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

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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®.

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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.

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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

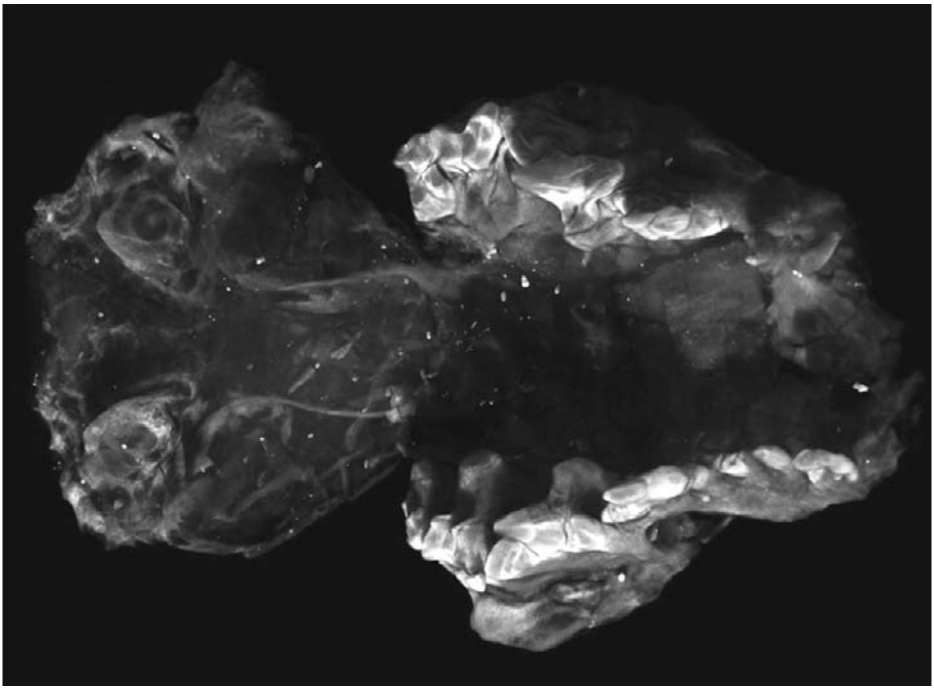

Figure 1.3 Viverravidae. Ventral view of a computerised microtomography rendering of the cranium of *Viverravus acutus* (UM 67326) from the Early Eocene of the Bighorn Basin, Wyoming (Polly *et al.*, 2006). Rendering by G. R. Davis, Queen Mary, University of London, using Drishti Volume Exploration and 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

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(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 sabre-toothed cats', nimravids are distinguished by their long, laterally compressed upper canines, mandibular flange, and reduced or absent m2, similar to sabre-toothed 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