulo* enter, soon followed by the machairodont felid *Megantereon*. The nimravid cats and simocyonine arctoids are absent and presumably extinct. A diverse group of smaller felids (*Lynx*, *Adelphailurus*, *Pratifelis*) and the large *Nimravides* are joined for the first time in North America by several machairodont felids (*Machairodus*, *Megantereon*), and this coexistence of machairodonts and the less specialized felines continues into the late Pleistocene. Modern procyonids (*Procyon*) also make their first appearance. The canids *Epicyon*, *Borophagus*, and *Carpocyon* continue through this interval, suggesting that the endemic canid assemblage is largely unperturbed, simply receiving occasional pulses of immigrant stocks from Eurasia.

However, a number of extinctions of characteristic taxa occur at the end of the interval at ~4.5–4.7 Ma (Hemphillian-Blancan boundary). The felids *Machairodus* and *Nimravides*, the ursid *Agriotherium*, and the canids *Epicyon* and *Carpocyon* are missing from Interval F, representing a significant shift in the carnivoran guild in the early Pliocene.

EARLY CANID-FELID-URSID ASSOCIATION WITH MACHAIRODONT AND HYAENOID CANID (Interval F: ~4.5–3 Ma)

At ~4.5 Ma the earlier Blancan faunas include species of felids, canids, and ursids that reflect at least to some degree the modern representatives of these families in North America. *Ursus* appears near the beginning of the interval (~4.3–4.5 Ma), as does *Puma* (Martin, 1998). *Ursus* is accompanied by the tremarctine bear *Plionarctos*, marking the initiation of a shared occupation of North America by *Ursus* and tremarctines that will extend to the Holocene. The canine canids that arise in the Hemphillian begin to radiate into the lines leading toward modern foxes, coyotes, and wolves, but most Blancan canines (the ancestral coyote *Canis lepophagus*, the small wolflike *Canis edwardii*, and foxes) are small.

Archaic holdovers that remain in the interval include the tremarctine ancestor *Plionarctos*, the machairodont *Megantereon*, and the hyaenoid canid *Borophagus*.

MODERN CANID-FELID-URSID ASSOCIATION WITH MACHAIRODONT AND HYAENID (Interval G: ~3 Ma–Holocene)

The presence of modern groups ancestral or closely related to the living North American canids (*Canis*, *Vulpes*, *Urocyon*), felids (*Felis*, *Lynx*, *Puma*, *Panthera*), and ursids (*Ursus sensu lato*) characterize the interval. The tremarctine ursid *Tremarctos* first occurs at ~2.5 Ma in California and Idaho, and its sister taxon the arctodont bear *Arctodus*, the largest land carnivoran to have ever existed, appears late in the interval at ~1 Ma, accompanying the much smaller species of New World *Ursus*.

The late Cenozoic radiation of the canine canids (subfamily Caninae), stemming from the small early and mid-Miocene *Leptocyon*, was initiated in the Hemphillian. Only small foxes (*Urocyon*, *Vulpes*) coexisted with coyote-sized “*Canis*” *davisi* (Berta, 1987) in the Hemphillian, and so canines did not yet rival in size the large carnivorans of the latest Miocene in North America. Canine diversification took place in North and possibly Central America from ~6 to 3 Ma (Berta, 1987). By ~3.5 Ma in the Blancan a coyote-

sized canid, *Canis lephagus*, was widely distributed and is a possible ancestor of *Canis latrans* (Kurtén and Anderson, 1980). No wolf-sized canids were present in the New World at this time. Early wolves, *Canis etruscus*, evolved in the Old World in the early Pleistocene from the *C. arnensis*–*C. lephagus* group of Holarctic coyotelike canines (Kurtén and Anderson, 1980). A small wolf-like canid does not occur in North America until the appearance of *Canis edwardii* in the late Blancan and *Protocyon texanus* (known only from the American Southwest) in the early Irvingtonian. These small wolves are followed by the larger *C. armbrusteri* in the late Irvingtonian, and the arrival of *Canis lupus*, the gray wolf, in the latest Irvingtonian and Rancholabrean. The large dire wolf (*Aenocyon dirus*) of North America is contemporary with the gray wolf in the Rancholabrean. Thus, large wolf-sized canids are a relatively recent phenomenon in North America, appearing only in the early Pleistocene (Irvingtonian) and continuing to the present. These wolves do not become important in the large carnivoran assemblage of North America until the extinction of the hunting hyena *Chasmaporthetes* at ~1.5 Ma in the early Irvingtonian and the disappearance of the canid *Borophagus* at or shortly after ~2 Ma.

