1

Introduction to Carnivora

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Why Carnivora?

The placental mammal order Carnivora encompasses many charismatic taxa, from dogs and cats to bears, otters, hyaenas, and seals. Perhaps more than any other mammalian clade, carnivorans are a source of fascination for humans, partially due to our intimate observation of the domesticated species that reside in many of our own homes. Beyond our quirky cats and loyal dogs, however, carnivorans have long and often been the subject of a variety of studies and documentaries of natural history concerning behaviour, ecology, and evolution, and for many good reasons. With over 260 living species, Carnivora is one of the most species-rich clades of mammals. It should be noted that the term 'carnivoran' is a phylogenetic classification, in contrast to 'carnivore', an ecological classification describing any meat-eater.

Evolutionarily, Carnivora is divided into two major branches (Flynn *et al.*, this volume, Chapter 2, Figure 2.2): Feliformia (including cats, linsangs, civets, mongooses, fossas, falanoucs, and hyaenas; Figure 1.1) and Caniformia (encompassing dogs, bears, seals, sea lions, walruses, the red panda, raccoons, skunks, weasels, badgers, otters, and wolverines; Figure 1.2) (Wozencraft, 2005; Myers *et al.*, 2008). As that list suggests, this taxonomic diversity is well matched by their ecological breadth. While the name Carnivora usually conjures up images of tigers and wolves, carnivorans range in diet from pure carnivores to species that specialise on fruit, leaves, and insects, as well as the full spectrum of mixed diets; carnivorans are represented by omnivorous bears, frugivorous raccoons, and even insectivorous hyaenas. Even better for students of evolution, many carnivoran families have given rise to multiple different ecomorphs. This ecological diversity is possibly best exemplified by the species-poor but ecologically diverse bears, which have evolved folivorous, frugivorous, omnivorous, insectivorous, and hypercarnivorous forms (Wozencraft, 2005). In fact, as discussed by Holliday (this volume, Chapter 7), the hypercarnivorous forms

Figure 1.1 Feliformia. A, Felidae; *Panthera leo*, lion; B, Felidae: *Smilodon fatalis*, sabre-toothed cat; C, Viverridae: *Arctictis binturong*, binturong; D, Hyaenidae: *Crocuta crocuta*, spotted hyaena; E, Herpestidae: *Mungos mungo*, banded mongoose; F, Eupleridae: *Cryptoprocta ferox*, fossa. Photo credits: A, D, A. Goswami; B, P. Goswami; C, Klaas Lingbeek-van Kranen, iStockphoto®; E, N. Smit, iStockphoto®; F, J. Weston, iStockphoto®.
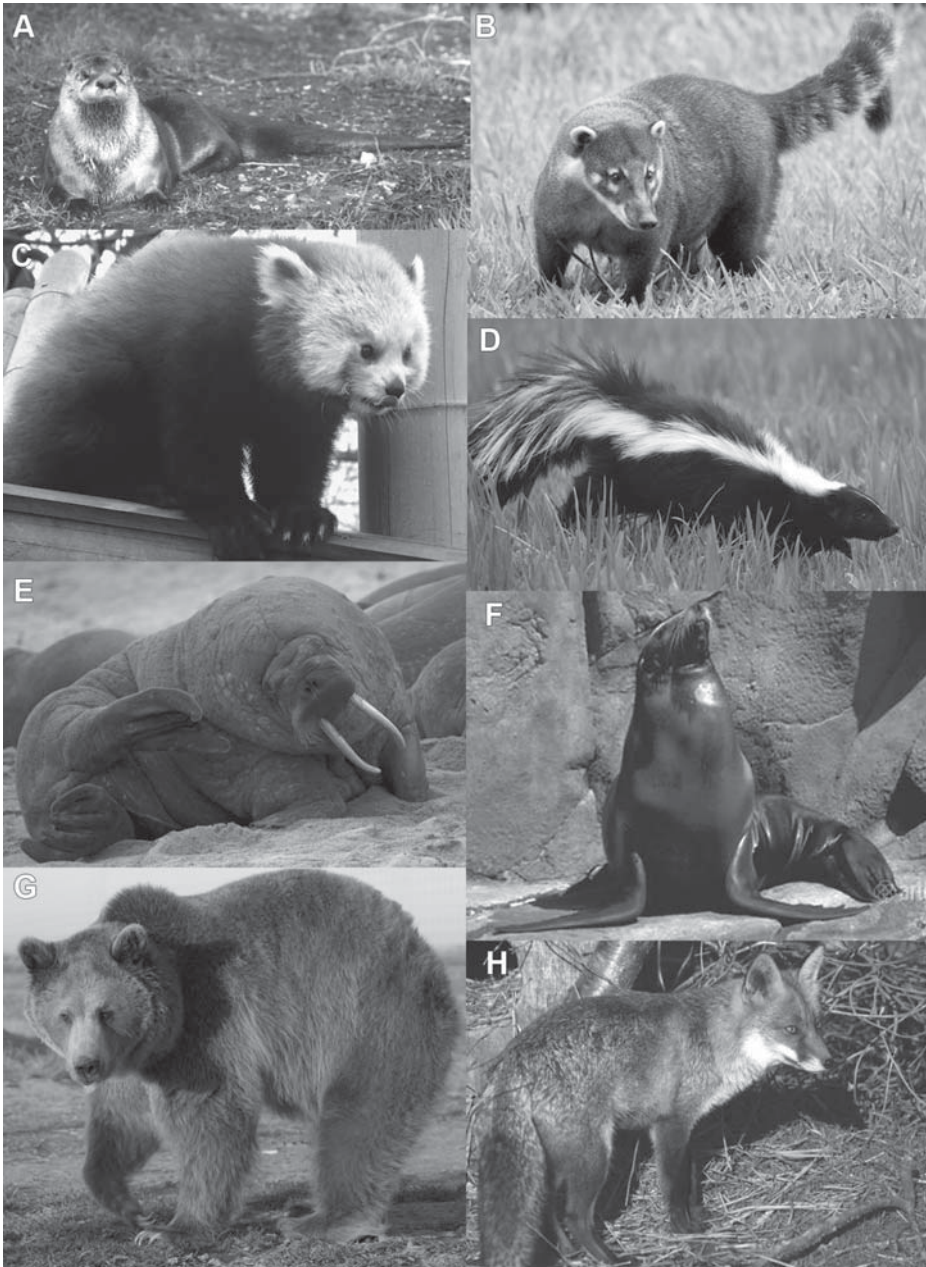
Figure 1.2 Caniformia. A, Mustelidae: *Lontra canadensis*, northern river otter; B, Procyonidae: *Nasua narica*, coati; C, Ailuridae: *Ailurus fulgens*, red panda; D, Mephitidae: *Mephitis mephitis*, striped skunk; E, Odobenidae: *Odobenus rosmarus*, walrus; F, Otariidae: *Zalophus californianus*, California sea lion; G, Ursidae: *Ursus arctos*, brown bear; H, Canidae: *Vulpes vulpes*, red fox. Photo credits: A, F, H, FreeDigitalPhotos.net; B, G. Brzezinski, iStockphoto®; C, S. Peigné; D, J. Coleman, iStockphoto®; E, T. Shieh, iStockphoto®; G, K. Livingston, iStockphoto®.

that we usually think of as representing Carnivora may well be the least successful members of the clade.

