

# MAJOR PATTERNS IN THE HISTORY OF CARNIVOROUS MAMMALS

*Blaire Van Valkenburgh*

Department of Organismic Biology, Ecology, and Evolution, University of California, Los Angeles, CA 90095-1606; e-mail: bvanval@ucla.edu

KEY WORDS: carnivores, evolutionary trends, mammalian adaptations, competition, predation

---

## ABSTRACT

The history of carnivorous mammals is characterized by a series of rise-and-fall patterns of diversification in which declining clades are replaced by phylogenetically distinct but functionally similar clades. Seven such examples from the last 46 million years are described for North America and Eurasia. In three of the seven turnover events, competition with replacement taxa may have driven the decline of formerly dominant taxa. In the remaining four this is less likely because inferred functional similarity was minimal during the interval of temporal overlap between clades. However, competition still may have been important in producing the rise-and-fall pattern through suppression of evolution within replacement taxa; as long as the large carnivore ecospace was filled, the radiation of new taxa into that ecospace was limited, only occurring after the extinction of the incumbents. The apparently inevitable decline of incumbent taxa may reflect the tendency for clades of large carnivorous mammals to produce more specialized species as they mature, leading to increased vulnerability to extinction when environments change.

---

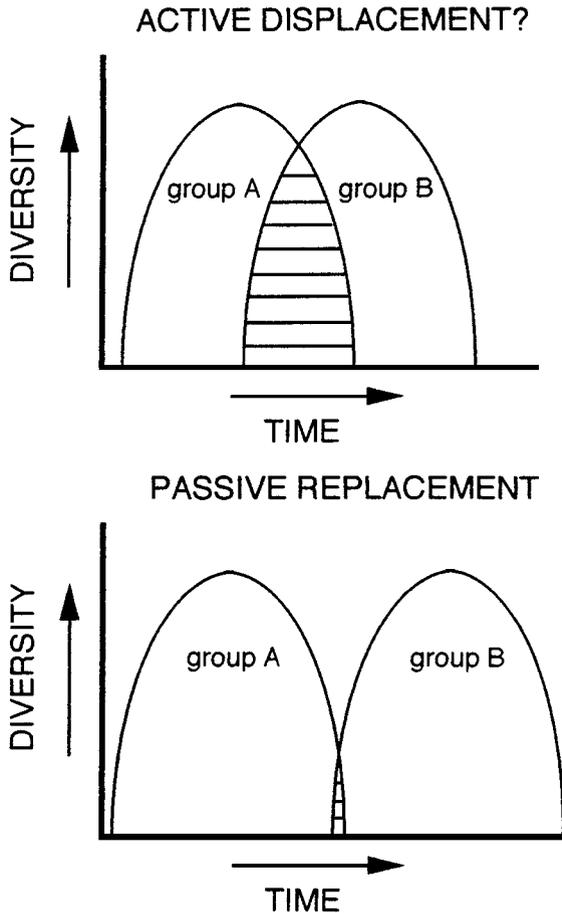
## *Introduction*

Carnivorous mammals include some of the most popular and well-known mammalian species, such as lions, tigers, wolves, and, of course, domestic cats and dogs. Undoubtedly this has encouraged study of their evolutionary history, and they have been the subject of several recent reviews (Martin 1989, Hunt 1996, Werdelin 1996a). Their limited diversity, relative to herbivores, for example, also make them a fairly tractable group to review, and their potential roles as competitors and predators has made them the subject of numerous studies of

possible competition and coevolution in the fossil record (Bakker 1983, Van Valkenburgh 1988, 1991, Janis & Wilhelm 1993, Werdelin 1996b, Werdelin & Turner 1996).

The focus of this review is on carnivorous mammals that eat vertebrates frequently; at a minimum, their diet should be or have been 50 percent vertebrates but it can range upward to 100 percent. In addition, the emphasis is on non-marine species that are or were jackal size (about 7 kg) and larger. The focus on relatively large species that rely substantially to entirely on vertebrate prey delimits a group of mammals that tend to be highly interactive, both over ecological and evolutionary time (Eaton 1979, Van Valkenburgh 1988, 1995). In extant ecosystems, groups or guilds (Root 1967) of sympatric large carnivores are often characterized by the regular occurrence of interspecific predation and interference competition, despite the fact that carnivore population densities are currently reduced due to human activities (Eaton 1979, Van Valkenburgh 1985, 1995). These negative interactions among species appear to influence the distribution and abundance of the less dominant species, suggesting that selection should favor behavioral and morphological attributes that minimize competition and dangerous interspecific encounters (cf. Van Valkenburgh 1985, 1988; Dayan & Simberloff 1996). Over evolutionary time, intense competition and intraguild predation (cf. Polis and Holt 1996) might be capable of driving the replacement of one clade by another.

In the fossil record, the replacement of one clade by another produces a "double-wedge" pattern (Figure 1), in which the rise and fall of an earlier clade is followed by or overlaps the rise of a second clade (Krause 1986, Benton 1987). If the rise of the second clade overlaps the fall of the first clade in time and space, then competition as a cause is implied, and the turnover might be ascribed to "active displacement" or "competitive replacement" (Benton 1987). However, the same pattern could result from chance or an environmental (biotic or physical) change that favored one clade and not the other. If there is little or no temporal overlap between successive clades, it is considered to be "passive replacement" (Benton 1987). In fact, double-wedge patterns do characterize the fossil record of large carnivores (Van Valkenburgh 1991, Werdelin & Solounias 1991, Werdelin 1996a, Werdelin & Turner 1996), and temporal overlap between declining and expanding clades is typical. Whether such reciprocal trends in diversity are due to active displacement as opposed to alternate responses to some external factor, such as climate change, is difficult to assess. However, if double-wedge patterns occur repeatedly in the history of carnivorous mammals and if not all such replacements are associated with significant climate change, the argument for competition (and intraguild predation) as causal agents is strengthened. As I describe here, it more often appears that the previously dominant clade suppressed the diversification of the replacement clade,



*Figure 1* Hypothetical examples of double-wedge patterns of reciprocal diversity trends in two groups of organisms. (*top*) Active displacement or competitive displacement is implied because of the extensive temporal overlap between the two groups. (*bottom*) Passive replacement of group A by group B is implied because of the near absence of temporal overlap.

suggesting a competitive advantage of incumbency (Rosenzweig & McCord 1991) rather than extinction caused by competition.

In addition to competition and intraguild predation, the history of large carnivorous mammals likely has been affected by the evolution of their prey, but the impact seems to have been limited. Although an "arms race" between predator and prey might be expected (e.g. Simpson 1944, Dawkins & Krebs 1979), it has yet to be well documented in the mammalian fossil record. Over the course

of the Cenozoic, ungulates have tended to evolve longer, more erect limbs and presumably faster speeds, as the world shifted from the more tropical, closed-habitat world of the Paleogene to the more arid, savannahlike world of the late Cenozoic (Webb 1977, Bakker 1983, Janis & Wilhelm 1993). Interestingly, the limbs of carnivores do not exhibit a parallel trend and instead remain relatively short and flexible until quite late, approximately five million years ago (Bakker 1983, Janis & Wilhelm 1993).

Although carnivorous mammals do not seem to track climate change closely, there are examples where severe temperature declines appear to have altered their evolutionary history. In several instances, sea level falls associated with global cooling exposed land bridges between continents and allowed interchange between formerly isolated flora and fauna (Tedford et al 1987, Webb & Opdyke 1995). It is these sporadic events of interchange that played a more significant role in the history of carnivorous mammals than the long-term cooling and drying trend. As I describe here, in some cases access to new territory with apparently unoccupied ecological space resulted in a rapid adaptive radiation within the immigrant clade. More often, however, the immigrant taxa exist at low diversity in their new continent for some period of time and then replace formerly dominant carnivores as they disappear for reasons that are not usually clear. Although this might be ascribed to competitive replacement of the native by the immigrant, such a conclusion is not often justified because of substantial differences in body size and ecomorphology between the putative competitors.

This review of the major events in the history of carnivorous mammals focuses on the turnover events between “dynasties,” that is, the decline of formerly dominant clades and their replacement. Most of the examples will come from North America and Eurasia, because that is where the Cenozoic fossil record is best documented and understood.

### *The Cast of Characters*

Before going further into the history of carnivorous mammals, it is useful to place the key taxa within a phylogenetic framework. Without this, it is difficult to appreciate the magnitude of convergent evolution that has occurred. Most of the species and families of mammals that are mentioned are members of the order Carnivora, and are labeled “carnivorans” to distinguish them from other carnivorous mammals outside the order. The order Carnivora includes both marine species, pinnipeds (seals, sea lions, and walruses), and terrestrial species, fissipeds, which are the subject of this paper. Carnivora is split into two major branches, the Feliformia (such as cats, hyenas, civets, mongooses, and the extinct catlike nimravids) and the Caniformia (such as bears, weasels, skunks, badgers, raccoons, dogs, pinnipeds, and the extinct bear-dogs) (Figure 2 and Table 1) (Flynn et al 1988, Wyss & Flynn 1993). This fundamental

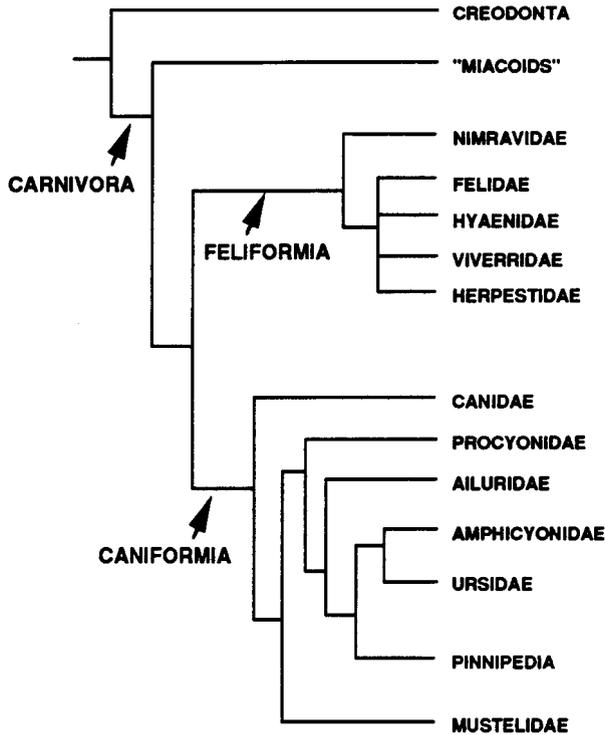


Figure 2 Phylogenetic tree of the order Carnivora. The extinct order Creodonta is the closest sister order, and together they form a group known as the Ferae (Wyss & Flynn 1993). The tree is based on molecular and morphological evidence as presented in Wyss & Flynn (1993).

subdivision was complete by the late Eocene (about 40 MYA) and may have occurred much earlier in the late Cretaceous or earliest Paleocene (70–60 MYA) (Flynn & Galiano 1982, Hunt & Tedford 1993). The sister group relationships within each of the two subdivisions are not fully resolved, but recent molecular and morphological studies have made significant advances. It is now widely accepted that (a) pinnipeds are monophyletic, (b) mustelids and procyonids are sister taxa, (c) the red panda, *Ailurus fulgens*, is a monotypic lineage, and (d) mongooses deserve family rank as Herpestidae (Wyss & Flynn 1993, Hunt & Tedford 1993, Vrana et al 1994, Lento et al 1995, Flynn & Nedbal 1998).