An archaic and rather exotic component remains early in the interval: in the later Blancan faunas the ailurid *Parailurus* in the Pacific Northwest and a number of aeluroid carnivores appear from ~3.5 to 2.8 Ma, including the Old World hyaenid *Chasmaporthetes* (the only hyaenid to ever reach the New World), the machairodont *Homotherium*, and the felines *Dinofelis* and *Miracinonyx*. The machairodont *Megantereon* persists from the early Blancan and is believed to evolve into the late Blancan and Irvingtonian *Smilodon* at ~2.4 Ma.

The advent of the mass extinctions at the Pleistocene-Holocene boundary sees the demise of many of the great carnivorans of Intervals F and G: gone are *Homotherium* in the Wisconsinan; *Miracinonyx* at ~19,000–20,000 years; *Arctodus* at ~12,000–13,000 years; *Smilodon* at ~8,000 years. Earlier last occurrences in the interval included the

hyaenids at ~1.5 Ma and the felid *Dinofelis* at ~2–2.3 Ma.

OXYGEN ISOTOPES, CENOZOIC GLOBAL CLIMATE, AND INTERVALS A–G

Although the fossil history of larger carnivorans and creodonts is punctuated by numerous temporal gaps in the Cenozoic non-marine sedimentary record of North America, the richer sampling of lineages made possible by renewed field efforts and the opening of the Frick Collection in New York, together with a progressively more refined lithostratigraphy and biochronology of North America mammals, make possible an improved assessment of faunal turnover in these groups. Most striking in the compilation of table 11.1 is the relative duration of these intervals through time. Intervals A through C are significantly longer than those to follow (13.3, 6.2, 8.5 m.y. versus 3.0, 1.5, 1.5, and 3.0 m.y.). Although the boundary between intervals is not always sharply defined, with some taxon ranges overlapping and others beginning or ending diachronously, the composition of the guilds of larger carnivores reflects an evident measure of faunal stability over these temporal intervals.

Recent advances in our understanding of global climate and tectonism during the Cenozoic provide a template against which we can evaluate Intervals A through G. Earth's climate has been profoundly affected by the orbital behavior of the planet, and by crustal movements and deformation generated by plate tectonics. Insight into Cenozoic climate change has been considerably enhanced by the development of deep-ocean oxygen and carbon isotopic records that supply detailed information on long-term as well as abrupt, or "transient", shifts in global climate (Miller et al., 1987, 1991; Prentice and Matthews, 1988; Denton, 1999; Zachos et al., 2001). Earlier discussions of Cenozoic climate tended to emphasize a nearly continuous climatic cooling from the early Paleogene into the Pleistocene. Newer high-resolution isotopic data have revealed a more complex and varying climatic signal characterized by intervals of broad climatic stability of variable duration that record cooling and warming events. These intervals are themselves made up of

shorter oscillating periods of cooling and warming, some exceedingly brief (10^4 – 10^5 years).

Here I compare the North American Intervals A–G (fig. 11.1) with the recently published deep-sea stable oxygen isotope record for benthic foraminifera compiled from over 40 ocean drilling sites that sampled the Cenozoic record of sedimentation (fig. 11.2, from Zachos et al., 2001). These intervals compare reasonably well with the $\delta^{18}\text{O}$ curve; several large carnivore faunal turnover events occur at evident shifts in oxygen isotope values of the deep-sea curve. Moreover, subevents (e_1 – e_3) within Intervals C and D appear to correspond to abrupt, or “transient”, oxygen isotope enrichment events suggestive of marked climatic cooling. Next I discuss the more detailed correspondence of Intervals A–G with the Zachos et al. (2001) curve.