Carnivoran diversity does not end with diet, as carnivorans display a broad range in styles of locomotion, including cursorial, arboreal, fossorial, and aquatic species. Carnivorans inhabit all of the world's oceans and five of the continents, with only Australia and Antarctica lacking native terrestrial carnivorans, prior to introduction by humans. However, aquatic members of the clade have colonised those regions as well. The semi-aquatic to fully aquatic species, including otters, walruses, sea lions, and seals, have evolved systems to extract molluscs from their shells, filter krill, and mate on sea ice (Myers *et al.*, 2008). The deepest diving carnivoran, the northern elephant seal, can reach depths of over a kilometre, while its distant relative, the cheetah, can cross that distance on land in less than a minute. Arboreal forms are no less specialised, with prehensile tails evolving multiple times in carnivoran evolution, including in living kinkajous and binturongs, as well as possibly in some fossil forms (Flynn *et al.*, this volume, Chapter 2).

This last point highlights one of the primary reasons that research into carnivoran evolution is such an exciting field of scientific research: in addition to their remarkable living diversity, carnivorans have an excellent fossil record, spanning almost the whole of the Cenozoic (Flynn and Wesley-Hunt, 2005). We know of nearly three times as many extinct carnivoran genera as extant genera (approximately 355 and 129, respectively; McKenna and Bell, 1997). The precise origins of Carnivora are poorly understood, but one possibility is that they evolved from a *Cimolestes*-like ancestor, a late Cretaceous–early Paleocene insectivorous mammal. The earliest known stem carnivorans, or the first carnivoramorphans, as defined by Wyss and Flynn (1993), are from the earliest Paleocene (65–61 Mya) of North America (Fox and Youzwyshyn, 1994). These stem carnivorans are very different from the forms seen today, but they share with living carnivorans a characteristic dental modification called carnassials. Carnassials are the blade-like upper fourth premolar and lower first molar, which shear against each other for enhanced meat-slicing ability. While some of the frugivorous and folivorous carnivorans have subsequently modified their carnassials, it is the key character uniting crown group and stem carnivorans in Carnivoramorpha (Wyss and Flynn, 1993; Flynn and Wesley-Hunt, 2005; Flynn *et al.*, this volume, Chapter 2).

The relationship of Carnivora to other placental mammals

The recent proliferation of molecular phylogenetics has vastly changed our understanding of carnivoran relationships, both to other mammals and to each other. Recent studies divide placental mammals into four superorders.

Carnivora falls within the superorder Laurasiatheria, which also includes the orders Perissodactyla (horses, tapirs, and rhinoceroses), Cetartiodactyla (whales and even-toed ungulates), Chiroptera (bats), Soricomorpha (shrews and moles), and Pholidota (pangolins). The other placental mammal superorders are Euarchontaglires (primates, rodents, rabbits, tree shrews, and colugos), Afrotheria (elephants, sea cows, hyraxes, aardvarks, tenrecs, and sengis), and Xenarthra (sloths, armadillos, and anteaters). Together, Laurasiatheria and Euarchontaglires form the clade Boreoeutheria, reflecting their hypothesised northern hemisphere origin (Murphy *et al.*, 2001, 2007). Among the most surprising results of these analyses is the possibility that pangolins, scaly anteater-like mammals, are the closest living relatives to Carnivora (Murphy *et al.*, 2001).

Introduction to the major carnivoran clades and their fossil record

Stem carnivorans

The earliest fossil representatives of the living families of Carnivora appeared in the late Eocene. However, as noted above, there are many earlier fossils with the diagnostic carnassial teeth that represent the stem leading to the living families. There are two major groups of stem carnivorans: Viverravidae (not to be confused with civets in the family Viverridae) and Miacoidea. It was previously thought that feliforms evolved from viverravids, and caniforms from miacoids. However, many new well-preserved fossils of Paleocene (65–55 Mya) and Eocene (55–34 Mya) carnivorans have resolved much of the early history of the group (Wesley-Hunt and Flynn, 2005).

Viverravids (Figure 1.3) are probably the most basal group of Carnivoramorpha and were small- to medium-sized terrestrial animals that incorporated insects as a large part of their diet (Flynn *et al.*, this volume, Chapter 2). Miacoidea is a group of terrestrial and arboreal early carnivoramorphan species that appear to represent a series of intermediate forms between the more basal viverravids and the true (=crown clade) carnivorans. New fossils support a single origin of the living carnivoran families from 'Miacoidea', which suggests that the living families may have separated almost 15 million years later than previously thought, although the precise interrelationships are still contentious (Wesley-Hunt and Flynn, 2005; Polly *et al.*, 2006; Flynn *et al.*, this volume).

By the late Paleocene (61–55 Mya), viverravids and miacoids are known from Asia and North America, spreading to Europe by the early Eocene (55–49 Mya). Both Viverravidae and 'Miacoidea' were extinct by the late Eocene (37–34 Mya). Also in the late Eocene (37–34 Mya), the first representatives of several
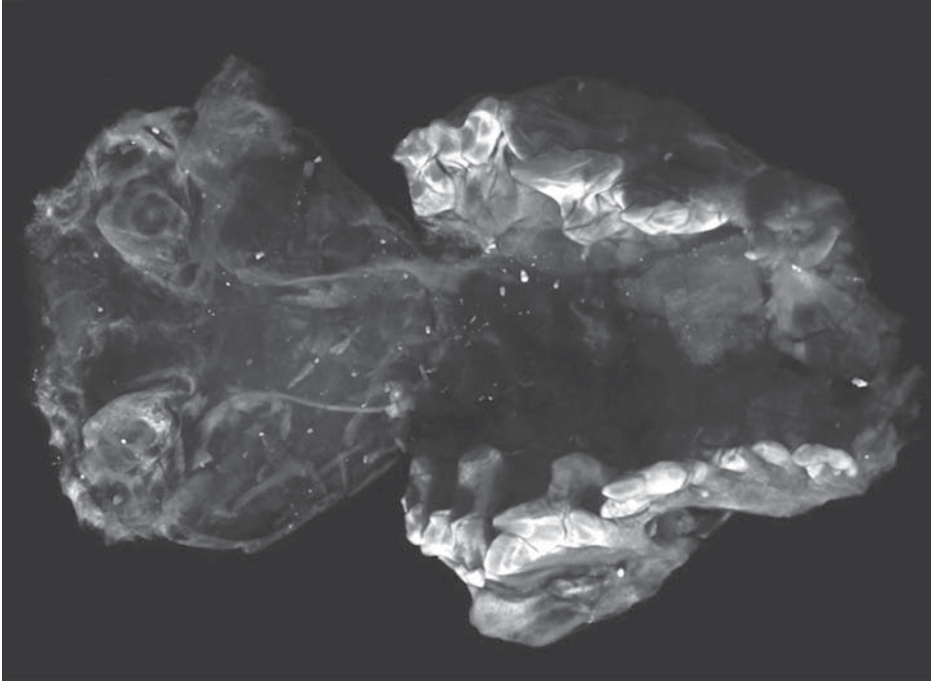
Figure 1.3 Viverravidae. Ventral view of a computerised microtomography rendering of the cranium of *Viverravus acutus* (UM 67326) from the Early Eocene of the Bighorn Basin, Wyoming (Polly *et al.*, 2006). Rendering by G. R. Davis, Queen Mary, University of London, using Drishti Volume Exploration and Presentation Tool (A. Limaye, Australia National University).

crown group carnivoran families (Canidae, Mustelidae, Ursidae, Amphicyonidae, and Nimravidae) appear on the northern continents, discussed in more detail below; however, modern feliform families do not appear until the Oligocene (34–24 Mya). Carnivorans do not invade the southern continents (Africa and South America) until the Miocene (24–5 Mya). While all caniform families have a global distribution, feliforms, except for Nimravidae and Felidae, are largely restricted to the Old World throughout their history (Flynn and Wesley-Hunt, 2005).