In addition to the Carnivora, several extinct groups of carnivorous mammals are relevant. Creodonts and mesonychids were the first large carnivores after the demise of the dinosaurs some 65 MYA, and they had a worldwide distribution,

**Table 1** Brief description of carnivorous mammals discussed in this paper

	Extant representatives	Extinct representatives
Family Mesonychidae	—	Terrestrial, doglike omnivores
Order Creodonta		
Limnocyonidae	—	Civetlike creodonts
Oxyaenidae		Short-faced robust creodonts with flexible limbs
Hyaenodontidae	—	Terrestrial doglike creodonts with some cursorial adaptations
Order Carnivora		
Nimravidae	—	Saber-toothed catlike predators
Viverridae	Civets	
Herpestidae	Mongoose	
Hyaenidae	Hyenas, aardwolf	Diverse array of civetlike and wolflike species
Felidae	Felinae: cats	Machairodontinae: saber-toothed cats
Canidae	Caninae: wolflike dogs and foxes	Hesperocyoninae and Borophaginae
Procyonidae	Raccoons, coatis, kinkajous	
Ailuridae	Red panda	
Amphicyonidae		"Bear-dogs:" a diverse group of terrestrial carnivorans, most of which had flexible, fairly robust limbs
Ursidae	Bears	Hemicyoninae: an extinct group of highly carnivorous, fairly cursorial species
Pinnipedia	Seals, sea lions, walruses	
Mustelidae	Weasels, badgers, skunks, and otters	Oligobuninae: medium to large mustelids, some of which were hypercarnivorous

exclusive of South America, Australia, and the poles (Bakker 1983, Janis et al 1998a). Creodonts and carnivorans are probably sister taxa (Wyss & Flynn 1993), but mesonychids are more closely related to ungulates and were the probable progenitors of cetaceans (Thewissen 1994, Gingerich et al 1994).

In addition to these two groups, carnivorous marsupials should be mentioned. During South America's long isolation the carnivorous mammal role was filled by a somewhat dog-like group of marsupials known as borhyaenids, which ultimately produced a saber-tooth cat analog, *Thylacosmilus* (Marshall 1976, 1978). The borhyaenids were joined by the occasional large didelphid (possum) as well as giant predatory ground birds, known as phorusrhacids (Marshall 1977). In Australia the typical marsupial carnivores tended to be

small and omnivorous, with a few exceptions such as the cat-like wombat relative, *Thylacoleo*, and the dog-like Tasmanian wolf, *Thylacinus* (Archer 1982, Rich 1991). Notably, as in South America the large predator adaptive zone was partially filled by an unexpected group. In this instance giant reptiles (such as lizards and snakes) rather than birds were the dominant large predators for much of Australia's Cenozoic history (Molnar 1991).

### *The Paleogene*

As was true for all mammals, the first major event in the history of carnivorous mammals was the extinction of the dinosaurs at the Cretaceous-Tertiary boundary. The removal of these giants that had dominated the landscape for the first 150 million years of mammalian history resulted in an ecological release for their furry successors. Nevertheless, considerable time passed (approximately 10 million years) before the first large, specialized meat eaters appeared (Gunnell 1998). In the interim, fairly generalized animals such as mesonychids seemed to be the most carnivorous species within the community. Perhaps the first genus that would fit the definition of carnivorous mammal used in this paper is the coyote-sized mesonychid, *Dissacus*, which was present in North America and Europe in the mid-Paleocene, about 62 MYA (Janis et al 1998a). Mesonychids had a somewhat doglike appearance, but a closer look at their teeth and limbs reveals them to be quite different from modern canids. Their limbs were shorter, more robust, and more flexed than typical canids and their teeth were much less specialized for carnivory (Bakker 1983, O'Leary & Rose 1995a, b). The lower tooth row of mesonychids consisted of a series of premolar-like teeth, similar in shape with relatively blunt cusps and weakly developed cutting blades (Figure 3, top). There are no modern analog taxa with this type of dentition, and so it is difficult to infer mesonychid diets with confidence, but they were probably omnivorous. Mesonychids persist at low diversity into the latest Eocene in the New World and slightly later in Asia (O'Leary & Rose 1995a, Archibald 1998). Over their history they tend to become larger and more cursorial, with some genera achieving the size of black bears (Bakker 1983, O'Leary & Rose 1995a).

The mesonychids were joined in the late Paleocene by the earliest known creodonts, described as civetlike in their diets, preying on relatively small mammals, birds, and perhaps arthropods (Gunnell 1998). Clearly, the creodonts had a dentition more specialized for carnivory than the mesonychids. All their lower molars were narrow and bladelike with obvious shearing facets caused by the scissorlike occlusion of lower and upper teeth (Figure 3, middle). The creodonts reached maximum diversity in the early and middle Eocene and produced a diverse array of species including probable bone crackers (e.g. *Patriofelis*), small saber-tooth cat analogs (e.g. *Machaeroides*), and foxlike

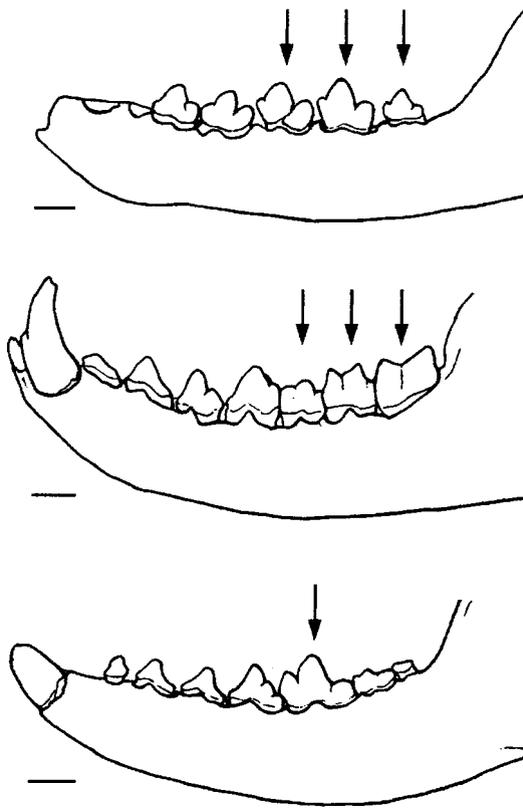


Figure 3 Lateral view of the lower jaws of (top) *Dissacus*, a mesonychid, (middle) *Hyaenodon crucians*, a creodont, and (bottom) *Hesperocyon gregarius*, a canid carnivoran. Arrows indicate molar teeth specialized for cutting. *Dissacus* is from Figure 1 (O'Leary & Rose 1995b); the others are from color transparencies.

forms (e.g. *Limnocyon*). In terms of locomotor adaptations, creodonts fall into two basic types: robust, short-limbed wolverinelike forms (e.g. oxyaenids) and slender-limbed, semicursorial forms (e.g. hyaenodontids) (Mellett 1977, Gunnell and Gingerich 1991, Gebo and Rose 1993, Gunnell 1998). Creodonts and mesonychids coexisted throughout the Eocene, with little or no evidence of competitive displacement (Figure 4).

The first carnivorans appear in the fossil record about 62 MYA, along side the first mesonychids (Flynn 1998, Janis et al 1998a). However, these early carnivorans, called miacoids, were small, weasel- to perhaps fox-size animals, many of whom probably spent part of the day foraging or resting in trees (Heinrich

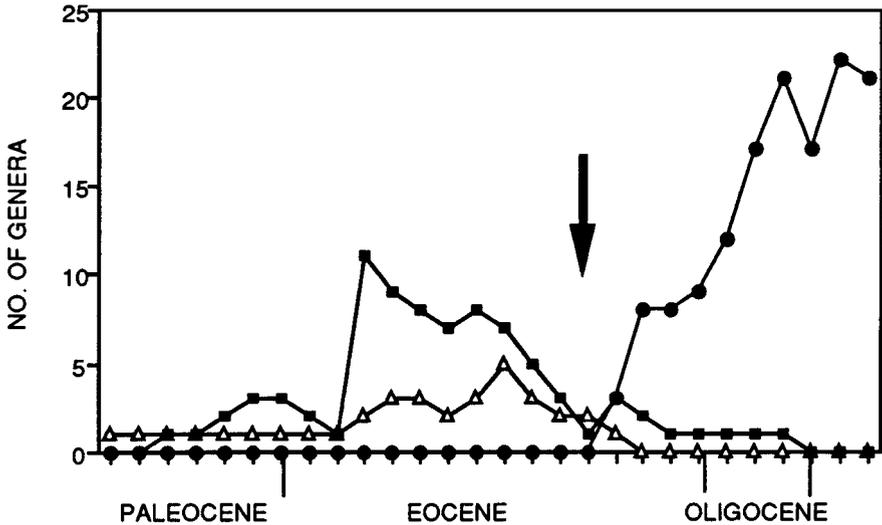


Figure 4 Generic diversity in North American creodonts (*solid squares*), mesonychids, (*open triangles*), and carnivorans (*solid circles*) over time. Arrow indicates approximate time when declining clade(s) diversity is exceeded by that of the replacement clade(s). Unlabeled temporal units correspond to intervals used throughout Janis et al (1998b). (Data are from Gunnell 1998, Archibald 1998, and Flynn 1998.)

and Rose 1995, 1997, Rose 1990). They differ most from the creodonts and mesonychids in their teeth. Miacoids display a key diagnostic feature of the order Carnivora: a single pair of cutting teeth, the carnassials (upper fourth premolar, P4, and lower first molar, m1). This differs from both creodonts, which have two or three pairs of cutting teeth, and mesonychids, which have a series of similar looking premolarized molars (Figure 3).

The significance of the carnivoran configuration is that it seems to have allowed greater evolutionary plasticity in the long term. The molars behind the carnassial remain as less specialized crushing teeth, and the premolars anterior to the carnassial are retained as modified cones for puncturing, holding, or crushing food. By enhancing either the cutting aspects of their teeth (i.e. the carnassials) or the crushing aspects (i.e. the postcarnassial molars), carnivorans can move into hypercarnivorous (meat specialists) or hypocarnivorous (plant matter specialists) niches, respectively. Both the creodonts and the mesonychids modify all their molars for similar function early in their evolutionary history, and this may have constrained them in terms of their adaptive diversity. In particular, the loss of crushing function in creodont molars might have limited them to hypercarnivorous diets. Interestingly, marsupial carnivores (dasyurids)

also have all their lower molars modified as cutting blades, and their adaptive diversity is much more limited than that of the Carnivora. Werdelin (1987, 1996a) has argued that the pattern of dental eruption in marsupials, in which molars erupt in sequence over an individual's life span, has acted as a developmental constraint on the evolution of dietary diversity. This is likely true, but even without such an unusual eruption pattern, the examples of the mesonychids and creodonts suggest that the restriction of all molars to a cutting blade function, which involves a significant loss of tooth complexity, may itself act as an evolutionary constraint.