Oxygen isotope curves for the Cenozoic (Miller et al., 1987; Prentice and Matthews, 1988; Zachos et al., 2001) record an evident shift toward greater enrichment in $\delta^{18}\text{O}$ ratios (e.g., 0.0 to 1.8‰, Zachos et al., 2001) from the end of the early Eocene (~49 Ma) to the beginning of the late Eocene (~37 Ma). The shift from mid- to late Eocene corresponds to the advent of the Chadronian carnivore fauna in North America characterized by the large carnivore guild of Interval A (Hunt, 1996: fig. 2). Prior to Interval A, the Paleocene-Eocene carnivores of North America, the miacoids and creodonts, were not large mammals, most much less than 50 kg and many much smaller (~1–20 kg).² The shift from a miacoid-creodont dominated fauna in the Paleocene and earlier Eocene to the fauna of Interval A corresponds to the global climatic changes now documented at the end of the middle Eocene (~37 Ma, Berggren et al., 1995; Prothero and Emry, 1996: 679).

A more moderate shift occurred in North America at the Eocene-Oligocene boundary

at ~33.7 Ma (extinction of brontotheres, the creodont *Hemiposalodon*, several species of hyaenodonts, the archaic amphicyonids *Daphoenictis* and *Brachyrhynchocyon*, oromyacid artiodactyls, and cylindrodont rodents), here designated as the Chadronian-Orellan boundary between subintervals A₁ and A₂ (fig. 11.2). In the Old World the Eocene-Oligocene mammalian faunal shift was a more pronounced event (Grand Coupure, ~33.7 Ma, Montanari et al., 1988; Lévêque, 1993).

From the EECO (early Eocene climatic optimum, 50–52 Ma) a 17-million-year trend toward cooler climate is indicated by a 3.0‰ enrichment in $\delta^{18}\text{O}$ from 50 to 34 Ma (early Eocene to early Oligocene). Prior to the late Eocene this enrichment is attributed to a 7°C decline in deep ocean temperature (Zachos et al., 2001). All later $\delta^{18}\text{O}$ change is regarded as the combined effects of ice-volume and temperature, “particularly for the rapid enrichment event at 34 Ma” (Zachos et al., 2001).

The Oligocene oxygen isotope curve from ~34 to 26 Ma shows $\delta^{18}\text{O}$ values of 2.4 to 3.0‰, indicating a marked enrichment in $\delta^{18}\text{O}$ over the Eocene interval where values were between 0.0 and 2.0‰ (Zachos et al., 2001). Permanent ice sheets with mass as great as 50% of the present-day ice sheet are inferred during this early to mid-Oligocene interval (Zachos et al., 1994, 2001). From ~33.7 Ma to ~26 Ma, the mammals of the Orellan, Whitneyan, and early Arikarean NALMAs represent a uniform faunal aggregate of species evolving without major interruption in faunal content; this is likewise an interval of uniform $\delta^{18}\text{O}$ values until the late Oligocene warming event—the Zachos et al. (2001) curve places this event at ~26–24 Ma, immediately prior to the Miocene Mi-1 glaciation.

Within Interval A₂, a warming spike at ~28.3 Ma coincides with an episode of major erosional incision in the central Great Plains in which much of the upper White River Group is removed at a number of localities in the late Oligocene, followed by deposition of the lower Arikaree Group. This event is coincident with a prominent fall in sea level recorded during the initiation of supercycle TB1 in the stratigraphic record (Haq

² Mesonychians, long considered creodonts but now removed from that order (McKenna and Bell, 1997), existed in North America from the early Paleocene to mid-Eocene and undoubtedly filled a scavenging, omnivorous, if not strictly carnivorous role for most species. Placed in three families (Mesonychidae, Hapalodectidae, Triisodontidae), they were nearly all larger than contemporary miacoids and many creodonts.

et al., 1988: fig. 14; Woodburne and Swisher, 1995: fig. 3).

From ~26 to 24 Ma, a marked warming trend is recorded in the $\delta^{18}\text{O}$ values, which fall to between 1.4‰ and 2.0‰. From ~26 Ma until the mid-Miocene (~14–15 Ma), oxygen isotope values are believed to indicate reduced global ice volume and cooler bottom-water temperatures, punctuated by several brief glaciations (Mi events). These glaciations and concomitant lowering of sea level may have allowed brief migrations at these times via the Bering land bridge.