Feliformia (Figure 1.1)

Feliforms are often thought of as less diverse than caniform carnivorans, although there is little support for this view in terms of modern taxonomic diversity; there are 56 extant feliform genera and 73 extant caniform genera (Myers *et al.*, 2008). However, when extinct genera are included, caniforms far

outnumber feliforms, with 244 extinct caniform genera to 76 extinct feliform genera, if nimravids are included with feliforms (McKenna and Bell, 1997). This difference in taxonomic diversity is often coupled with the idea that feliforms are also ecologically and morphologically less diverse, perhaps driven by the observation that domestic cat breeds have a more limited range of variation than domestic dog breeds (Wayne, 1986). However, while feliforms lack the ecological and morphological breadth represented by some caniforms, particularly pinnipeds, there is much unappreciated diversity in feliforms.

Felidae

The most speciose feliform clade is, perhaps surprisingly, Felidae, with 41 extinct and extant genera (McKenna and Bell, 1997; Myers *et al.*, 2008). Felids are generally hypercarnivorous, with some of their distinguishing features including a short, blunt rostrum, retractable claws, well developed carnassials, and reduction of the postcarnassial dentition. The earliest records of felids are from the Oligocene of Eurasia, but in the Miocene, felids expand their range to include every continent other than the isolated Australia, Antarctica, and South America (which they quickly invaded following the formation of the isthmus of Panama in the late Pliocene) (Marshall *et al.*, 1982; McKenna and Bell, 1997; Flynn and Wesley-Hunt, 2005).

Extant felids (Figure 1.1a) are perhaps some of the rarest and most captivating of animals, being generally solitary, stalking predators with exquisite camouflage. Extinct felids are comparably fascinating, including some of the most popular fossils, machairodontine sabre-toothed cats (Figure 1.1b). However, felid diversity is often dismissed with the observation that lions are essentially scaled-up house cats (Wayne, 1986; Sears *et al.*, 2007). While there is certainly some truth to this generalisation, Benoit (this volume, Chapter 6) and Lewis and Lague (this volume, Chapter 14) demonstrate that felid allometry is not as straightforward as previously thought.

Viverridae

After Felidae, the most taxonomically diverse feliforms are the much-revised Viverridae, with 28 recognised genera (McKenna and Bell, 1997), even after removal of taxa now incorporated in the families Nandiniidae (West African palm civet), Prionodontidae (Asian linsangs), Herpestidae (mongooses), and Eupleridae (Malagasy carnivorans), as discussed by Veron (this volume, Chapter 3). As its long history as a wastebasket taxon suggests, Viverridae is a group of relatively generalised, medium-sized carnivorans restricted to the Old World. Civets have well-developed carnassials and long, pointed snouts, and one of their most distinguishing characters is the presence of a perineal gland.

Most are arboreal and nocturnal, feeding on a variety of small vertebrates and invertebrates, but there are some interesting specialisations within this clade. Many of the palm civets (Paraxodurinae) are primarily frugivorous and highly arboreal, and, as noted above, one member of this clade, *Arcticis binturong* (Figure 1.1c), has evolved a prehensile tail (Myers *et al.*, 2008). Viverrids have a lengthy fossil record, first appearing in Eurasia in the Oligocene before spreading into Africa in the Miocene (McKenna and Bell, 1997; Flynn and Wesley-Hunt, 2005).

Hyaenidae

Hyaenidae is the next most speciose feliform clade, with 20 extinct genera representing a far greater taxonomic diversity than the 4 extant genera, all of which are now confined to Africa and South to Southwest Asia (McKenna and Bell, 1997; Myers *et al.*, 2008). The first hyaenids appear in the early Miocene of Europe and Africa, quickly moving to Asia by the middle Miocene, and briefly invading North America in the late Pliocene (McKenna and Bell, 1997; Flynn and Wesley-Hunt, 2005). While many of the extinct hyaenids were bone-crackers, similar to the better-known modern species (Figure 1.1d), some converge on canid morphologies, possibly occupying a similar niche to that of modern dogs in the Miocene and Pliocene of Eurasia and Africa (Werdelin, 1996b; Van Valkenburgh, 2007). The only hyaenid to make it to North America, *Chasmaporthetes*, was one of these 'hunting hyaenas', with a more canid-like stance and dentition well adapted for cursoriality and pursuit predation (Berta, 1981).

One of the most unusual living feliforms is a hyaenid, *Proteles cristata*, the aardwolf. In contrast to the massive molars observed in most hyaenids, the aardwolf has drastically reduced their postcanine dentition to a variable number of peg-like premolars and molars. Aardwolves eat termites almost exclusively, a specialisation that is reflected in its reduced dentition, broad tongue, sticky saliva, and small body size (Wozencraft, 2005). There is disagreement on the divergence date of aardwolfs from the other modern hyaena species, with estimates ranging from the middle to late Miocene (Werdelin and Solounias, 1991; Koepfli *et al.*, 2006), but it certainly represents an extreme shift in ecology and morphology from its hypercarnivorous ancestors.

Herpestidae

Herpestidae, a clade of relatively small and primarily African feliforms, has 14 extant and only a single extinct genus. Most herpestids are carnivorous, feeding on a variety of small vertebrates and insects, although they are often associated with the ability of some species to kill snakes. The social mongooses

(Figure 1.1e), several closely related genera of herpestids, are well known for having evolved complex social systems, most famously *Suricata suricatta*, the meerkat (Flynn *et al.*, 2005; Myers *et al.*, 2008), although many other herpestids are solitary. Some species, including meerkats, are semi-fossorial, while others are semi-aquatic, such as *Atilix paludinosis*, the marsh mongoose. For the most part, herpestids are terrestrial and relatively generalised, although agile, carnivores (Myers *et al.*, 2008).

With their similarly long, pointed snouts, herpestids were originally considered a subclade of Viverridae. In fact, herpestids are most closely related to the Malagasy carnivorans and to hyaenids (Veron, Chapter 3; Flynn *et al.*, Chapter 2). Herpestids first appear in the early Miocene of Europe and Africa, moving into Asia by the late Miocene (McKenna and Bell, 1997; Flynn and Wesley-Hunt, 2005).

Eupleridae

The Malagasy carnivorans, Eupleridae, include several genera that were originally included in Herpestidae, commonly described as Malagasy mongooses, as well as three taxa that were included in Viverridae (Myers *et al.*, 2008). The cat-like *Cryptoprocta ferox* (Figure 1.1f) and the vermivorous and insectivorous *Eupleres goudotii* are some of the unusual forms that have evolved during this clade's long isolation on Madagascar, and their divergence from Herpestidae has been estimated to around 18–24 million years ago (Yoder *et al.*, 2003).

Nandiniidae

The most basal extant feliform clade is also the smallest, Nandiniidae. With only a single species, this taxon was previously, unsurprisingly, placed in Viverridae (Veron, this volume, Chapter 3). Recent molecular analyses confirm its basal position among extant feliform clades, although its primitive bullar and basicranial morphology had already hinted to many workers that it did not belong with viverrids (Hunt, 1987). Neither Nandiniidae nor Eupleridae have a pre-Recent fossil record.

Nimravidae

Nimravidae is a wholly extinct clade of large, cat-like predators that have often been identified as basal feliforms, but alternatively as stem carnivorans or stem caniforms (Flynn *et al.*, this volume, Chapter 2). Commonly called 'false sabretoothed cats', nimravids are distinguished by their long, laterally compressed upper canines, mandibular flange, and reduced or absent m2, similar to sabretoothed felids. With approximately nine genera, nimravids are well represented in the fossil record from the late Eocene in Asia and North America, invading Europe by the Oligocene (Bryant, 1991; McKenna and Bell, 1997; Peigné, 2003;

Flynn and Wesley-Hunt, 2005). Nimravids persist in these three regions until the late Oligocene.