The second major event in the history of carnivorous mammals occurred in the late Eocene, and as was true of the first event, this one affected many mammalian groups. In general, many of the groups that dominated Paleocene and Eocene communities went extinct and were replaced by representatives of orders that survived to the present (Janis 1993). The last 10 million years or so of the Eocene (43–33 MYA) witnessed two relatively rapid and severe cooling events, separated by a slight warming trend (Prothero and Berggren 1992, Prothero 1994), and these shifted the planet from the mostly warm, moist tropical world of the Paleogene toward the cooler, seasonally arid world of the Neogene (Wolfe 1992, Wing 1998). The transition was made in steps, with each temperature drop associated with sea lowering and intercontinental migrations, both between North America and Europe and between Europe and eastern Asia (Webb & Opdyke 1995). North American oxyaenid and limnocyonid creodonts made their last stand in the Uintan (circa 39.5–45.9 MYA), and they were followed by the mesonychids and miacoids in the Duchesnean and early Chadronian (35.5–39.5 MYA) (Gunnell 1998, Flynn 1998, Archibald 1998). Nearly simultaneously with or soon after the loss of these taxa, new predators appeared, including hyaenodontid creodonts, the first canids, amphicyonids, nimravids, and mustelids (Hunt & Tedford 1993, Janis et al 1998a). Although it might seem that the new predators outcompeted the archaic species, the excellent North American record indicates that the decline of the mesonychids and creodonts began well before the first appearance of the replacement taxa (Figure 4). This transition from a mesonychid/diverse creodont/miacoid guild to a predominantly nimravid/hyaenodontid creodont guild presents us with the first double-wedge pattern of turnover.

The causes for this turnover event remain murky. Clearly, it overlapped with a major climatic shift and the extinction of numerous potential prey species such as primitive artiodactyls, condylarths, brontotheres, and plesiadapiform primates (Janis 1993). However, these losses were matched by the arrival of many new taxa, some via migration between continents (Prothero 1994, Webb & Opdyke 1995). Rodents, lagomorphs (rabbits), and various artiodactyls diversified in the late Eocene and should have served as acceptable prey substitutes.

The new predators do not exhibit any obvious morphological advantages (e.g. larger body size, larger brains, better senses, or longer limbs) over those they replaced, except perhaps the presence of a single carnassial pair in the Carnivora. However, that hardly seems likely to have given them a competitive advantage on ecological time scales. Moreover, the wolf-like hyaenodontid creodonts are the largest and most common predators in the late Eocene and early Oligocene, and they bore three carnassial pairs. Thus the cause of the decline of the first dynasty of carnivorous mammals remains a mystery.

### *The Neogene*

The new late Eocene-Oligocene dynasty of predators included an array of species that differed more from one another in feeding and locomotor morphology (and inferred behavior) than the previous dynasty. For the first time there were definitive catlike forms, nimravids, with short snouts, no crushing postcarnassial molars, retractile claws, and elongate upper canine teeth. Although the nimravids were once labeled as true cats (Felidae), aspects of their basicranial anatomy demonstrate that the nimravids belong in their own family (Hunt 1987, Bryant 1991). The convergence in form is remarkable and has been well described previously (Matthew 1910, Martin 1980, Emerson & Radinsky 1980). Nimravids shared the niche of hypercarnivore with the hyaenodontid creodonts, which were more doglike in their post-cranial skeletons but still probably rushed prey from a short distance (Mellett 1977, Van Valkenburgh 1985, Janis & Wilhelm 1993). Also present for the first time at moderate body size were the amphicyonids or bear dogs, an extinct family of caniform carnivorans that reached maximum diversity in the Miocene (Viranta 1996, Hunt 1998b). In the Oligocene the amphicyonids of the Old and New World tended to be coyote size or smaller, with flexible limbs and fairly generalized dentitions, suggesting a moderately omnivorous diet (Van Valkenburgh 1985, Hunt 1998b). The earliest canid, *Hesperocyon*, was present in North America throughout the Oligocene but was a small, civet-like animal that probably climbed trees occasionally and ate a mixed diet of small vertebrates and plant matter (Van Valkenburgh 1985, 1987, Munthe 1998, Wang 1993).

For most of the Oligocene, there was little interchange between the Old and New World despite a sharp temperature drop (and inferred sea lowering) about 33 MYA that clearly increased seasonal aridity in some areas, such as the interior of North America (Hutchison 1996, Prothero 1994, Retallack 1992, Webb and Opdyke 1995). In fact, the faunal composition of central North America was so stable between approximately 37 and 27 MYA that it has been recognized as the "White River Chronofauna" (Emry 1981, Emry et al 1987). Within the North American predator guild, there were numerous species extinctions and replacements, but diversity varied little, and replacement taxa tended to be sister

taxa of those they replaced (Van Valkenburgh 1994). The stability of structure of the guild is quite remarkable given that floral and sedimentological evidence indicates a significant vegetational shift toward more savannahlike open habitats (Retallack 1992, Wolfe 1992, Prothero & Heaton 1996). Similar data are not yet available for the Old World, but it appears that faunal evolution was more dynamic. There was a major extinction event among European mammals at approximately 32–33 MYA (the “Grand Coupere”), which was associated with global cooling and the arrival of many immigrant taxa from Asia as a result of the drying of the Turgai Straits (Hooker 1992, Legendre and Hartenberger 1992, Janis 1993, Prothero 1994).

The third major event in the history of carnivorous mammals is the replacement of the Oligocene nimravid/hyaenodontid creodont guild. In North America it was largely replaced by canids, amphicyonids, and ursids, whereas in the Old World it was replaced by hyaenids, amphicyonids, and ursids. In both regions the transition between dynasties is not well documented in the fossil record but is characterized by the absence of either catlike nimravids or true cats. In North America the last Oligocene nimravids disappear at the Oligocene-Miocene boundary, approximately 23 MYA, and catlike species are absent until 17.5 MYA, when a felid immigrated from the Old World (Van Valkenburgh 1991, Hunt 1996). In Europe the timing is not as clear, but there is a significant period of time in the late Oligocene when nimravids are absent and felids have yet to appear (Werdelin 1996a).

During or just prior to this “cat gap,” numerous caniform species evolve catlike features indicative of hypercarnivory, such as reduced snouts, somewhat enlarged canines, and fairly extreme reduction of their crushing molars (Van Valkenburgh 1991). In North America the first caniform group of moderate body size to move in the direction of hypercarnivory were the endemic hesperocyonine canids, with three genera (*Parenhydrocyon*, *Enhydrocyon*, and *Mesocyon*), ranging in size from jackals to small coyotes, appearing in the early Arikareean (circa 28 MYA) (Wang & Tedford 1996, Munthe 1998). Notably, these three evolved alongside the last hyaenodont and the remaining three nimravids, two of which were puma-sized. The small hypercarnivorous canids were soon joined by and ultimately replaced by numerous species from other families which also had evolved more specialized meat-eating teeth and skulls (Van Valkenburgh 1991). These included at least three larger genera of similarly adapted amphicyonids, one endemic (*Daphoenodon*) and two from the Old World (*Temnocyon* and *Mammocyon*), a leopard-sized mustelid (*Megalictis*) as well as two hypercarnivorous bears, the hemicyonines *Cephalogale* and *Phoberocyon* (Hunt & Skolnick 1996, Hunt 1998a, b). The hypercarnivorous amphicyonids and ursids were more cursorial than the canids; all had a digitigrade stance and some were incapable of supination of the forepaw, suggesting

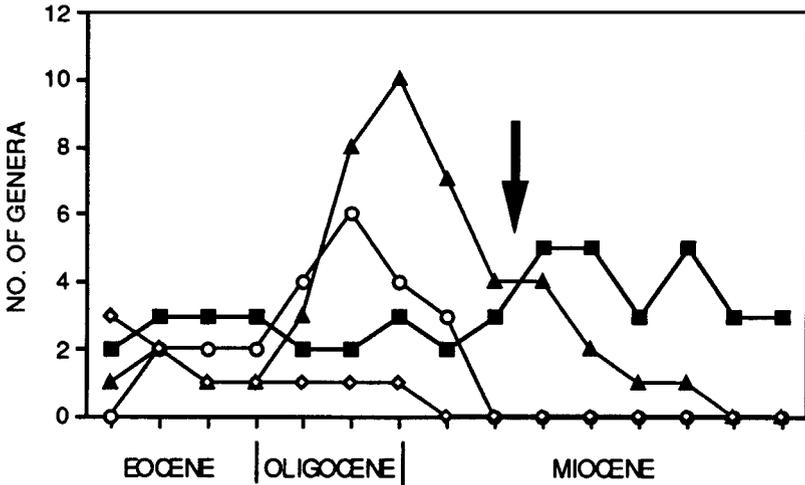


Figure 5 Generic diversity in North American creodonts (*open diamonds*), nimravids (*open circles*), highly carnivorous canids (*solid triangles*), and highly carnivorous amphicyonids and hemicyonine bears (*solid squares*) over time. Arrow indicates approximate time when declining clade(s) diversity is exceeded by that of the replacement clade(s). Unlabeled temporal units correspond to intervals used throughout Janis et al (1998b). Data are from Martin (1998a), Munthe (1998), and Hunt (1998a, 1998b).

specialization for terrestrial locomotion and perhaps greater speed (Hunt 1998a, b). In contrast, the contemporaneous canids tended to be more short-limbed robust forms, some of which likely were capable of climbing (Wang 1993, Munthe 1998). The rise and fall of nimravids and creodonts, followed by hesperocyonine canids, alongside a rise in amphicyonids and ursids presents another example of the double-wedge pattern, with significant temporal overlap between the declining and expanding wedges (Figure 5). Because many of the replacement taxa were similar in body size or larger than those they replaced, competitive displacement might have been responsible, particularly in the decline of the hypercarnivorous canids.

In the Old World, the late Oligocene-early Miocene record is not as good as that of North America, but a similar radiation of nonfeliform hypercarnivores may have occurred. Several of the North American immigrants with hypercarnivorous adaptations were members of Old World subfamilies that have been characterized as specialized meat eaters (e.g. temnocyonine amphicyonids, hemicyonine ursids; Hunt 1998a, 1998b). Consequently, it is likely that the Old World ancestors of the North American immigrants were hypercarnivorous as well. The apparent tendency of taxa to evolve toward hypercarnivory

suggests that this is a consistently lucrative niche that is rapidly filled when formerly dominant occupants decline. Interestingly, as will be discussed further below, a similar but less extensive radiation occurred when canids invaded South America approximately 2–3 MYA and found themselves on a cat-free continent (Van Valkenburgh 1991).

The remainder of the Miocene saw a gradual transition in the composition of the predator guild that was not punctuated by any notable events. The catlike feliforms return in the form of nimravids and felids, but their impact is felt gradually. Whereas the early Miocene was characterized by predator guilds dominated by caniform taxa (amphicyonids, ursids, and canids), the late Miocene featured guilds dominated more by feliform taxa (felids and doglike hyaenids in Eurasia; felids and borophagine canids in North America) (Hunt & Tedford 1993, Hunt 1996). There was no single climatic event associated with this transition, and occasional faunal interchange between the continents took place several times over the span of approximately 20 million years (Tedford et al 1987, Webb & Opdyke 1995). Notably, Cenozoic land mammal diversity in North America and western Europe peaked in the mid-Miocene (11–16 MYA) but declined sharply by the latest Miocene (Webb 1983, Stucky 1990, Van Valkenburgh & Janis 1993, Fortelius et al 1996). In Europe, the decline has been ascribed to severe reductions in habitat diversity and increased seasonality as savannahlike conditions came to dominate (Fortelius et al 1996), and similar arguments have been made for North America (Janis 1993, Webb 1983).