At approximately the Oligocene-Miocene boundary (23.7–24.0 Ma), a marked cooling event occurs (Mi-1 glaciation, fig. 11.2), evidenced by an enrichment spike in the $\delta^{18}\text{O}$ ratio to 2.6‰. The turnover of large carnivores between Intervals A and B is closely tied to the Oligocene-Miocene boundary, and to the transformation of the early to late Arikareean mammal fauna within North America, an event that coincides with the strong global temperature decline recorded in the oxygen-isotope curves. This also coincides with a major erosional interval in the Great Plains between lower Arikaree Group sediments and the upper Arikaree Group. $^{40}\text{Ar}/^{39}\text{Ar}$ dating of a tuff in the Harrison Formation in northwestern Nebraska indicates an age of ~23 Ma (sanidine, 22.9 ± 0.08 ; Izett and Obradovich, 2001) above a major unconformity with lower Arikaree sediments. The composition of the Harrison mammal fauna demonstrates a profound alteration of taxa from the early Arikareean assemblage that preceded it. Thus, the agreement of the faunal shift, the regional erosional event within the Arikaree Group, and the $\delta^{18}\text{O}$ enrichment spike at ~24 Ma are particularly compelling in suggesting a major climatic shift at the Oligocene-Miocene boundary that may be coupled with a marked global lowering of sea level that takes place from ~23 to 20 Ma (Prentice and Matthews, 1988). Sea level fall associated with the Mi-1 glaciation probably made possible a migration event via the Bering route in which late Arikareean carnivores (*Ysengrinia americana*, *Cephalogale*, *Zodiolestes*, *Cynelos*) and other mammals (chalicothere *Moropus*, entelodont *Dinohyus*, rhinoceros *Menoceras*, small dro-

momerycids and moschids) entered the New World.

Thereafter, a warming climate persists from the early Miocene until the mid-Miocene climatic optimum (fig. 11.2, MMCO; Zachos et al., 2001), which ends at ~14 Ma. Within this interval additional warming is indicated from ~17.5 to ~16.2–16.0 Ma (Box Butte–Sheep Creek interval of the Hemingfordian NALMA). An abrupt $\delta^{18}\text{O}$ enrichment event occurs at ~16 Ma, followed again by climatic warming from ~16 to ~15 Ma. From ~15 Ma a steady climatic deterioration begins that continues to the present, during which $\delta^{18}\text{O}$ values increase from 1.6‰ in the mid-Miocene to 3.0–5.0‰ in the Pleistocene, accompanied by the development of the Antarctic and Arctic ice sheets.

At ~15–14 Ma the steady and pervasive enrichment in $\delta^{18}\text{O}$ values marks the end of the mid-Miocene climatic optimum (Zachos et al., 2001). A dramatic shift in the large amphicyonids (e_1 event, fig. 11.2) and the progressive rise of the borophagine canids at this time suggests that the great beardedogs of the late Hemingfordian and early Barstovian were somehow tied to the stable climatic interval of the early and mid-Miocene. Within Interval C, the e_1 event marks a pronounced transition within the large carnivoran community. At ~14 Ma the *Amphicyon-Cynelos-Pliocyon* group was replaced by equally large *Pseudocyon* and *Ischyrocyon* species, preceded somewhat earlier by extinction of the last hesperocyonine canids. The ~14 Ma event marks the beginning of an $\delta^{18}\text{O}$ enrichment phase that persists until ~9 Ma, with $\delta^{18}\text{O}$ values steadily increasing from +2.0 to +3.0 ‰. The extinction of amphicyonids and hemicyonine ursids coincides with the 9 Ma date.

From ~9 to ~6 Ma (Interval D), there is a period of more uniform $\delta^{18}\text{O}$ values in the Zachos curve corresponding to the Hemphillian NALMA. The preceding period of global cooling may have contributed to aridification of the North American continental interior at this time, and development of the interior grassland faunas of the late Miocene. Two subevents during Interval D appear to coincide with abrupt oxygen isotope enrichment spikes. They occur within a brief warming trend from ~9 to ~7 Ma. At ~8

Ma the appearance of the migrant Old World ursid *Indarctos* corresponds to subevent e_2 . At ~ 7 Ma, an abrupt enrichment event accompanies a significant sea level fall that coincides with the immigration of several Eurasian carnivores (*Machairodus*, *Simocyon*, *Plesiogulo*, ?*Plionarctos*) via the Bering route into North America. Similar abrupt enrichment events also occur in the Zachos $\delta^{18}\text{O}$ curve at ~ 6 Ma and ~ 4.5 Ma, which mark the boundaries between Intervals D–E and E–F. Zachos et al. (2001) recognized a “subtle warming trend” from 6 to ~ 3.2 Ma, “when oxygen isotope values increased reflecting the onset of Northern Hemisphere Glaciation”. Sea level fall in Beringia may have contributed to the migration events recorded at these times.