Barbourofelines, another clade of sabre-toothed forms with approximately five named genera, have recently been removed from Nimravidae, with suggestions that they are more closely related to Felidae (Morlo *et al.*, 2004). These specialised carnivorans are geographically widespread but temporally restricted to the Miocene. They first appear in Africa and Europe in the early Miocene, but spread to Asia and North America before going extinct at the end of the Miocene (Bryant, 1991).

Caniformia (Figure 1.2)

Turning to the other major branch of Carnivora, we encounter a few clades that are far more speciose than their feliform relatives.

Mustelidae

Mustelidae is the most taxonomically diverse carnivoran family-level clade, with 107 recognised genera, even after the exclusion of Mephitidae (skunks and stink badgers). Mustelidae presently includes many familiar and fascinating animals, including otters (Figure 1.2a), sea otters, martens, weasels, ferrets, polecats, honey badgers, wolverines, and New and Old World badgers (Myers *et al.*, 2008). Mustelids are well-represented in the fossil record from the early Oligocene, with at least 84 extinct genera. They first appear in Eurasia, spreading to North America and Africa by the late Oligocene or early Miocene (Wolsan, 1993; McKenna and Bell, 1997). Unlike raccoons, mustelids do not enter South America prior to the formation of the Panamanian land bridge in the late Pliocene (Marshall *et al.*, 1982). Studies of mustelid evolution suggest that most of their diversification has occurred in Eurasia, with multiple invasions of the other continents from that region (Koepfli *et al.*, 2008).

While most mustelids are small- to medium-sized animals, there are several large species that reach 30–40 kg, and the clade displays an order of magnitude range in body size (Finarelli and Flynn, 2006). Mustelids are generally short-faced and elongate, with short limbs. They have successfully invaded arboreal, riverine, and marine habitats, but few mustelids deviate from a carnivorous diet. They do, however, demonstrate remarkable specialisations in the acquisition and consumption of prey, with one of the most interesting being sea otters, which regularly use rocks to break open shells of their prey (Myers *et al.*, 2008).

Relationships among mustelids and other arctoid caniforms have been revised extensively in recent years, as discussed by Flynn *et al.* (Chapter 2). Mephitidae, Procyonidae, and Phocidae have all been suggested as either

subclades within Mustelidae or close relatives, although several of these controversies have been settled with new molecular data (Flynn and Nedbal, 1998; Flynn *et al.*, 2000, 2005; Koepfli *et al.*, 2008) or with total evidence analyses that incorporate the many problematic fossil taxa previously described as basal arctoids or basal musteloids (Finarelli, 2008).

Procyonidae

The closest relatives to Mustelidae appear to be raccoons (Procyonidae). This clade consists of approximately 18 genera, although only 6 are extant and the affinities of the fossil forms are highly disputed. The earliest uncontested record of procyonids comes from the early Miocene of Europe, with their appearance in North America soon after. In the late Miocene, procyonids invade South America, where they are one of the few mammalian clades to invade that island continent prior to the closure of the Panamanian isthmus (Marshall *et al.*, 1982). While the extinct Simocyoninae, from the Miocene of North America, Europe, and Asia, have been placed in Procyonidae, some argue for a closer relationship to Ailuridae (Morlo and Peigné, this volume, Chapter 4), which suggests that true procyonids never colonised Asia. Procyonids disappear from Europe by the end of the Miocene, after which they are strictly a New World clade (McKenna and Bell, 1997).

Although they are not particularly taxonomically diverse and are all medium-sized, primarily nocturnal, and at least partially arboreal, living procyonids do display interesting variation in both morphology and ecology. Perhaps the most familiar forms are the omnivorous raccoons of North America, but the South American species in particular have more specialised diets. Olingos (*Bassaricyon*) and kinkajous (*Potos*) are primarily frugivorous and highly arboreal, while coatis (*Nasua*; Figure 1.2b) are more terrestrial and insectivorous (Myers *et al.*, 2008). They also display great variation in skull shape, from very short-snouted forms like kinkajous to the long-snouted coatis. As noted above, kinkajous are also one of the two living carnivorans to bear a prehensile tail, demonstrating their highly arboreal nature.

Ailuridae

Red pandas (Figure 1.2c) and allies (Ailuridae) have often been placed in Procyonidae, and the superficial resemblance in size, general shape, and pelage is striking. However, as discussed by Morlo and Peigné (this volume, Chapter 4), molecular, morphological, and fossil evidence strongly supports ailurids as a distinct clade, and many molecular studies place Ailuridae as the sister clade to other musteloids (Mephitidae, Procyonidae, and Mustelidae; Flynn *et al.*, this volume, Chapter 2). As mentioned above, simocyonines may represent the

extinct sister clade to ailurines, which would extend the temporal range of this family to the middle Miocene. Both clades are found in Europe, North America, and Asia, although simocyonines do not extend beyond the late Miocene or early Pliocene. Ailurines are first observed in the middle Miocene of Europe and early Pliocene of North America, but are extinct in both regions by the late Pliocene and are currently found only in Asia. The fossil record of ailurids has grown extensively in recent years, with multiple new genera identified along with great extension of their geographic and temporal range (Morlo and Peigné, this volume, Chapter 4). As only one species of Ailuridae survives today, *Ailurus fulgens*, and is quite specialised for bamboo-feeding, these new fossil forms will have important implications for understanding the evolution of their unusual living relative.

Mephitidae

The last of the musteloid clades, Mephitidae (skunks and stink badgers), was only recently recognised as a separate clade from Mustelidae (Dragoo and Honeycutt, 1997; Flynn and Nedbal, 1998). Mephitids are known from the early Miocene of Europe and the late Miocene of North America, with a single genus, *Promephitis*, known from the late Miocene to early Pliocene of Asia. Skunks persist only in the New World today, but stink badgers (*Mydaus*) are found in Indonesia and the Philippines (Myers *et al.*, 2008). Like most carnivorans, mephitids invade South America as part of the Great American Biotic Interchange after the formation of the Panamanian land bridge in the late Pliocene (Marshall *et al.*, 1982; McKenna and Bell, 1997). Represented today by only 4 genera, there are 11 recognised fossil mephitid genera, primarily from Europe and North America.

Like most musteloids, mephitids are small- to medium-sized, but they generally have fairly stocky bodies, pointed snouts, and large digging claws (Figure 1.2d). Of course, mephitids are best known for the noxious odours that they produce from their anal glands when threatened, and they all bear conspicuous markings, usually white or yellow stripes or spots on a brown or black coat, to warn potential predators (Myers *et al.*, 2008). Most mephitids are omnivorous, but several species, particularly stink badgers, are primarily insectivorous, using their strong claws to dig for prey.

Pinnipedia

These four musteloid families are united with Pinnipedia (seals, sea lions, and walruses) and Ursidae (bears) in Arctoidea, although historically the exact interrelationships among arctoids have been highly contentious. A long debate has raged on the monophyly of pinnipeds, with some arguing

that Phocidae (seals) were more closely related to mustelids, while Otariidae (sea lions and fur seals) and Odobenidae (walruses) were closer to bears. More recent studies, including several molecular analyses, demonstrate that pinnipeds are monophyletic and are likely the sister clade to Musteloidea (see Flynn *et al.*, this volume, Chapter 2). Pinnipeds are a fascinating group, representing a major transition to a primarily aquatic life that is accompanied by a large radiation (Jones and Goswami, this volume, Chapter 12). Extant pinnipeds comprise 21 genera, but there are at least 48 extinct genera recognised from the late Oligocene of North America (McKenna and Bell, 1997; Deméré *et al.*, 2003). Perhaps the best known is *Enaliarctos*, which already has well-developed flippers, from the late Oligocene to early Miocene of western North America and Asia (Berta *et al.*, 1989), but a recent discovery of an early Miocene pinniped from the Canadian Arctic provides an exceptionally preserved transitional fossil. *Puijila darwini* shows several skull characters linking it to pinnipeds but has large, possibly webbed feet, and an unspecialised tail (Rybczynski *et al.*, 2009). The precise relationships among fossil forms and even extant clades are highly debated, with disagreement on the affinities of odobenids, in particular, but *Puijila* and *Enaliarctos* both provide morphological support that quadrapedal swimming was likely the primitive condition for all pinnipeds. Today, odobenids continue to use quadrapedal locomotion in the water, while phocids use hindlimb-powered swimming and otariids rely instead on their forelimbs for propulsion and manoeuvering in the water.