There is a double-wedge pattern in the Miocene that is associated with the return of catlike feliforms. Felids show up first in the Old World, approximately 24 MYA in the form of *Proailurus*, a felid the size of a bobcat. (Hunt & Tedford 1993). *Proailurus* is very rare but is succeeded by a more successful genus, *Pseudaeleurus*, which evolved in the Old World at least 20 MYA and immigrated to North America around 18 MYA (Martin 1998b). Nimavid saber-toothed cats reappear as well, first in Eurasia about 18 MYA and subsequently in North America by immigration around 11 MYA. (Martin 1989, 1998a, Werdelin 1996a). In both Eurasian and North American faunas the felids (often saber-toothed forms) increase in both diversity and body size over the course of the Miocene, perhaps displacing, or at least replacing, many of the caniform hypercarnivores (Van Valkenburgh 1991, Werdelin 1996a). These parallel diversifications are accompanied by a radiation of medium- to large-size dog-like predators, hyaenids in the Old World and borophagine canids in North America (Figure 6). The possible victims of the felid, hyaenid, and borophagine radiations seem to have been the hemicyonine bears and amphicyonids, both of which completely disappear by the latest Miocene (Figures 6 and 7). The amphicyonids also may have been affected negatively by the arrival of large

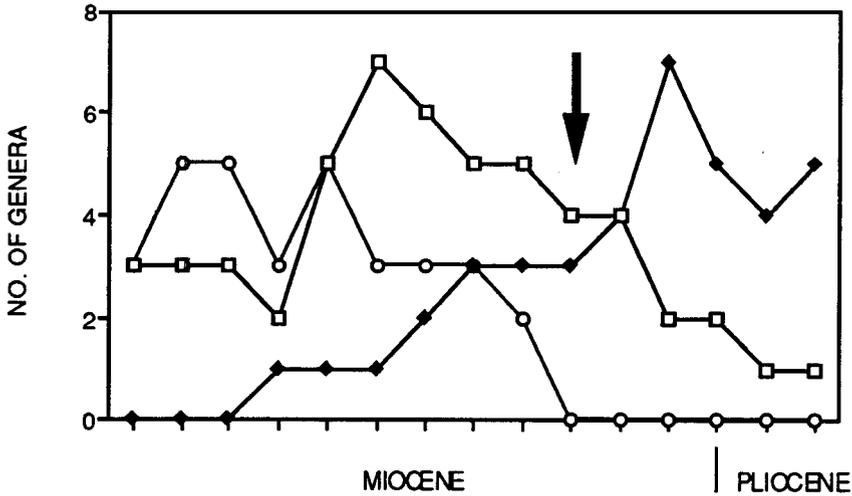


Figure 6 Generic diversity in North American borophagine canids (*open squares*), felids and nimravids, (*solid diamonds*), and amphicyonids and hemicyonine bears (*open circles*) over time. Arrow indicates approximate time when declining clade(s) diversity is exceeded by that of the replacement clade(s). Unlabeled temporal units correspond to intervals used throughout Janis et al (1998b). Data are from Martin (1998a, 1998b), Munthe (1998), and Hunt (1998a, 1998b).

omnivorous agriotherine ursids approximately 12 MYA in Eurasia and then 8 MYA in North America (Viranta 1996, Werdelin 1996a, c). It is interesting that the last amphicyonids, who were jack-of-all-trades massive predators with both blade-like carnassials and large crushing molars, were replaced by taxa, such as the hyaenids, felids, and agriotherine bears, that were more specialized for either carnivory (felids and hyaenids) or omnivory (ursids) (Viranta 1996, Werdelin 1996b).

The next and final major turnover within Holarctic, large mammalian predator guilds occurs relatively rapidly and sets the stage for the predator guilds of the present, which are composed of large felids, wolflike and foxlike canids, bone-cracking hyaenids (in the Old World), and omnivorous ursids. In this case, the turnover was associated with a major extinction event that removed 60 to 70 percent of Eurasian genera and 70 to 80 percent of North American genera (Webb 1983, 1984; Savage & Russell 1983). In both regions the extinctions occur near the Mio-Pliocene boundary (circa 5–8 MYA) and are correlated with a significant climatic event, the desiccation of the Mediterranean Sea (the Messinian salinity crisis) and the associated spread of seasonally arid grasslands in place of more mesic woodlands (Janis 1993).

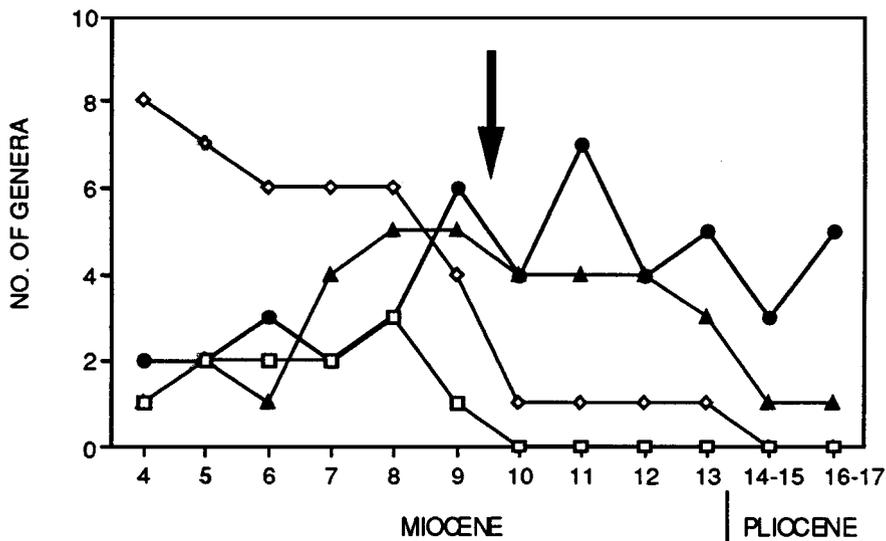


Figure 7 Generic diversity in Eurasian hemicyonine bears (open squares), amphicyonids, (open diamonds), felids and nimravids (solid circles), and non-bone-cracking hyaenids (solid triangles) over time. Arrow indicates approximate time when declining clade(s) diversity is exceeded by that of the replacement clade(s). Temporal units are numbered according to European Neogene Mammal Faunal Zones (MN units); for explanation, see Bernor et al (1996). (Diversity data are from Werdelin & Solounias 1991, 1996; and Werdelin 1996c.)

In Eurasia, the transition to the Pliocene predator guild is marked by a startling decline in hyaenid diversity from 22 species in the Turolian (9–5.3 MYA) to just 5 species in the Ruscinian (5.3–3 MYA) (Figure 7; Werdelin & Turner 1996). The extinctions are almost entirely of the more civet-like and dog-like species rather than the bone crackers (Werdelin & Turner 1996). In North America the borophagine canids undergo a similar drop in diversity from a maximum of five genera in the early late-Miocene to a single genus by latest Pliocene (Munthe 1998).

Again it is the more dog-like ecomorphs that disappear first, leaving only the genera most convergent with bone-cracking hyaenids. Certainly, the fact that bone-cracking species were favored both among the hyaenids and the borophagine canids 5–7 MYA suggests that food (prey) was scarce and the ability to use a carcass more fully was advantageous.

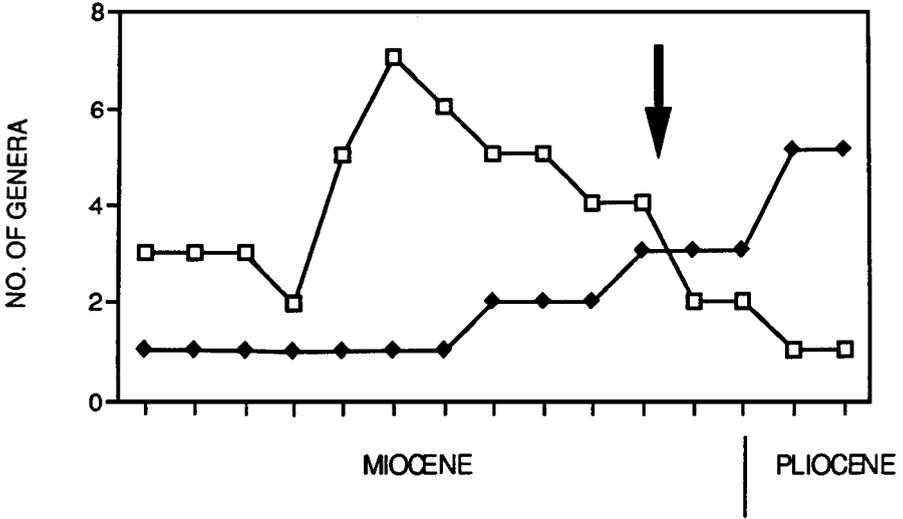
The group that eventually takes over the ecospace formerly held by borophagine dogs and hyaenids is the same in both Eurasia and North America, the modern subfamily of canids, the Caninae (Munthe 1998, Werdelin & Solounias 1991, Werdelin 1996a, 1996c, Werdelin & Turner 1996, Flynn et al 1991).

Canids spent the first 30 million years of their history entirely in North America, finally dispersing in the late Miocene, with a single species, "*Canis*" *cipio*, emerging in the Old World fossil record approximately 7–8 MYA in Spain. This is followed by a gradual diversification of fox-like and wolf-like forms (Werdelin & Turner 1996). In North America, an early fox-like genus of Caninae, *Leptocyon*, coexisted alongside the Borophagine throughout their Miocene heyday, finally beginning to diversify around 7–8 MYA (Hunt 1996, Munthe 1998). So, in both Old and New Worlds, the replacement canids overlap with the taxa they replace, creating another double-wedge pattern (Figure 8). However, the early canines that might have been potential competitors of Eurasian hyaenids or North American borophagines are much smaller in body size and exceedingly rare in the fossil record. In this case, it seems the double wedge is best explained as simple replacement rather than competitive displacement.

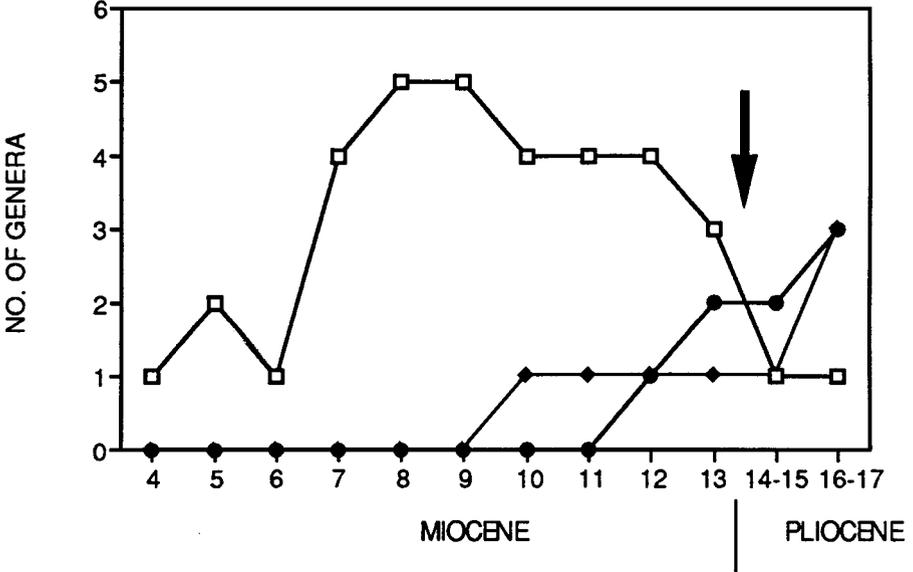
Saber-toothed ecomorphs also suffer declines in the latest Miocene but much more so in Eurasia than North America. The nimravids made their final stand approximately 9 MYA in Eurasia and so were already gone by the Mio-Pliocene extinction event (Werdelin 1996a, 1996c). However, there were seven genera of felids in the late Miocene that exhibit elongate, flattened upper canine teeth to varying degrees. That number declined to two in the Pliocene, *Megantereon* and *Homotherium*, while the number of felid genera with more rounded canines (the conical-tooth cats or Felinae) increased from one to three over the same interval (Werdelin & Turner 1996). In North America the picture was different. The last nimravid, *Barbourofelis*, arrived from the Old World in the late mid-Miocene but vanished by 6 MYA, about one million years before the Mio-Pliocene boundary. Across this boundary, there is only a slight decline in felid diversity, from seven to five genera, and both extinctions occur among non-saber-toothed forms (Martin 1998b). The final chapter in the global history of the felids is the dwindling of saber-tooth diversity and the expansion of big cats with more conical canine teeth. Although saber-toothed felids were never very diverse, with most paleocommunities containing two or at most three species, it does seem odd that this successful ecomorph should decline to extinction. The obvious explanation is competition with the larger conical-toothed felines in the genus *Panthera*, but it is not clear what advantage the felines had over the massive, well-equipped saber-toothed forms. An analysis of changes in body size and locomotor adaptations among the potential prey species might provide insight into the causes of the decline of saber-toothed cats.