It becomes evident that as $\delta^{18}\text{O}$ values continue to increase on average through the Pliocene and Pleistocene, many instances of sea level lowering provide avenues across Beringia for mammal migration. Episodic appearances in the New World of large carnivores with Eurasian affinities are likely tied to such climatic events.

From 4.5 to ~ 3.2 Ma the climate in the early Pliocene remains somewhat stable and warm, but after ~ 3 Ma a cooling trend begins. From ~ 3.2 to ~ 2 Ma the effect of global cooling and the full development of both Antarctic and northern hemisphere ice masses undoubtedly influenced the mammalian fauna of the northern continents, and resulted in the shift to a modern assemblage of large carnivores in which large canids, ursids, and felids became the dominant species. The marked shift to oxygen isotope values $> +3.0$ occurs from ~ 3.2 to 2 Ma and corresponds to the transition from Interval F to G.

At the beginning of the Pleistocene at ~ 1.8 Ma the oscillations in the $\delta^{18}\text{O}$ values increase noticeably, and a succession of glacial-interglacial events continues from ~ 2.4 Ma to the present. Such climatic oscillations are likely related to (and perhaps largely responsible for) shifts in carnivoran ranges, and also for certain speciation events and extinctions, on the northern continents.

COMPARISON OF INTERVALS A–G WITH CENOZOIC MAMMAL MIGRATION EVENTS

Intervals A to G are broadly comparable with land mammal migration episodes in the

Cenozoic of North America identified by Webb and Opdyke (1995). Timing of these migration events was compared to the Prentice-Matthews (1988) $\delta^{18}\text{O}$ curve for the Cenozoic, based on equatorial planktonic foraminifera. Correspondences were also noted with the sequence stratigraphic onlap-offlap chronology of Haq et al. (1988). Boundaries of Intervals D through G generally correspond to the migration episodes of Webb and Opdyke for the Hemphillian and Blancan land mammal ages, including the Clarendonian-Hemphillian boundary. More recent work on faunas of the late Oligocene–early Miocene Arikaree and Hemingford Groups of the central Great Plains has improved the resolution of taxon ranges of large carnivores and other mammals for Intervals A–C.

Webb and Opdyke (1995) noted important mammalian immigration events in the early Miocene, two first-order and one second-order, placed at 21, 20, and 18 Ma. These occurred in the latest Arikarean (six genera), early Hemingfordian (14 genera), and medial Hemingfordian (10 genera). They remarked on the close temporal spacing of the two events at ~ 21 and ~ 20 Ma. The placement of the three events can be revised here so that they occur at 23.0, 19.2, and 18.8–18.5 Ma. The ~ 23 Ma date is based on $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Agate Ash (Izett and Obradovich, 2001) in the Harrison Formation, marking the initiation of upper Arikaree Group deposition in the Great Plains. The ~ 19.2 Ma date (FT, zircon) establishes the earliest Upper Harrison deposition in the same region (Hunt et al., 1983); and ~ 18.8 –18.5 Ma defines the earliest Runningwater Formation sediments based on paleomagnetic calibration (MacFadden and Hunt, 1998). The mammalian taxa associated with these intervals are listed in table 11.2.

Webb and Opdyke’s (1995) “latest Arikarean” event is better placed at or near the Oligocene-Miocene boundary at ~ 23 –23.7 Ma (Interval A–B boundary). This event is coincident with a major sea level fall (Haq et al., 1988) that could have made possible the introduction of Eurasian large carnivores and other mammals (table 11.2) into North America via the Bering land bridge. In the central Great Plains, Interval B includes 3 principal lithostratigraphic units: the two for-

TABLE 11.2

First and Last Occurrences of Early Miocene Mammals in the Harrison, Upper Harrison, and Runningwater Lithostratigraphic Units of Western Nebraska and Southeastern Wyoming

LOWER ARIKAREE GROUP: Last occurrence of nimravid cats (Nimravinae), amphicyonid *Daphoenus*, hyaenodont creodonts, leptachenine oreodonts, archaeothere entelodonts, and miohippine horses.