Odobenidae
Odobenids are today represented by only a single species, the walrus (Figure 1.2e), but there are as many as 14 extinct genera of odobenids, ranging back to the middle Miocene of Asia and North America and the early Pliocene of Europe (Deméré *et al.*, 2003). Most early odobenids do not show greatly enlarged canines and appear to have retained a more typical piscivorous diet, rather than sharing the specialisations for suction-feeding of molluscs observed in extant walruses (Berta *et al.*, 2006). Walruses are divided into two monophyletic clades: odobenines, including the extant walrus, and dusignathines. The extinct dusignathines are known only from the late Miocene to the early Pliocene of North America. Unlike modern odobenids, dusignathines show enlargement of both upper and lower canines and likely evolved suction feeding independently from odobenines (Adam and Berta, 2002). Modern walruses are highly gregarious animals confined to the Arctic region. They live primarily on ice floes and are large, conspicuous animals, where both genders bear large canines for fighting, cutting ice, and even tearing apart occasional vertebrate prey (Myers *et al.*, 2008).

Otariidae

Molecular analyses often ally Odobenidae with Otariidae (sea lions and fur seals), in the clade Otarioidea (Flynn *et al.*, 2005), although morphological analyses often prefer a topology uniting Odobenidae with Phocidae (seals) in Phocamorpha (Berta *et al.*, 2006). Otariids (Figure 1.2f) retain the most terrestrial morphology among extant pinnipeds, in that they are able to rotate their hind flippers under their bodies while on land and can only mate and breed on land, unlike phocids and odobenids. Otariids are large and gregarious, with most species displaying great sexual size dimorphism, but they are relatively uniform in ecology. Most species are generalists, eating fish, small vertebrates, and cephalopods, and, while they inhabit a broad geographic range, their requirements of land for breeding restricts them from parts of the Arctic and Antarctic where phocids flourish. With only seven extant and three extinct genera known, otariids are the least speciose of the three pinniped families. Otariids also have the latest appearance of the extant pinnipeds, with the first unambiguous otariid from the late Miocene of California. The record for crown Otariidae is even worse, with no unambiguous representatives prior to the late Pliocene or early Pleistocene. Otariids are generally split into Arctocephalinae (fur seals) and Otariinae (sea lions), although the monophyly of these groups is debated (Deméré *et al.*, 2003).

Phocidae

The last of the extant pinniped clades is Phocidae, which is the most diverse and well-represented in the fossil record. If desmatophocines are accepted as phocids (Berta *et al.*, 2006), there are approximately 24 extinct and 10 extant genera in Phocidae, with a first appearance in the early Miocene. Phocids are generally split into two clades – phocines and monachines (Davis *et al.*, 2004) – although other groupings have also been suggested (Wyss, 1988). Phocids are highly derived for aquatic life, with several species able to mate at sea and breed on ice, freeing them from the terrestrial realm. Several phocids display exceptional diving abilities, and many have evolved specialised diets, such as krill-feeding in *Lobodon carcinophaga*, large vertebrate carnivory in *Hydrurga leptonyx*, and suction feeding in *Erignathus barbatus* (Adam and Berta, 2002; Jones and Goswami, this volume, Chapter 12). Unlike otariids, both of the phocid subclades are represented in the fossil record as early as the middle Miocene of Europe and North America, although none of the extant genera appear prior to the late Pliocene. Phocids are currently distributed in all of the world's oceans, including several species that are exclusively polar, and one freshwater species in Lake Baikal.

Ursidae

The last of the arctoid caniform families is Ursidae. Bears are not a particularly speciose clade, with only five genera and eight species (Myers *et al.*, 2008). However, bears have a long and interesting fossil record, with approximately 20 extinct genera ranging back to the late Eocene of Europe and North America. While relationships are, as usual, contentious, bears and their fossil relatives are typically divided into three chronologically distinct groups: Amphicynodontinae, a likely paraphyletic group from the late Eocene to the early Oligocene of Europe, Asia, and North America; Hemicyoninae, from the early Oligocene to the late Pliocene of Asia, Europe, and North America; and Ursinae, from the early Miocene of Asia, Europe, and North America, spreading to Africa in the late Miocene and to South America in the early Pleistocene (Marshall *et al.*, 1982; Hunt, 1998).

Amphicynodontines (not to be confused with amphicyonids) are relatively small- to medium-sized dog-like animals, displaying some arboreality, but remaining relatively generalised. Hemicyonines, in contrast, evolve a larger body size and more predatory morphology and ecology, with a digitigrade stance that suggests that they were capable runners and hunted down large vertebrate prey. While the hemicyonines successfully invaded North America from Eurasia in the Miocene, potentially displacing other carnivores, such as creodonts and nimravids, these carnivorous bears disappear by the end of the Miocene, leaving their more generalised relatives to continue the bear lineage (Hunt, 1998). Ursinae is an unusual clade of large-bodied, primarily omnivorous forms (Figure 1.2g), with many species with extreme specialisations. Pandas, of course, are well known for bamboo feeding, while sloth bears feed primarily on ants and termites. Spectacled bears are more frugivorous, and polar bears are entirely carnivorous. Thus, for a clade of only eight living species, bears show exceptional ecological diversity.

Among crown ursids, pandas (*Ailuropoda* and allies) are the first to diverge, with molecular clock estimates dating this split at 12 Mya (Wayne *et al.*, 1991), while the first fossil evidence of the distinct ailuropodine lineage is in the late Miocene. The first tremarctine bears, including *Arctodus*, the giant short-faced bear, and *Tremarctos*, the modern spectacled bear, also appear in the late Miocene (McKenna and Bell, 1997), with molecular clock estimates dating the split between tremarctines and ursines also in the Miocene, approximately 6 Mya. Ursini, including the rest of the extant bears (sloth bears, sun bears, polar bears, and black and brown bears), experiences its major radiation into the modern forms around the Miocene–Pliocene boundary (Wayne *et al.*, 1991; Krause *et al.*, 2008).

Canidae

The last of the extant caniform clades, Canidae (Figure 1.2g), is one of the most diverse, with approximately 47 named genera and one of the best fossil records, dating from the middle Eocene (Munthe, 1998). Canids are perhaps the most familiar of all of carnivorans, as they have invaded human homes as successfully as they have invaded every continent except Antarctica (albeit Australia with human help). Canids are a well-studied group, with three major clades providing an ideal system for studying macroevolutionary patterns (Finarelli, 2007). The earliest canids are the hesperocyonines, with at least 10 genera known from the middle Eocene to the middle Miocene of North America (Wang, 1994). While the earliest forms are small- to medium-sized, large, hypercarnivorous forms evolve during the Oligocene, with hesperocyonines achieving their maximum diversity in the late Oligocene.