The Plio-Pleistocene predator guild differed from all previous guilds in that it included a variety of carnivorans that were clearly built for long-distance pursuit. In Eurasia, long-limbed, running hyaenas ("chasmoporthetines") had been present at low diversity since the mid-Miocene, but there were no similarly built carnivorans in North America until the Plio-Pleistocene, when the Caninae

North America



Eurasia



diversified. The long legs, relatively inflexible forelimbs, and compact paws of the Caninae label them as specialized for terrestrial locomotion, more so than perhaps any previous caniforms (Janis & Wilhelm 1993). In addition to the dogs, cheetahlike felids evolve in parallel in both North America (*Miracinonyx*) and Eurasia (*Acinonyx*), and a running hyena (*Chasmoporthetes*) migrates from the Old to the New World (Berta 1981, Van Valkenburgh et al 1990, Hunt 1996). Finally, in the Pleistocene of North America, even the ursids produce a long-legged, gigantic short-faced bear (*Arctodus*). All this provides the large predator guild with a greater diversity of locomotor types than seen previously, running cats, hyaenas, dogs, and bears alongside robust saber-toothed felids and more typical felids.

The apparent increase in the number of cursorial hunters in the Plio-Pleistocene cannot be correlated with a similar pattern among their potential prey. In North America, a study of the evolution of cursorial adaptations among carnivorans and herbivores demonstrated that among herbivores the transition to long, slender limbs and compact, interlocking joints occurred quite early, approximately 20 million years before similarly specialized carnivores appear (Janis & Wilhelm 1993). Apparently, it was not necessary for predators to evolve markedly specialized limbs to keep up with their prey for much of the Cenozoic. It seems that something was different in the Pliocene; perhaps the vegetation structure was significantly more open with more extensive, short grasslands than previously existed. A very open structure makes ambush more difficult and would favor long-distance pursuit abilities among predators. More detailed data on vegetation structure before and after the Mio-Pliocene boundary would help resolve this issue, but such data are difficult to acquire. In addition, better osteological indicators of stamina and running abilities might reveal whether in fact, most pre-Pliocene predators were incapable of long-distance pursuit, as has been suggested (Bakker 1983, Janis & Wilhelm 1993).

### *Beyond North America and Eurasia*

South America, Africa, and Australia existed as isolated continents to varying degrees over the Cenozoic with Africa having the most contact with a larger

---

*Figure 8* (top) Generic diversity in North American borophagine canids (*open squares*) and canine canids (*solid diamonds*). Unlabeled temporal units correspond to intervals used throughout Janis et al (1998b). (Data are from Munthe 1998.) (bottom) Generic diversity in European bone-cracking hyaenids (*solid diamonds*), non-bone-cracking hyaenids (*open squares*), and canids (*solid circles*). Arrow indicates approximate time when declining clade(s) diversity is exceeded by that of the replacement clade(s). Temporal units for Eurasia are numbered according to European Neogene Mammal Faunal Zones (MN units). For explanation see Bernor et al (1996). (Data are from Werdelin & Solounias 1991, Werdelin 1996c, Werdelin & Turner 1996.)

landmass via a land bridge, South America somewhat less, and Australia none. Both Africa and South America made important contributions to Cenozoic carnivore history, especially in the Plio-Pleistocene.

The African land mammal record is interrupted by numerous gaps that make it difficult to reconstruct the history of connections to Eurasia. Nevertheless, it is clear that the Neogene sequence of carnivorous mammals in Africa was not too different from that of Eurasia; creodonts and nimravids were replaced by amphicyonids, felids, and hyaenids in the Miocene and then by canids, felids, and hyaenids in the Plio-Pleistocene (Savage & Russell 1983). In several instances, predator clades make their final appearance in Africa after having gone extinct elsewhere, suggesting that Africa served as a refuge from Eurasian conditions (changing climate and competitive milieu). This was true for the hyaenodontid creodonts, amphicyonids, and the doglike hyaenids (Werdelin & Solounias 1991, Viranta 1996, Gunnell 1998, Werdelin & Turner 1996). Perhaps Africa's most significant contribution to the history of carnivorous mammals is that at present it contains the most diverse large predator guild and therefore has served as a model for much of the work on paleoecology of carnivore guilds (e.g. Van Valkenburgh 1987, 1988, Werdelin & Turner 1996, Lewis 1997). It appears likely that three of the major players in both modern and Pleistocene predator guilds evolved in Africa: the lion, leopard, and spotted hyena (Turner 1990). Pleistocene lions are known from every continent except Australia, making them the most widespread carnivoran species to have ever existed (if they are all the same species) (Kurtén 1968, Kurtén and Anderson 1980).

The most significant event in the history of carnivorous mammals in South America was the opening of a substantial land bridge to Central and North America approximately 2-3 MYA. Just prior to the emergence of the Panamanian isthmus, the South American predator community consisted of one bear-like procyonid carnivoran, three species of carnivorous didelphid marsupials (one of which was the size of a coyote), and a gigantic, predaceous ground bird (Marshall 1977). With the possible exception of the rare ground bird, none of these species was a specialized hypercarnivore. Consequently, carnivorans from the north were entering a cat-free world, and not surprisingly, there was a radiation of hypercarnivorous forms within one of the first families to arrive, the canids. Over the interval from 2.5 MYA to 10 KYA, 16 new species of canids appeared, seven of which were adapted for hypercarnivory (Berta 1988, Van Valkenburgh 1991). Felids appear in the South American fossil record at the same time as canids but apparently do not diversify to the same degree, with only three new species found in the Plio-Pleistocene record (Berta and Marshall 1978). The reasons for this are unclear; it is possible that the early record is incomplete and canids arrived much earlier to South America and won

the advantage of incumbency. What seems clear is that the radiation of South American canids is an excellent example of adaptive radiation in the face of ecological opportunity. Even today, despite late Pleistocene extinctions, the canid fauna of South America is the most diverse of any continent.

### *Discussion*

The dominant feature of the history of carnivorous mammals is the repeated occurrence of double-wedge patterns of replacement in which formerly dominant clades are replaced by clades that were previously absent or at low diversity. In many cases, the replacement taxa are similar in morphology to those they replace, thus providing multiple examples of functional convergence among carnivores over the course of the Cenozoic.

Seven examples of double-wedge patterns were provided (Table 2), here listed in chronological order, by the declining or outgoing dynasty: (a) Eocene mesonychid/diverse creodont/miacoid; (b) Oligocene nimravid/hyaenodontid creodont (Eurasia and North America); (c) early Miocene hesperocyonine canid/amphicyonid/hemicyonine ursid (North America) andhyaenid/amphicyonid/hemicyonine ursid (Eurasia); and (d) late Miocene borophagine canid/felid (North America) and dog-likehyaenid/felid (Eurasia). The demise of the last two dynasties occurred near the Mio-Pliocene boundary and was followed by the establishment of similar dynasties in both Eurasia and North America that included canine canids, conical-toothed and saber-toothed felids, and bone-crackinghyaenids (in Eurasia only).

The causes of these turnovers are unlikely to be the same in each instance. Double-wedge patterns in which the expanding clade temporally and spatially overlaps the declining clade suggest the possibility of competitive displacement. Such an overlap existed in most or all of the examples mentioned, and given the incompleteness of the fossil record the observed time span of overlap is a minimum value. Consequently, in all cases, the overlap was likely of sufficient duration to have allowed competition to drive the decline of the formerly dominant group. However, even when there is substantial temporal and spatial overlap, it is critical to examine whether the morphology and body size of the newcomers are consistent with the notion that they might have outcompeted the incumbents (cf Krause 1986, Maas et al 1988). For carnivorous mammals the key parameters are body size, diet, and locomotor mode, all of which can be deduced for extinct species from morphology (cf. Van Valkenburgh 1987, 1988, 1990, Lewis 1997). If the newcomers differ greatly from the incumbents in inferred body size, diet, and locomotor mode, a conclusion of competitive displacement is not well justified. Moreover, when possible, the relative abundance of both newcomers and incumbents should be examined. Ideally, if competition were important, the fossil record would record a decline in the

**Table 2** Turnover events with declining and replacement taxa shown

Location and approximate time of turnover	Declining taxa	Replacement taxa	Competition as cause of turnover <sup>a</sup>
1) North America and Eurasia: late Eocene–Oligocene, 46–35 MYA	Mesonychids, non-hyaenodontid creodonts, miacoid carnivorans	Hyaenodontid creodonts, canids, amphicyonids, nimravids	Doubtful
2) North America: late Oligocene–early Miocene, 30–20 MYA	Hyaenodontid creodonts, nimravids	Hesperocyonine canids, amphicyonids, hemicyonine ursids	Possible
3) Eurasia: late Oligocene–early Miocene, 30–20 MYA	Hyaenodontid creodonts, nimravids	Amphicyonids, hemicyonine ursids, hyaenids	Possible
4) North America: mid-late Miocene, 13–6 MYA	Amphicyonids, hemicyonine ursids	Borophagine canids, felids	Possible
5) Eurasia: mid-late Miocene, 12.5–9.5 MYA	Amphicyonids, hemicyonine ursids	Doglike hyaenids, felids	Possible
6) North America: late Miocene–Pliocene, 5–2 MYA	Borophagine canids	Canine canids, conical-toothed and saber-toothed felids	Doubtful
7) Eurasia: late Miocene–Pliocene, 7–4 MYA	Doglike hyaenids	Canine canids, conical-toothed and saber-toothed felids, bone-cracking hyaenids	Doubtful

<sup>a</sup>Competition is not considered to have been important as a cause of turnover in cases where temporal overlap is minimal and/or replacement taxa differ significantly in body mass or inferred diet from the declining taxa. See text for further explanation.

numbers of individuals of incumbents along side a rise in those of newcomers. However, the fossil record of carnivores tends to be patchy, and it is unlikely that changes in abundance would be clear.