HARRISON FORMATION: First occurrence of *Ysengrinia*, *Cephalogale*, *Daphoenodon*, *Zodiolestes*, *Moropus*, *Menoceras*, *Dinohyus*, small moschid and dromomerycid deer, *Merychyus*, *Hypsiops*, *Promerycochoerus*, *Syndyoceras*.
Last occurrence of *Palaeocastor*, *Promerycochoerus*, *Zodiolestes*.

UPPER HARRISON BEDS (AGATE LOCAL FAUNA): First occurrence of *Cynelos*, *Daphoenodon superbus*, *Parahippus nebrascensis*.
Last occurrence of *Daphoenodon superbus*.

UPPER HARRISON BEDS (NIOBRARA CANYON LOCAL FAUNA): First occurrence of *Daphoenodon falkenbachi*, *Merycochoerus matthewi*, *Aletomeryx*, *Cynorca*, *Hesperhys*. Last occurrence of *Merycochoerus matthewi*, *Megalictis*, *Nanotragulus*.

RUNNINGWATER FORMATION: First occurrence of *Edaphocyon*, *Amphicyon*, *Ursavus*, *Potamotherium*, *Brachypsalis*, *Leptarctus*, *Parahippus tylei*, *P. pawniensis*, *Merycochoerus magnus*, *M. proprius*, *Machaeromeryx*, and merycodont antilocaprids.
Last occurrence of *Borocyon*, *Parahippus tylei*, *P. pawniensis*, *Merycochoerus*, *Miotapirus*, and entelodonts.

mations of the upper Arikaree Group (Harrison Formation, "Upper Harrison" beds) and the oldest unit of the Hemingford Group (Runningwater Formation). Mammals from these rock units have collectively been named the "Runningwater Chronofauna" (Webb and Opdyke, 1995) because of an evident faunal continuity through the interval, particularly among the ungulate lineages (e.g., camels, oreodonts, rhinos, horses, protoceeratids, dromomerycids).

Within this chronofauna, Webb and Opdyke (1995) identified one of the most significant (first-order) migration events in the later Cenozoic, involving the appearance of 14 genera of mammals in the Runningwater Formation of western Nebraska. This event occurs within Interval B, herein dated at ~18.8–18.5 Ma based on the paleomagnetic calibration of the initiation of Runningwater deposition in western Nebraska by MacFadden and Hunt (1998). A faunal shift among large amphicyonine carnivores (from subgroup I to II, fig. 11.1), the appearance of new lineages of daphoenines (*Borocyon*), the first appearance of the Eurasian ursine bear *Ursavus*, and the extinction of temnocyonines and the giant mustelid *Megalictis* (Hunt and Skolnick, 1996) mark this event. Thus, Interval B can be subdivided into B₁ and B₂ segments (fig. 11.1: B₁, ~23 to ~18.8–18.5 Ma; B₂, ~18.8–18.5 to 17.5 Ma).

A profound change in the style of sedi-

mentation is observed in the Great Plains at the boundary between Intervals B₁ and B₂, influencing faunal composition of the upper Arikaree units relative to the fauna of the Runningwater Formation. Arikaree Group sedimentation is primarily fine-grained eolian volcanoclastic sands and silts deposited over a level aggrading landscape east of the Rocky Mountain uplifts (Hunt, 1990). Fluvial deposits are largely limited to broad shallow streams that reworked the fine-grained eolian materials but remained confined to localized linear valley tracts. In contrast, Runningwater sediments include a much greater proportion of granitic, epiclastic coarse sediment derived from the uplifts to the west (Cook, 1965; Yatkola, 1978), deposited within an enormous and deep paleovalley complex that can be traced from southeastern Wyoming through northwest Nebraska to southwestern South Dakota. This "sudden" appearance of riparian fluvial environments at ~18.8 Ma is the signature of Runningwater sedimentation, and these beds are replete with fish, alligator, salamander, aquatic turtles, frogs, and mammals in numerous local channel deposits that remain richly fossiliferous. Such depositional environments are very rare in Arikaree rocks. It is uncertain how many of the "migrant" mammals of the Runningwater are the result of the new wetter environments or whether they truly represent relatively synchronous introduction of Old World taxa into North

America at this time. Many of these first appearances might be predicted in such riparian settings (e.g., the aquatic arctoid *Potamothereium*, otter *Mionictis*, mustelid *Leptarctus*, the ursine bear *Ursavus*, weasels and other small arctoid carnivores, the procyonid *Edaphocyon*, small merycodont antilocaprids, and several insectivores).