The second major radiation is that of the borophagine dogs. Borophagines are also exclusively North American, with the earliest members appearing in the early Oligocene (Wang et al., 1999). However, borophagines exhibit their maximum diversity in the Miocene, during which 13 of the approximately 15 recognised genera exist. Although borophagines are typically thought of as bone-crackers, similar to modern hyaenas, this morphology really characterises the later forms that dominated in the late Miocene and Pliocene. Among the early to middle Miocene forms, several taxa show signs of hypocarnivory or omnivory, with some even suggested as primarily frugivorous. Indeed, the small-bodied borophagine *Cynarctus* was originally placed in Procyonidae based on its hypocarnivorous dentition (Wang et al., 1999). However, by the late Miocene and into the Pliocene, borophagines decline quickly, likely due to competition with canines, and the large-bodied carnivorous or bone-cracking forms are the last of the borophagine radiation to go extinct at the end of the Pliocene (Munthe, 1998).

Canines are the last and only extant canid radiation, with approximately 13 extant and 7 extinct genera, and the only ones to expand beyond North America. Canines first appear in the early Miocene of North America, spreading to Europe in the late Miocene, then to Africa and Asia in the Pliocene. They do not colonise South America until the late Pliocene or early Pleistocene, after the emergence of the Panamanian land bridge (Marshall et al., 1982). Canine generic diversity remains low for most of the Miocene, with a pulse of diversification in the late Miocene, correlated with a decline in borophagine diversity in North America and hyaenid diversity in Eurasia, and a larger pulse, particularly in species diversification, in the early Pliocene (Munthe, 1998; Van Valkenburgh, 1999; Finarelli, 2007). Modern

canids are generally medium-sized and relatively omnivorous, with long rostra and a digitigrade stance (Figure 1.2h). They are specialised for long-distance pursuit and are generally gregarious, forming packs with complex social systems.

Amphicyonidae

The last caniform clade is the problematic Amphicyonidae, or 'bear-dogs'. This extinct clade is taxonomically diverse, with 34 genera, and a long fossil record spanning the Eocene to the Miocene (McKenna and Bell, 1997). Amphicyonids first appear in North America and Eurasia in the Eocene, only invading Africa in the Miocene. These medium- to large-bodied predators show a range of dental and locomotor morphologies similar to both canids and ursids, driving the confusion on their phylogenetic placement (Hunt, 1996). While early forms appear to be more cursorial, like canids, later amphicyonids display a more bear-like, semi-plantigrade stance, perhaps related to a trend of increasing body size that is well documented in this clade (Finarelli and Flynn, 2006).

Non-carnivoran carnivores

It is worth noting here that many other clades of mammals have also evolved carnivorous forms, allowing for many interesting studies of ecomorphology and convergence. An extinct group with particular relevance to carnivoran evolution is the order Creodonta, composed of two families, Oxyaenidae and Hyaenodontidae (McKenna and Bell, 1997). Creodonts were carnivorous mammals that were the dominant predators for much of the early Cenozoic, before going extinct in the late Miocene (~8 Mya). The largest terrestrial, mammalian carnivore was a hyaenodontid creodont, *Megistotherium osteothlastes*, with a skull length of over a metre and an estimated body size of over 800 kg (Rasmussen *et al.*, 1989). Creodonts share carnassials with carnivorans, suggesting common ancestry, although this interpretation is heavily debated. However, the molars of creodonts became carnassials, with no premolar carnassials, as seen in Carnivora, leaving creodonts without grinding ability on the molars. Because of the great temporal and geographic overlap between creodonts and carnivorans, one might suspect competition. However, given the rapid diversification of carnivorans into their modern range of niches, noted above, there is little evidence that creodonts suppressed early carnivoran evolution through competition (Wesley-Hunt, 2005). Instead, carnivorans may well have outcompeted creodonts (Friscia and Van Valkenburgh, this volume, Chapter 11).

Carnivory has also evolved at least three times in marsupial mammals, with perhaps even more extreme specialisations than are observed in any placental carnivoran. The South American borhyaenid marsupials evolved forms that converge on the morphology of mustelids, bears, dogs, hyaenas, and perhaps most strikingly, sabre-toothed cats. *Thylacosmilus atrox*, the sabre-toothed marsupial, goes even further than sabre-toothed felids, in evolving massive carnassials and open-rooted, evergrowing canines (Riggs, 1934). *Thylacoleo carnifex*, the marsupial lion of Australia, also shows unique specialisations, with the largest carnassials of any carnivorous mammal, and enlarged, procumbent incisors acting as canines (Argot, 2004). Unfortunately, Australia's marsupial carnivores have not fared well since the arrival of humans, with the marsupial wolf, *Thylacinus cynocephalus*, going extinct in the twentieth century. In the last chapter of this volume, Wroe (this volume, Chapter 15) uses finite element analysis to compare these marsupial predators to the more familiar placental carnivorans.

Ecomorphology and macroevolutionary patterns

Because of their living diversity and excellent fossil record, Carnivora has been the focus of many studies in recent years. As described in several chapters in this volume, some of the greatest advances in the understanding of carnivoran evolution involve resolving the relationships of the living and extinct species, providing a framework for more detailed study of their evolutionary history. These phylogenetic studies provide a solid foundation for studies of carnivoran evolution. A strong phylogenetic framework is essential to rigorous assessment of evolutionary trends, to isolate the effects of external influences from patterns that simply reflect ancestral conditions. Several studies in this volume employ recent phylogenies to assess, for example: patterns of body and brain size evolution in Carnivora (Flynn *et al.*, Chapter 2); the effects of character correlations on phylogenetic analyses (Goswami and Polly, Chapter 5); the influence of specialisation on subsequent morphological evolution (Holliday, Chapter 7); the relationship between ecology and cranial shape in aquatic carnivorans (Jones and Goswami, Chapter 12); and the relationship between habitat and limb morphology in terrestrial carnivorans (Polly, Chapter 13).

Ecomorphology and competition in particular have been studied extensively in the fossil record of carnivorans (Van Valkenburgh, 1985, 1989, 1999; Werdelin, 1996a; Wesley-Hunt, 2005). Teeth reflect diet and ecology (Lucas, 1979), and studies of fossil teeth reveal much about paleoecology and its relationship to evolutionary diversity, as many chapters in this volume discuss in detail (Werdelin and Wesley-Hunt, Chapter 8; Wesley-Hunt *et al.*, Chapter 9; Morlo

et al., Chapter 10; Friscia and Van Valkenburgh, Chapter 11). The early fossil record of carnivoran dentition shows that diversity increased rapidly in the early Cenozoic (Wesley-Hunt, 2005). Interestingly, by the late Eocene–early Oligocene, the early carnivorans had filled most of the same ecological niches occupied by living species. Although different clades are dominant at different times, entirely new forms and consequently entirely new ecological niches are rare. Even what we think of as a highly specialised morphology, sabre-toothery, evolved independently in both Felidae and Nimravidae, as well as in marsupials, discussed further below. This lack of novelty in the carnivoran record perhaps reflects the stability of prey as a food source, in contrast to the environment-driven shifts affecting herbivore diets (Van Valkenburgh, 1999).

Large hypercarnivorous forms in particular have evolved several times. Large cat-like forms have evolved in at least six different families, from short-faced bear-dogs to leopard-sized mustelids. Bone-cracking forms have evolved at least twice, in hyaenas and dogs. Wolf-like forms have evolved at least five times, in dogs, bears, red pandas, bear-dogs, and hyaenas (Van Valkenburgh, 1999, 2007). However, despite the repeated evolution of hypercarnivorous forms, it has been demonstrated that hypercarnivory is often an evolutionary dead end. Large hypercarnivores diversify quickly, but also decline and go extinct relatively quickly, often being replaced by another hypercarnivorous group. It has been suggested that this pattern is due to the increasing special-isation limiting the group's ability to generalise or expand into other niches, thus increasing their extinction risk (Van Valkenburgh, 1999; Van Valkenburgh *et al.*, 2004; Holliday, this volume, Chapter 7). Correspondingly, recent studies have shown that hypercarnivores are always less morphologically diverse than their closest non-hypercarnivorous relatives (Holliday and Steppan, 2004). Thus, while the sabre-toothed cat may be the classic image of the carnivoran radiation, the raccoon may well be the better model for success in carnivoran evolution.