In three of the examples, the decline of the Eocene and the two late Miocene dynasties, competition does not seem likely to have been the driving force. In the Eocene example the decline of the mesonychids and creodonts was already well underway by the time most replacement taxa appeared. In the late Miocene, the replacement clade, the Caninae, overlapped with the incumbents, borophagine and hyaenids, but these early canines were smaller and much rarer than the incumbents. The major diversification of the Caninae took place after the extinction of the groups they replaced, implying an opportunistic replacement rather than active displacement. Interestingly, in all three of these

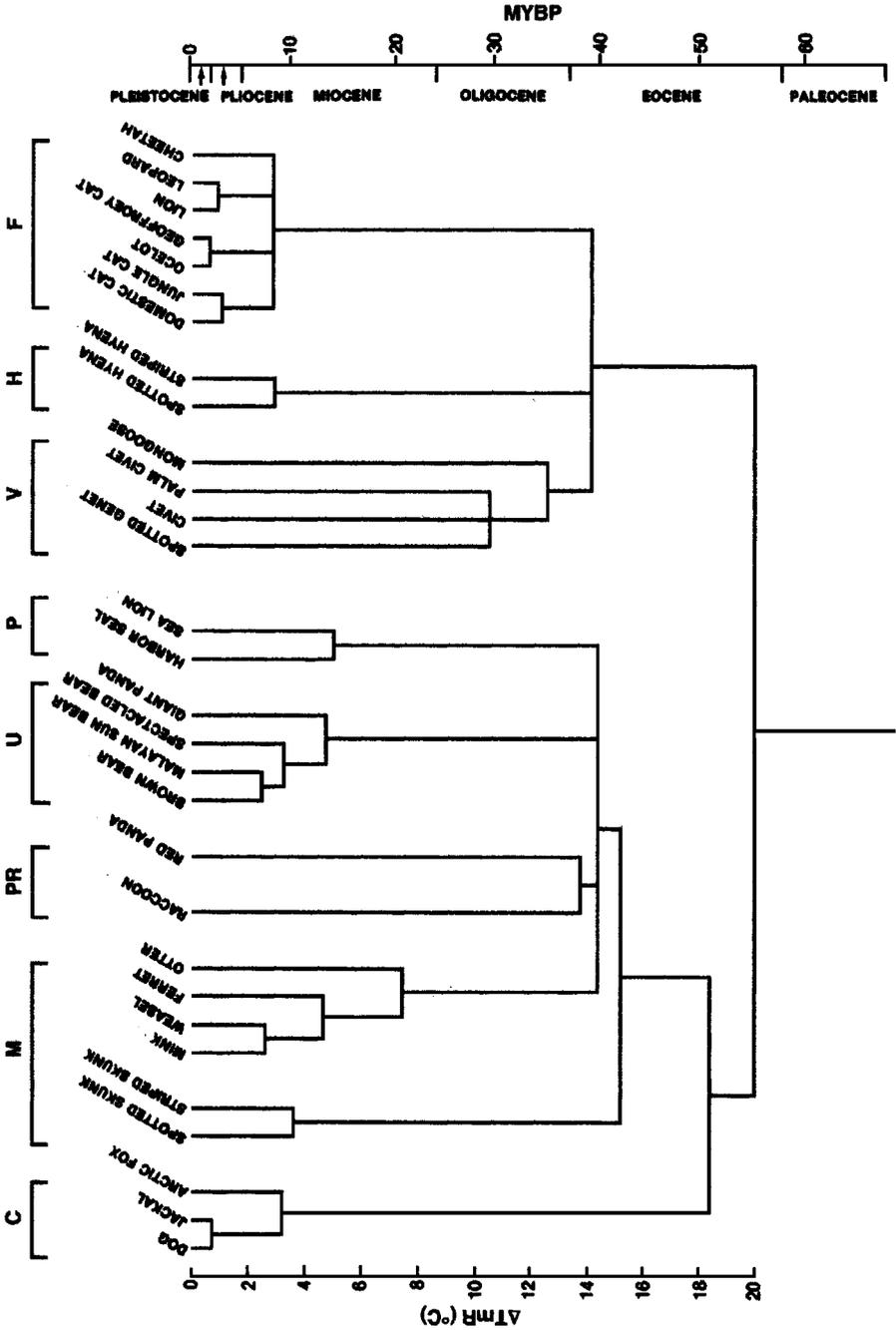
examples the turnover is associated with significant extinction and turnover among other land mammals, as well as a major temperature drop and increasing seasonality.

In the remaining three double-wedge examples, the case for competitive displacement is stronger but not certain. In North America the hypercarnivorous canids and amphicyonids that replaced the late Oligocene hypercarnivorous nimravids and hyaenodonts were of moderate size in the early Arikarean, when all four groups were present. Similarly, the gradual turnover in the mid-Miocene of Eurasia involved reciprocal diversity trends between similarly sized amphicyonids and dog-like hyaenids, both of which had dentitions indicative of moderate carnivory (Viranta 1996; Werdelin 1996a, 1996c; Werdelin & Solounias 1996). The parallel turnover that occurred in North America was also between taxa of similar size and diet, amphicyonids and borophagine canids. None of these three examples is associated with such severe climate shifts as those in the late Eocene and late Miocene.

One interesting pattern emerging from this review is that each predator dynasty tends to be composed of a few subfamilies of carnivores, such as borophagine canids, hemicyonine ursids, and hyaenodontid creodonts. As a result, these subfamilies share similar histories of a fairly rapid rise in diversity followed by a decline to extinction, with their heyday of high diversity having lasted perhaps 10 to 15 million years. Interestingly, such short life spans do not seem to characterize the subfamilies of most of the smaller carnivorans. The fossil record of small carnivorans is more difficult to reconstruct than that of larger species because of the limited amount of material and taxonomic uncertainties caused by the fragmentary nature of many specimens. However, it is possible to compare subfamily durations of large and small carnivorans from a molecular-based phylogeny.

In a tree based on hybridization of unique sequence DNA (Wayne et al 1989) the splitting of families within the Carnivora is shown to have occurred nearly simultaneously, with the exception of the Canidae, which split some 10 million years earlier (Figure 9). This is in partial agreement with the fossil record; the earliest canids, mustelids, ursids, nimravids, and amphicyonids all appear approximately 37-40 MYA (Janis et al 1998a).

Subsequent to these basal divisions on the DNA hybridization tree, the families vary in their branching patterns. Among the larger, more carnivorous families (canids, felids, and hyaenids), all the extant species appear to have diverged less than 10 MYA. Not surprisingly, all the extant taxa within each of these families belong to the same subfamily. In contrast, among the smaller and more omnivorous forms, the splits tend to be much deeper in the tree, and these deep splits often correspond to subfamily (or proposed family) subdivisions. For example, the raccoon (*Procyon lotor*) and red panda (*Ailurus fulgens*)



are now considered to belong to different families (Flynn and Nedbal 1998). Among the four species grouped as viverrids in this tree, mongooses are usually given family rather than subfamily status, as the Herpestidae (Flynn & Nedbal 1998). The deep splits are most extreme among the Viverridae but are also apparent within the Mustelidae and less so among the Ursidae. This reflects the fact that each of these three families is today represented by two or more subfamilies.

The fact that extant canids, felids, and hyaenids include but one subfamily each reflects their dynamic history as members of the large predator guild. Previous subfamilies have gone extinct, such as the borophagine canids, machairodont (saber-toothed) felids, and doglike hyenas. The alternative pattern of persistence of subfamilies among the smaller and/or more omnivorous carnivorans is likely due to at least three factors. First, as smaller taxa, they tend to exist at higher diversity, and therefore entire subfamilies are unlikely to disappear. Second, as smaller, more omnivorous forms, they are less specialized, and this also might favor persistence when environments change. Third, levels of interspecific competition are not likely to be as high as that within the large predator guild, and consequently, displacement is less likely. On the other hand, clades that evolve into the large predator adaptive zone are likely to find that greater body size and dental specialization are advantageous in the short run, despite the consequent loss of evolutionary versatility and species diversity. Natural selection is not prescient, and adaptations for current conditions may prove detrimental when the environment changes, particularly if those adaptations involve significant specialization. Evolution within the large carnivore niche may behave like a ratchet, with interspecific competition favoring increasing body mass and dental specialization, which together are likely to make the species more vulnerable to extinction if the environment changes. In relation to smaller species, large carnivores exist at lower population densities, making them more vulnerable to extinction, and tend to disperse widely, discouraging genetic isolation and thereby speciation (Stanley 1979, p. 278). Consequently, as predator clades age, they produce fewer new taxa, and eventually, extinction rate exceeds speciation rate, sending them into a decline.

The idea that evolution might proceed in a ratchetlike manner is usually considered with reference to the advantage of sex. The hypothesis, known as

---

←

*Figure 9* Phenetic tree of carnivoran relationships based on thermal stability of DNA hybrids from Wayne et al (1989). *C*, Canidae; *M*, Mustelidae; *PR*, Procyonidae and Ailuridae; *U*, Ursidae; *P*, Pinnipedia; *V*, Viverridae and Herpestidae; *H*, Hyaenidae; and *F*, Felidae. The timescale was based on a divergence time of approximately 40 MYA for all the carnivoran families except the Canidae. (From Wayne et al 1989, published with permission of Cornell University Press.)

Muller's ratchet, states that populations of clonal organisms will accumulate deleterious mutations over time due to drift and the fact that back mutations are extremely rare (Futuyma 1998 p. 610). Consequently, the population becomes dominated by more and more inferior genotypes over time, and these are less likely to persist through an environmental perturbation. Recombination, or sex, tends to rid the population of deleterious mutations and thereby provides a long-term advantage for survival of the lineage. The parallel ratchet for the carnivores is a macroevolutionary one, in which new species are budded off rather than cloned. In the carnivore example, the ratchet works by the loss of generalized features (small body mass, versatile dentition) as speciation tends to produce more specialized forms. Given that evolutionary reversals are uncommon, clades that have become dominated by specialized forms are hypothesized to be at a disadvantage during an environmental perturbation (but see Armbruster & Baldwin 1998).

In support of this hypothesis, a tendency for mean body size to increase within subfamilies and/or families of carnivores has been reported for North American amphicyonids (Hunt 1998b) and hyaenodontids (Mellett 1977), as well as Eurasian felids and hyaenids (Werdelin & Solounias 1991, Werdelin 1996a). Similarly, the last representatives of subfamilies or families are often described as exhibiting relatively specialized dentitions for their clade: for example, amphicyonids (Viranta 1996, Hunt 1998b), nimravids (Martin 1998a), North American hyaenodonts (Mellett 1977), and borophagine dogs (Munthe 1998). Rates of extinction and speciation over the life span of each subfamily have yet to be quantified; it would be especially useful to document whether extinction rate increased as each clade aged and the replacement taxa appear.

### *Conclusion*

The key to understanding the history of carnivorous mammals over evolutionary time lies in fundamental characteristics of the large predator adaptive zone that have changed little over the last 65 million years. First, there are a fairly limited number of ways to hunt, kill, and consume prey, and consequently, sympatric predators have tended to diverge along the same lines, no matter where or when they lived. There are bone crackers, meat specialists, and omnivores. Moreover, unlike the situation for herbivores, the material properties of the food of carnivores did not change over the course of the Cenozoic. Although the prey may have acquired longer legs and tougher teeth, they were still composed of skin, muscle, bone, and viscera, and so their predators continued to evolve the blades, daggers, and hammers to eat them. On different continents and at different times the same kinds of carnivores appear, often bearing remarkably similar adaptations despite independent evolutionary histories, such as

saber-like canine teeth and bone-cracking cheek teeth (Werdelin 1996a, Martin 1989).