Nonetheless, there is an integrity to the faunas of the upper Arikaree Group and Runningwater beds that is terminated by the hiatus between this latter formation and the Box Butte Formation of the medial Hemingfordian, which rests disconformably on the terminal paleosol ("Platy Bench") of the Runningwater at many localities in western Nebraska (Galusha, 1975). Box Butte mammals show a greater affinity with the superjacent fauna of the Sheep Creek Formation (Tedford et al., 1987; Galusha, 1975). The break between the Runningwater and Box Butte faunas was recognized by Webb and Opdyke (1995) as a first-order migration event (with 10 migrant genera), corresponding to the Interval B–C boundary of this study. In the Great Plains this boundary is marked by the appearance of hypsodont horses with cement-covered cheek teeth, the arrival of the first true felids, a new large aceratherine rhinoceros and new mustelids, and the extinction of many taxa belonging to Interval B (table 11.2).

Interval C represents a period of relative stability in North American Miocene faunas, culminating in the mid-Miocene climatic optimum (MMCO), after which the steady increase in $\delta^{18}\text{O}$ values heralds the initiation of global cooling and the development of large-volume Antarctic ice. Near the onset of climatic deterioration, the e_1 subevent records the replacement of the large amphicyonine fauna (*Amphicyon*, *Cynelos*, *Pliocyon*) of the early Barstovian by the large amphicyonines (*Pseudocyon*, *Ischyrocyon*) of the medial-late Barstovian (Hunt, 1998b). Webb and Opdyke (1995) remarked on the notable decline in diversity of browsing and mixed feeding ungulates following the mid-Miocene cooling, and their replacement by grazing forms. The cooling event seems to favor the radiation of borophagine canids in North America as appropriate predators of the grazing ungulates.

The Interval C–D boundary marks the end

of the Clarendonian NALMA, where a shift to the Hemphillian faunas has long been recognized (Tedford et al., 1987). Among the most striking extinctions at this time are the loss of the great amphicyonines and hemicyonines that characterize much of the Miocene of North America. Similarly, the aelurodontine and cynarctine canids also fail to survive the Clarendonian (Wang et al., 1999).

Within Interval D, Webb and Opdyke recognized as a second-order event the migration of the great bear *Indarctos* at ~ 8 Ma, and also events at ~ 7 and ~ 6 Ma. The ~ 8 Ma event (e_2 event, fig. 11.2) corresponds to Mi-7 (Miller et al., 1991) and the sea level fall TB3.2 (Haq et al., 1988). The events at ~ 7 Ma (e_3 event, fig. 11.2) and ~ 6 Ma (Interval D–E boundary) also now appear to correspond to oxygen isotope excursions of the Zachos et al. (2001) $\delta^{18}\text{O}$ curve.

Also identified by Webb and Opdyke is a first-order migration episode at ~ 5 Ma that appears to correspond to Interval E (from ~ 6 to ~ 4.5 Ma). Moreover, their event at ~ 2.5 Ma, during the development of major Northern Hemisphere ice sheets, correlates approximately with the start of Interval G at ~ 3 – 3.2 Ma. Despite slight differences in the timing of these events, there is an evident correspondence between the migration events for Cenozoic mammals identified by Webb and Opdyke (1995) and the large carnivore intervals proposed here.

The correlation of mammal migration events to the oxygen isotope record from marine deposits of the global ocean was discussed by Webb and Opdyke (1995) as the probable result of development of land bridges (in the Neogene via the Bering Route) coincident with lowered sea level, accompanied by climate shifts that in and of themselves transformed the North American ecosystem. The continuing refinement of mammalian biochrons in North America, based on new collections and intensive study of older materials, and accompanied by more detailed field geological efforts, will provide a steadily improving database for such investigations.

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