Locomotor styles also reflect diversity in carnivoran paleoecology, espe-cially when there is significant dietary overlap among coexisting predators (Morlo *et al.*, this volume, Chapter 10; Polly, this volume, Chapter 13). Coexisting carnivorans in modern ecosystems can partition resources by inhabiting different locomotor niches defined by habitat (arboreal or terres-trial) or hunting style (pursuit or ambush). Studies of fossil carnivoran ecomorphology have shown that the locomotor diversity of coexisting carni-vorans is similar in fossil and Recent ecosystems (Van Valkenburgh, 1985; Andersson and Werdelin, 2003). Although the species are different, the ecological structure is similar, demonstrating that extinct taxa partitioned resources similarly to living species.

As described above, these ecological niches are not exclusive to Carnivora; several other mammalian clades have evolved carnivorous forms. Yet, while these other ecological carnivores dominate for long periods on some continents, none approach the taxonomic and ecological diversity and temporal persistence of Carnivora. Why some clades diversify and flourish while others wither is a question of interest not only for evolutionary biology, but also for conservation, and Holliday (this volume, Chapter 7) and Friscia and Van Valkenburgh (this volume, Chapter 11) touch on the answer. Specialisation for hypercarnivory in members of the order Carnivora often involves narrowing and lengthening of the carnassials into shearing blades and reduction or complete loss of post-carnassial molars. In creodonts and marsupial carnivores, all of the molars are specialised for carnivory, either through reduction of all post-carnassial dentition or, more often, modification of all of the molar teeth into carnassials. In contrast, most carnivorans retain at least some post-carnassial grinding dentition, and many of the herbivorous carnivorans, most notably the giant panda, greatly expand the grinding surface of their molars and reduce their carnassials. While all of their competitors specialised further and further towards hyper-carnivory, carnivorans never develop shearing dentition beyond the original P4/m1 carnassial pair, and this combination of shearing and grinding dentition has served Carnivora well (Van Valkenburgh, 1999). The dental flexibility conferred by the carnivoran dental arrangement may well be the secret to its success. While many carnivoran lineages have gone down the path of greater specialisation, through reduction of the post-carnassial dentition, the greater diversity of carnivorans rests with those that, morphologically and ecologically, keep their options open (Holliday, this volume, Chapter 7).

Conclusions

In closing, there are many reasons why carnivorans are one of the most interesting clades for studies of evolutionary biology. With their great taxonomic, morphological, and ecological diversity, excellent fossil record and well-studied phylogeny, they provide an ideal system for studying convergence and ecomorphology, macroevolutionary patterns, and even life history evolution. This volume brings together some of the most exciting and broad studies, using an array of methods, to examine the evolutionary history of Carnivora and, in doing so, displays the cutting edge of vertebrate palaeontology. While their obvious charisma may lead people to dismiss the focus on carnivoran evolution as better suited to the popular media, the studies in this volume provide ample evidence that Carnivora truly is a model clade for macroevolutionary studies.

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REFERENCES

Adam, P. J. and Berta, A. (2002). Evolution of prey capture strategies and diet in the pinnipedimorpha (mammalia, carnivora). *Oryctos*, **4**, 83–107.

Andersson, K. and Werdelin, L. (2003). The evolution of cursorial carnivores in the Tertiary: implications of elbow-joint morphology. *Proceedings of the Royal Society of London, B*, **270**, s163–65.

Argot, C. (2004). Evolution of South American mammalian predators (Borhyaenoidea): anatomical and palaeobiological implications. *Zoological Journal of the Linnean Society*, **140**, 487–521.

Berta, A. (1981). The Plio-Pleistocene hyaena *Chasmaporthetes ossifragus* from Florida. *Journal of Vertebrate Paleontology*, **1**, 341–56.

Berta, A., Ray, C. E. and Wyss, A. R. (1989). Skeleton of the oldest known pinniped, *Enaliarctos mealsi*. *Science*, **244**, 60–62.

Berta, A., Sumich, J. L. and Kovacs, K. (2006). *Marine Mammals: Evolutionary Biology*, 2nd ed. Amsterdam: Elsevier.

Bryant, H. N. (1991). Phylogenetic relationships and systematics of the Nimravidae (Carnivora). *Journal of Mammalogy*, **72**, 56–78.

Davis, C. S., Delisle, I., Stirling, I., Siniff, D. B. and Strobeck, C. (2004). A phylogeny of the extant Phocidae inferred from complete mitochondrial DNA coding regions. *Molecular Phylogenetics and Evolution*, **33**, 363–77.

Deméré, T. A., Berta, A. and Adam, P. J. (2003). Pinnipedimorph evolutionary biogeography. *Bulletin of the American Museum of Natural History*, **279**, 32–76.

Dragoo, J. W. and Honeycutt, R. L. (1997). Systematics of mustelid-like carnivores. *Journal of Mammalogy*, **78**, 426–43.

Finarelli, J. A. (2007). Mechanisms behind active trends in body size evolution in the Canidae (Carnivora: Mammalia). *American Naturalist*, **170**, 876–85.

Finarelli, J. A. (2008). A total evidence phylogeny of the Arctoidea (Carnivora: Mammalia): relationships among basal taxa. *Journal of Mammalian Evolution*, **15**, 231–54.

Finarelli, J. A. and Flynn, J. J. (2006). Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): the effects of incorporating data from the fossil record. *Systematic Biology*, **55**, 301–13.

Flynn, J. J. and Nedbal, M. A. (1998). Phylogeny of the Carnivora (Mammalia): congruence versus incompatability among multiple data sets. *Molecular Phylogenetics and Evolution*, **9**, 414–26.

Flynn, J. J. and Wesley-Hunt, G. D. (2005). Carnivora. In *The Rise of Placental Mammals: Origins and Relationships of the Major Extant Clades*, ed. D. Archibald and K. Rose. Baltimore, MD: Johns Hopkins University Press, pp. 175–98.

Flynn, J. J., Nedbal, M. A., Dragoo, J. W. and Honeycutt, R. L. (2000). Whence the red panda? *Molecular Phylogenetics and Evolution*, **17**, 190–99.

Flynn, J. J., Finarelli, J. A., Zehr, S., Hsu, J. and Nedbal, M. A. (2005). Molecular phylogeny of the Carnivora (Mammalia): assessing the impact of increased sampling on resolving enigmatic relationships. *Systematic Biology*, **54**, 317–37.

Fox, R. C. and Youzwyshyn, G. P. (1994). New primitive Carnivorans (Mammalia) from the Paleocene of Western Canada, and their bearing on relationships of the order. *Journal of Vertebrate Paleontology*, **14**, 382–404.

Holliday, J. A. and Steppan, S. J. (2004). Evolution of hypercarnivory: the effect of specialization on morphological and taxonomic diversity. *Palaeobiology*, **30**, 108–28.

Hunt, R. M. (1987). Evolution of Aelurioidea Carnivora: significance of the ventral promontorial process of the petrosal and the origin of basicranial patterns in the living families. *American Museum Novitates*, **2930**, 1–32.

Hunt, R. M. (1996). Amphicyonidae. In *The Terrestrial Eocene–Oligocene Transition in North America*, ed. D. R. Prothero and R. J. Emry. Cambridge: Cambridge University Press, pp. 476–85.