A second feature of the large predator adaptive zone that has greatly influenced the evolutionary history of carnivores is the proclivity for interspecific competition and intraguild predation. Interspecific competition tends to be more intense among large carnivores because prey are often difficult to capture and can represent a sizable quantity of food that is worthy of stealing and defending. In addition, competition appears to be a motive for much intraguild predation because the victim often is not eaten (Cooper 1991, Johnson et al 1996). In many ecosystems today, interspecific relations among sympatric predators play a primary role in their distribution and abundance (Laurenson 1994, Johnson et al 1996, Creel & Creel 1996, Mills & Gorman 1997, White & Garrott 1997), so much so that for some species, such as the cheetah and wild dog, conservation may be dependent on density reduction among other larger species (Creel & Creel 1998, Laurenson 1994). Given such strong levels of interaction, it is not surprising to see parallels on the evolutionary time scale.

Visit the *Annual Reviews* home page at  
<http://www.AnnualReviews.org>

#### Literature Cited

- Archer M, ed. 1982. *Carnivorous Marsupials*. Mosman, N.S.W.: R. Zool. Soc. N.S.W.
- Archibald D. 1998. Archaic ungulates ("Condylarthra"). See Janis et al 1998b, p. 292–331
- Armbruster WS, Baldwin BG. 1998. Switch from specialized to generalized pollination. *Nature* 394:632
- Bakker RT. 1983. The deer flees, the wolf pursues: incongruities in predator-prey-coevolution. In *Coevolution*, ed. DJ Futuyma, M Slatkin, p. 350–82
- Benton MJ. 1987. Progress and competition in macroevolution. *Biol. Rev.* 62:305–38
- Bernor RL, Fahlbusch V, Mittmann H-W, eds. 1996. *The Evolution of Western Eurasian Neogene Mammal Faunas*. New York: Columbia Univ. Press
- Berta A. 1981. The Plio-Pleistocene hyaena *Chasmoporthetes ossifraga* from Florida. *J. Vertebr. Paleontol.* 1:341–56
- Berta A. 1988. Quaternary evolution and biogeography of the large South American Canidae (Mammalia: Carnivora). *Univ. Calif. Publ. Geol. Sci.* 132:1–149
- Berta A, Marshall LG. 1978. *South American Carnivora. Fossilium Catalogus I: Animalia, pars 125*. The Hague: W. Junk
- Bryant HN. 1991. Phylogenetic relationships and systematics of the Nimravidae (Carnivora). *J. Mammal.* 72:56–78
- Cooper SM. 1991. Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyaenas. *Afr. J. Ecol.* 29:130–36
- Creel S, Creel NM. 1996. Limitation of African wild dogs by competition with other carnivores. *Conserv. Biol.* 10:526–38
- Creel S, Creel NM. 1998. Six ecological factors that may limit African wild dogs, *Lycaon pictus*. *Anim. Conserv.* 1:1–9
- Dawkins R, Krebs JR. 1979. Arms races between and within species. *Proc. R. Soc. London Ser. B.* 205:489–511
- Dayan T, Simberloff D. 1996. Patterns of size separation in carnivore communities. In *Carnivore Behavior, Ecology and Evolution*, ed. JL Gittleman, p. 243–66. Ithaca, NY: Cornell Univ. Press
- Eaton RL. 1979. Interference competition among carnivores: a model for the evolution of social behavior. *Carnivore* 2:9–16
- Emerson SB, Radinsky LB. 1980. Functional analysis of sabertooth cranial morphology. *Paleobiology* 6:259–312
- Emry RJ. 1981. Additions to the mammalian fauna of the type Duchesnean, with

- comments on the status of the Duchesnean "age". *J. Paleontol.* 55:563–70
- Emry RJ, Bjork PR, Russell LS. 1987. The Chadronian, Orellan, and Whitneyan land mammal ages. In *Cenozoic Mammals of North America, Geochronology and Biostratigraphy*, ed. MO Woodburne, p. 118–52. Berkeley: Univ. Calif. Press
- Flynn JJ. 1998. Early Cenozoic Carnivora ("Micoidea"). See Janis et al 1998b, p. 110–23
- Flynn JJ, Galiano H. 1982. Phylogeny of early Tertiary Carnivora, with a description of a new species of *Parictis* from the middle Eocene of northwestern Wyoming. *Am. Mus. Novit.* 2725:1–64
- Flynn JJ, Nedbal MA. 1998. Phylogeny of the Carnivora (Mammalia): congruence vs. incompatibility among multiple data sets. *Mol. Phylogenet. Evol.* 9:414–26
- Flynn JJ, Neff NA, Tedford RH. 1988. Phylogeny of the Carnivora. In *The Phylogeny and Classification of the Tetrapods*. vol. 2: *Mammals*, ed. MJ Benton, p. 73–115. Syst. Assoc. Spec. Vol. 35B. Oxford, UK: Clarendon
- Flynn LJ, Tedford RH, Qiu ZX. 1991. Enrichment and stability in the Pliocene mammalian fauna of north China. *Paleobiology* 17:246–65
- Fortelius M, Werdelin L, Andrews P, Bernor RL, Humphrey L, et al. 1996. Provinciality, diversity, turnover and paleoecology in land mammal faunas of the later Miocene of western Eurasia. See Bernor et al 1996 p. 414–48
- Futuyma DJ. 1998. *Evolutionary Biology*, 3rd ed. Sunderland, MA: Sinauer
- Gebo DL, Rose KD. 1993. Skeletal morphology and locomotor adaptation in *Prolimnocyon atavus*, an early Eocene hyaenodontid creodont. *J. Vertebr. Paleontol.* 13:125–44
- Gingerich PD, Raza SM, Arif M, Anwar M, Zhou XY. 1994. New whale from the Eocene of Pakistan and the origin of cetacean swimming. *Nature* 368:844–47
- Gunnell GF. 1998. Creodonta. See Janis et al 1998b, p. 91–109
- Gunnell GF, Gingerich PD. 1991. Systematics and evolution of late Paleocene and early Eocene Oxyaenidae (Mammalia, Creodonta) in the Clarks Fork Basin, Wyoming. *Contrib. Mus. Paleontol. Univ. Mich.* 28:141–79
- Heinrich RE, Rose KD. 1995. Partial skeleton of the primitive carnivoran *Miacis petilus* from the early Eocene of Wyoming. *J. Mammal.* 76:148–62
- Heinrich RE, Rose KD. 1997. Postcranial morphology and locomotor behaviour of two early Eocene miacoid carnivorans, *Vulpavus* and *Didymictis*. *Palaeontology* 23:279–305
- Hooker JJ. 1992. British mammalian paleocommunities across the Eocene-Oligocene transition and their environmental implications. See Prothero & Berggren 1992, p. 494–515
- Hunt RM. 1987. Evolution of the aeleuroid Carnivora: significance of auditory structure in the nimravid cat *Dinictis*. *Am. Mus. Novit.* 2886:1–74
- Hunt RM. 1996. Biogeography of the order Carnivora. In *Carnivore Behavior, Ecology and Evolution*, ed. JL Gittleman, p. 485–541. Ithaca, NY: Cornell Univ. Press
- Hunt RM. 1998a. Ursidae. See Janis et al 1998b, p. 174–95
- Hunt RM. 1998b. Amphicyonidae. See Janis et al 1998b, p. 196–227
- Hunt RM, Skolnick R. 1996. The giant mustelid *Megalictis* from the early Miocene carnivore dens at Agate Fossil Beds National Monument, Nebraska: earliest evidence of dimorphism in New World Mustelidae (Carnivora, Mammalia). *Contrib. Geol. Univ. Wyo.* 31:35–48
- Hunt RM, Tedford RH. 1993. Phylogenetic relationships within the aeluroid Carnivora and implications of their temporal and geographic distribution. In *Mammal Phylogeny*, eds. FS Szalay, MJ Novacek, MC McKenna, p. 53–73. New York: Springer-Verlag
- Hutchinson JH. 1996. Testudines. See Prothero & Emry 1996, p. 337–53
- Janis CM. 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annu. Rev. Earth Planet. Sci.* 24:467–500
- Janis CM, Baskin JA, Berta A, Flynn JJ, Gunnell GF, et al. 1998a. Carnivora. See Janis et al 1998b, p. 73–90
- Janis CM, Scott KM, Jacobs LL, eds. 1998b. *Evolution of Tertiary Mammals of North America*. New York: Cambridge Univ. Press
- Janis CM, Wilhelm PB. 1993. Were there mammalian pursuit predators in the Tertiary? Dances with wolf avatars. *J. Mammal. Evol.* 1:103–25
- Johnson W, Fuller TK, Franklin WL. 1996. Sympatry in canids: a review and assessment. In *Carnivore Behavior, Ecology and Evolution*, ed. JL Gittleman, p. 189–218. Ithaca, NY: Cornell Univ. Press
- Krause DW. 1986. Competitive exclusion and taxonomic displacement in the fossil record: the case of rodents and multituberculates in North America. In *Vertebrates, Phylogeny, and Philosophy*, ed. KM Flanagan, JA Lillegraven, p. 95–118. *Univ. Wyo. Spec. Pap.* 3:119–30
- Kurtén B. 1968. *Pleistocene Mammals of Europe*. Chicago: Aldine
- Kurtén B, Anderson E. 1980. *Pleistocene Mammals of North America*. New York: Columbia Univ. Press

- Laurenson K. 1994. High juvenile mortality in cheetahs (*Acinonyx jubatus*) and its consequences for maternal care. *J. Zool.* 234:387–408
- Laurenson K. 1995. Implications of high offspring mortality for cheetah population dynamics. In *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem*, ed. ARE Sinclair, P. Arcese, p. 385–99. Chicago: Univ. Chicago Press
- Legendre S, Hartenberger J-L. 1992. The evolution of mammalian faunas in Europe during the Eocene and Oligocene. In *Prothero & Berggren 1992*, p. 516–28
- Lento GM, Hickson RE, Chambers GK, Penny D. 1995. Use of spectral analysis to test hypotheses on the origin of pinnipeds. *Mol. Biol. Evol.* 12:28–52
- Lewis ME. 1997. Carnivoran paleoguilds of Africa: implications for hominid food procurement strategies. *J. Human Evol.* 32:257–88
- Maas MC, Krause DW, Strait SG. 1988. The decline and extinction of Plesiadapiforms (Mammalia: Primates) in North America: displacement or replacement. *Paleobiology* 14:410–31
- Marker-Kraus L, Kraus D. 1997. Conservation of strategies for the long-term survival of the cheetah *Acinonyx jubatus* by the Cheetah Conservation Fund, Windhoek. *Int. Zoo Yearb.* 35:59–66
- Marshall LG. 1976. Evolution of the family Thylacosmilidae, fossil marsupial saber-tooths of South America. *PaleoBios* 23:1–20
- Marshall LG. 1977. Evolution of the carnivorous adaptive zone in South America. In *Major Patterns in Vertebrate Evolution*, ed. MK Hecht, PC Goody, BM Hecht, p. 709–21. New York: Plenum
- Marshall LG. 1978. Evolution of the Borhyaenidae, extinct South American predaceous marsupials. *Univ. Calif. Publ. Geol. Sci.* 117:1–89
- Martin LD. 1980. Functional morphology and the evolution of cats. *Trans. Nebr. Acad. Sci.* 8:141–54
- Martin LD. 1989. Fossil history of the terrestrial Carnivora. In *Carnivore Behavior, Ecology and Evolution*, ed. JL Gittleman, p. 536–68. Ithaca, NY: Cornell Univ. Press
- Martin LD. 1998a. Nimravididae. See Janis et al 1998b, p. 228–35
- Martin LD. 1998b. Felidae. See Janis et al 1998b, p. 236–42
- Matthew WD. 1910. The phylogeny of the Felidae. *Bull. Am. Mus. Nat. Hist.* 28:289–316
- Mellott JS. 1977. Paleobiology of North American *Hyaenodon* (Mammalia: Creodonta). *Contrib. Vertebr. Evol.* 1:1–134
- Mills MGL, Gorman ML. 1997. Factors affecting the density and distribution of wild dogs in the Kruger National Park. *Conserv. Biol.* 11:1397–406
- Molnar RE. 1991. Fossil reptiles in Australia. In *Vertebrate Palaeontology of Australasia*, ed. P Vickers-Rich, JM Monaghan, RF Baird, TH Rich, p. 605–702. Melbourne: Monash Univ. Publ.
- Munthe K. 1998. Canidae. See Janis et al 1998b, p. 124–43
- O'Leary MA, Rose KD. 1995a. Postcranial skeleton of the early Eocene mesonychid *Pachyaena* (Mammalia, Mesonychia). *J. Vertebr. Paleontol.* 15:401–30
- O'Leary MA, Rose KD. 1995b. New mesonychian dentitions from the Paleocene and Eocene of the Bighorn Basin, Wyoming. *Ann. Carnegie Mus.* 64:147–72
- Polis GA, Holt RD. 1996. Intraguild predation—the dynamics of complex trophic interactions. *Trends Ecol. Evol.* 7:151–54
- Prothero DR. 1994. The late Eocene-Oligocene extinctions. *Annu. Rev. Earth Planet. Sci.* 22:145–65
- Prothero DR, Berggren WA, eds. 1992. *Eocene-Oligocene Climatic and Biotic Evolution*. Princeton, NJ: Princeton Univ. Press
- Prothero DR, Emry RG, eds. 1996. *The Terrestrial Eocene-Oligocene Transition in North America*. New York: Cambridge Univ. Press
- Prothero DR, Heaton TH. 1996. Faunal stability during the early Oligocene climatic crash. *Palaeoogeogr. Palaoclimatol. Palaeoecol.* 127:257–83
- Retallack GJ. 1992. Paleosols and changes in climate and vegetation across the Eocene/Oligocene boundary. See Prothero & Berggren 1992, p. 382–98
- Rich TH. 1991. The history of mammals in Terra Australis. In *Vertebrate Palaeontology of Australasia*, ed. P Vickers-Rich, JM Monaghan, RF Baird, TH Rich, p. 893–1070. Melbourne: Monash Univ. Publ.
- Root RB. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr.* 37:317–50
- Rose KD. 1990. Postcranial skeletal remains and adaptations in early Eocene mammals from the Willwood Formation, Bighorn Basin, Wyoming. In *Dawn of the Age of Mammals in the Northern Part of the Rocky Mountain Interior of North America*, ed. TM Bown, KD Rose. *Spec. Pap. Geol. Soc. Am.* 243:107–34
- Rosenzweig ML, McCord RD. 1991. Incumbent replacement: evidence for long-term evolutionary progress. *Paleobiology* 17:202–13
- Savage DE, Russell DE. 1983. *Mammalian Paleofaunas of the World*. Reading, MA: Addison-Wesley

- Simpson GG. 1944. *Tempo and Mode of Evolution*. New York: Columbia Univ. Press
- Stanley SM. 1979. *Macroevolution: Pattern and Process*. San Francisco: WH Freeman
- Stucky RK. 1990. Evolution of land mammal diversity in North America during the Cenozoic. In *Current Mammalogy*, vol. 2, ed. HH Genoways, p. 375–432. New York: Plenum
- Tedford RH, Galusha T, Skinner MF, Taylor BE, Fields RW, et al. 1987. Faunal succession and biochronology of the Arikarean through Hemphillian interval (late Oligocene through earliest Pliocene Epochs) in North America. In *Cenozoic Mammals of North America, Geochronology and Biostratigraphy*, ed. MO Woodburne, p. 152–210. Berkeley: Univ. Calif. Press
- Thewissen JGM. 1994. Phylogenetic aspects of cetacean origins: a morphological perspective. *J. Mammal. Evol.* 2:157–84
- Turner A. 1990. The evolution of the guild of larger terrestrial carnivores during the Plio-Pleistocene in Africa. *Geobios* 23:349–68
- Van Valkenburgh B. 1985. Locomotor diversity within past and present guilds of large predatory mammals. *Paleobiology* 11:406–28
- Van Valkenburgh B. 1987. Skeletal indicators of locomotor behavior in living and extinct carnivores. *J. Vertebr. Paleontol.* 7:162–82
- Van Valkenburgh B. 1988. Trophic diversity within past and present guilds of large predatory mammals. *Paleobiology* 14:156–73
- Van Valkenburgh B. 1990. Skeletal and dental predictors of body mass in carnivores. In *Body Size in Mammalian Paleobiology*, ed. J Damuth, BJ MacFadden, p. 181–206. New York: Cambridge Univ. Press
- Van Valkenburgh B. 1991. Iterative evolution of hypercarnivory in canids (Mammalia: Canidae): evolutionary interactions among sympatric predators. *Paleobiology* 17:340–62
- Van Valkenburgh B. 1994. Extinction and replacement among predatory mammals in the North American late Eocene-Oligocene: tracking a guild over twelve million years. *Hist. Biol.* 8:1–22
- Van Valkenburgh B. 1995. Tracking ecology over geologic time: evolution within guilds of vertebrates. *Trends Ecol. Evol.* 10:71–76
- Van Valkenburgh B, Grady F, Kurtén B. 1990. The Plio-Pleistocene cheetah-like cat *Miracinonyx inexpectatus* of North America. *J. Vertebr. Paleontol.* 10:434–54
- Van Valkenburgh B, Janis CM. 1993. Historical diversity patterns in large mammalian herbivores and carnivores. In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, eds. R Ricklefs, D Shluter, p. 330–40. Chicago: Univ. Chicago Press
- Viranta S. 1996. European Miocene Amphicyonidae—taxonomy, systematics, and ecology. *Acta Zool. Fenn.* 204:1–61
- Vrana PB, Milinkovitch MC, Powell JR, Wheeler WC. 1994. Higher level relationships of the arctoid Carnivora based on sequence data and “total evidence”. *Mol. Phylogenet. Evol.* 3:47–58
- Wang X. 1993. Transformation from plantigrady to digitigrady: functional morphology of locomotion in *Hesperocyon* (Canidae: Carnivora). *Am. Mus. Novit.* 3069:1–23
- Wang X, Tedford RH. 1996. Canidae. See Prothero & Emry 1996, p. 433–52
- Wayne RK, Benveniste RE, Janczewski DN, O’Brien SJ. 1989. Molecular and biochemical evolution of the Carnivora. In *Carnivore Behavior, Ecology and Evolution*, ed. JL Gittleman, p. 465–94. Ithaca, NY: Cornell Univ. Press
- Webb SD. 1977. A history of savannah vertebrates in the New World. Part 1: North America. *Annu. Rev. Ecol. Syst.* 8:355–80
- Webb SD. 1983. The rise and fall of the late Miocene ungulate fauna in North America. In *Coevolution*, ed. MD Nitecki, p. 267–306. Chicago: Univ. Chicago Press
- Webb SD. 1984. Ten million years of mammal extinctions in North America. In *Quaternary Extinctions: a Prehistoric Revolution*, eds. PS Martin, RG Klein, p. 189–210. Tucson: Univ. Ariz. Press
- Webb SD, Opdyke ND. 1995. Global climatic influences on Cenozoic land mammal faunas. In *Effects of Past Global Change on Life*, ed. Board on Earth Sciences and Resources, National Research Council, p. 184–208. Washington, DC: Natl. Acad. Sci. USA
- Werdelin L. 1987. Jaw geometry and molar morphology in marsupial carnivores: analysis of a constraint and its evolutionary consequences. *Paleobiology* 13:342–50
- Werdelin L. 1996a. Carnivoran ecomorphology: a phylogenetic perspective. In *Carnivore Behavior, Ecology and Evolution*, ed. JL Gittleman, p. 582–624. Ithaca, NY: Cornell Univ. Press
- Werdelin L. 1996b. Community-wide character displacement in Miocene hyaenas. *Lethaia* 29:97–106
- Werdelin L. 1996c. Carnivores, exclusive of Hyaenidae, from the later Miocene of Europe and western Asia. See Bernor et al 1996, p. 271–89
- Werdelin L, Solounias N. 1991. The Hyaenidae: taxonomy, systematics and evolution. *Foss. Strata* 30:1–104
- Werdelin L, Solounias N. 1996. The evolutionary history of hyaenas in Europe and western Asia during the Miocene. See Bernor et al 1996, p. 290–306

- Werdelin L, Turner A. 1996. Turnover in the guild of larger carnivores in Eurasia across the Miocene-Pliocene boundary. *Acta Zool. Cracov.* 39:585-92
- White PJ, Garrott RA. 1997. Factors regulating kit fox populations. *Can. J. Zool.* 75:1982-88
- Wing SL. 1998. Tertiary vegetation of North America as a context for mammalian evolution. See Janis et al 1998b, p. 37-65
- Wolfe JA. 1992. Climatic, floristic, and vegetational changes near the Eocene/Oligocene boundary in North America. See Prothero & Berggren 1992, p. 421-36
- Wyss A, Flynn JJ. 1993. A phylogenetic analysis and definition of the Carnivora. In *Mammal Phylogeny*, eds. FS Szalay, MJ Novacek, MC McKenna, p. 32-52. New York: Springer-Verlag



## CONTENTS

Ups and Downs in Planetary Science, <i>Carolyn S. Shoemaker</i>	1
NATURE OF MIXED-LAYER CLAYS AND MECHANISMS OF THEIR FORMATION AND ALTERATION, <i>Jan Srodon</i>	19
Geologic Applications of Seismic Scattering, <i>Justin Revenaugh</i>	55
The Global Stratigraphy of the Cretaceous-Tertiary Boundary Impact Ejecta, <i>J. Smit</i>	75
Hubble Space Telescope Observations of Planets and Satellites, <i>Philip B. James, Steven W. Lee</i>	115
The Deglaciation of the Northern Hemisphere: A Global Perspective, <i>Richard B. Alley, Peter U. Clark</i>	149
K-Ar and $^{40}\text{Ar}/^{39}\text{Ar}$ Geochronology of Weathering Processes, <i>P. M. Vasconcelos</i>	183
Thermohaline Circulation: High Latitude Phenomena and the Difference Between the Pacific and Atlantic, <i>A. J. Weaver, C. M. Bitz, A. F. Fanning, M. M. Holland</i>	231
Kuiper Belt Objects, <i>David Jewitt</i>	287
STROMATOLITES IN PRECAMBRIAN CARBONATES: Evolutionary Mileposts or Environmental Dipsticks? <i>John P. Grotzinger, Andrew H. Knoll</i>	313
LINKING THERMAL, HYDROLOGICAL, AND MECHANICAL PROCESSES IN FRACTURED ROCKS, <i>Chin-Fu Tsang</i>	359
IMPACT CRATER COLLAPSE, <i>H. J. Melosh, B. A. Ivanov</i>	385
WESTERN UNITED STATES EXTENSION: How the West was Widened, <i>Leslie J. Sonder, Craig H. Jones</i>	417
MAJOR PATTERNS IN THE HISTORY OF CARNIVOROUS MAMMALS, <i>Blaire Van Valkenburgh</i>	463