Hunt, R. M. (1998). Ursidae. In *Evolution of Tertiary Mammals of North America*, ed. C. M. Janis, K. M. Scott and L. Jacobs. Cambridge: Cambridge University Press, pp. 174–95.

Koepfli, K.-P., Jenks, S. M., Eizirik, E., Zahirpour, T., Van Valkenburgh, B. and Wayne, R. K. (2006). Molecular systematics of the Hyaenidae: relationships of a relictual lineage resolved by a molecular supermatrix. *Molecular Phylogenetics and Evolution*, **38**, 603–20.

Koepfli, K.-P., Deere, K. A., Slater, G. J., *et al.* (2008). Multigene phylogeny of the Mustelidae: resolving relationships, tempo and biogeographic history of a mammalian adaptive radiation. *BMC Biology*, **6**, 10.

Krause, J., Unger, T., Nocon, A., *et al.* (2008). Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene–Pliocene boundary. *BMC Evolutionary Biology*, **8**, 220.

Lucas, P. W. (1979). The dental–dietary adaptations of mammals. *Neues Jahrbuch fur Geologie und Palaeontologie, Monatshefte*, **8**, 486–512.

Marshall, L. G., Webb, S. G., Sepkoski, J. J. and Raup, D. M. (1982). Mammalian evolution and the great American biotic interchange. *Science*, **215**, 1351–57.

McKenna, M. C. and Bell, S. K. (1997). *Classification of Mammals above the Species Level*. New York: Columbia University Press.

Morlo, M., Peigné, S. and Nagel, D. (2004). A new species of *Prosansansosmilus*: implications for the systematic relationships of the family Barbourofelidae new rank (Carnivora, Mammalia). *Zoological Journal of the Linnean Society*, **140**, 43–61.

Munthe, K. (1998). Canidae. In *Evolution of Tertiary Mammals of North America: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals*, ed. C. M. Janis, L. Jacobs and K. M. Scott. Cambridge: Cambridge University Press, pp. 124–43.

Murphy, W. J., Eizirik, E., Johnson, W. E., Zhang, Y. P., Ryder, O. A. and O'Brien, S. J. (2001). Molecular phylogenetics and the origins of placental mammals. *Nature*, **409**, 614–18.

Murphy, W. J., Pringle, T. H., Crider, T. A., Springer, M. S. and Miller, W. (2007). Using genomic data to unravel the root of the placental mammal phylogeny. *Genome Research*, **17**, 413–21.

Myers, P., Espinosa, R., Parr, C. S., Jones, T., Hammond, G. S. and Dewey, T. A. (2008). The animal diversity web (http://animaldiversity.ummz.umich.edu/).

Peigné, S. (2003). Systematic review of European Nimravinae (Mammalia, Carnivora, Nimravidae) and the phylogenetic relationships of Palaeogene Nimravidae. *Zoologica Scripta*, **32**, 199–229.

Polly, P. D., Wesley-Hunt, G. D., Heinrich, R. E., Davis, G. and Houde, P. (2006). Earliest know carnivoran auditory bulla and support for a recent origin of crown-group carnivora (Eutheria, Mammalia). *Palaeontology*, **49**, 1019–27.

Rasmussen, D. T., Tilden, C. D. and Simons, E. L. (1989). New specimens of the giant creodont *Megistotherium* (Hyaenodontidae) from Moghara, Egypt. *Journal of Mammalogy*, **70**, 442–47.

Riggs, E. S. (1934). A new marsupial saber-tooth from the pliocene of Argentina and its relationships to other South American predaceous marsupials. *Transactions of the American Philosophical Society*, **24**, 1–32.

Rybczynski, N., Dawson, M. R. and Tedford, R. H. (2009). A semi-aquatic mammalian carnivore from the Miocene epoch and origin of Pinnipedia. *Nature*, **458**, 1021–24.

Sears, K. E., Goswami, A., Flynn, J. J. and Niswander, L. (2007). The correlated evolution of *runx2* tandem repeats and facial length in carnivora. *Evolution and Development*, **9**, 555–65.

Van Valkenburgh, B. (1985). Locomotor diversity within past and present guilds of large predatory mammals. *Palaeobiology*, **11**, 406–28.

Van Valkenburgh, B. (1989). Carnivore dental adaptations and diet: a study of trophic diversity within guilds. In *Carnivore Behavior, Ecology, and Evolution,* ed. J. L. Gittleman. Ithaca, NY: Comstock Publishing Associates, pp. 410–36.

Van Valkenburgh, B. (1999). Major patterns in the history of carnivorous mammals. *Annual Review of Earth and Planetary Science*, **27**, 463–93.

Van Valkenburgh, B. (2007). Deja vu: the evolution of feeding morphologies in the Carnivora. *Integrative and Comparative Biology*, **47**, 147–63.

Van Valkenburgh, B., Wang, X. M. and Damuth, J. (2004). Cope's rule, hypercarnivory, and extinction in North American canids. *Science*, **306**, 101–04.

Wang, X. M. (1994). Phylogenetic systematics of the Hesperocyoninae (Carnivora: Canidae). *Bulletin of the American Museum of Natural History*, **221**, 1–207.

Wang, X. M., Tedford, R. H. and Taylor, B. E. (1999). Phylogenetic systematics of the Borophaginae (Carnivora: Canidae). *Bulletin of the American Museum of Natural History*, **243**, 1–391.

Wayne, R. K. (1986). Cranial morphology of domestic and wild canids: the influence of development on morphological change. *Evolution*, **40**, 243–61.

Wayne, R. K., Van Valkenburgh, B. and O'Brien, S. J. (1991). Molecular distance and divergence time in carnivores and primates. *Molecular Biology and Evolution*, **8**, 297–319.

Werdelin, L. (1996a). Carnivoran ecomorphology: a phylogenetic perspective. In *Carnivore Behavior, Ecology, and Evolution*, ed. J. L. Gittleman. Ithaca, NY: Cornell University Press, pp. 582–624.

Werdelin, L. (1996b). Community-wide character displacement in Miocene hyaenas. *Lethaia*, **29**, 97–106.

Werdelin, L. and Solounias, N. (1991). The Hyaenidae: taxonomy, systematics, and evolution. *Lethaia*, **30**, 1–105.

Wesley-Hunt, G. D. (2005). The morphological diversification of carnivores in North America. *Palaeobiology*, **31**, 35–55.

Wesley-Hunt, G. D. and Flynn, J. J. (2005). Phylogeny of the Carnivora: basal relationships among the carnivoramorphans, and assessment of the position of 'Miacoidea' relative to crown-clade carnivora. *Journal of Systematic Palaeontology*, **3**, 1–28.

Wolsan, M. (1993). Phylogeny and classification of early European Mustelida (Mammalia: Carnivora). *Acta Theriologica*, **38**, 345–84.

Wozencraft, W. C. (2005). Order Carnivora. In *Mammal Species of the World – A Taxonomic and Geographic Reference*, ed. D. E. Wilson and D. M. Reeder. Baltimore, MD: Johns Hopkins University Press, pp. 532–628.

Wyss, A. R. (1988). On 'retrogression' in the evolution of the Phocinae and phylogenetic affinities of the monk seals. *American Museum Novitates*, **2924**, 1–38.

Wyss, A. R. and Flynn, J. J. (1993). A phylogenetic analysis and definition of the Carnivora. In *Mammal Phylogeny*, ed. F. S. Szalay, M. J. Novacek and M. C. McKenna. New York: Springer Verlag, pp. 32–52.

Yoder, A. D., Burns, M. M., Zehr, S., *et al.* (2003). Single origin of Malagasy Carnivora from an African ancestor. *Nature*, **421**, 734–37.