



Studies and reconstructions of dire wolf (*Canis dirus*) and Grey wolf (*Canis lupus*) from late Pleistocene Rancholebre Tarpits, Los Angeles, California. Illustration by Pat Ortega.

## CHAPTER 2

# Ancestry

## Evolutionary history, molecular systematics, and evolutionary ecology of Canidae

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The evolutionary history of canids (Family Canidae) is a history of successive radiations repeatedly occupying a broad spectrum of niches ranging from large, pursuit predators to small omnivores, or even to herbivory. Three such radiations were first recognized by Tedford (1978), each represented by a distinct subfamily (Fig. 2.1). Two archaic subfamilies, Hesperocyoninae and Borophaginae, thrived in the middle to late Cenozoic from about 40 to 2 million years ago (Ma) (Wang 1994; Wang *et al.* 1999). All living canids belong to the final radiation, Subfamily Caninae, which achieved their present diversity only in the last few million years (Tedford *et al.* 1995).

Canids originated more than 40 Ma in the late Eocene of North America from a group of archaic carnivorans, the Miacidae (Wang and Tedford 1994, 1996). They were confined to the North American continent during much of their early history, playing a wide range of predatory roles that encompass those of the living canids, procyonids, hyaenids, and possibly felids. By the latest Miocene (about 7–8 Ma), members of the Subfamily Caninae were finally able to cross the Bering Strait to reach Europe (Crusafont-Pairó 1950), commencing an explosive radiation and giving rise to the modern canids of the Old World. At the formation of the Isthmus of Panama, 3 Ma, canids arrived in South America and quickly established themselves as one of the most diverse groups of carnivorans on the continent (Berta 1987, 1988). With the aid of humans, *Canis lupus dingo* was transported to Australia late in the Holocene. Since that time, canids have become truly worldwide predators, unsurpassed in distribution by any other group of carnivorans.

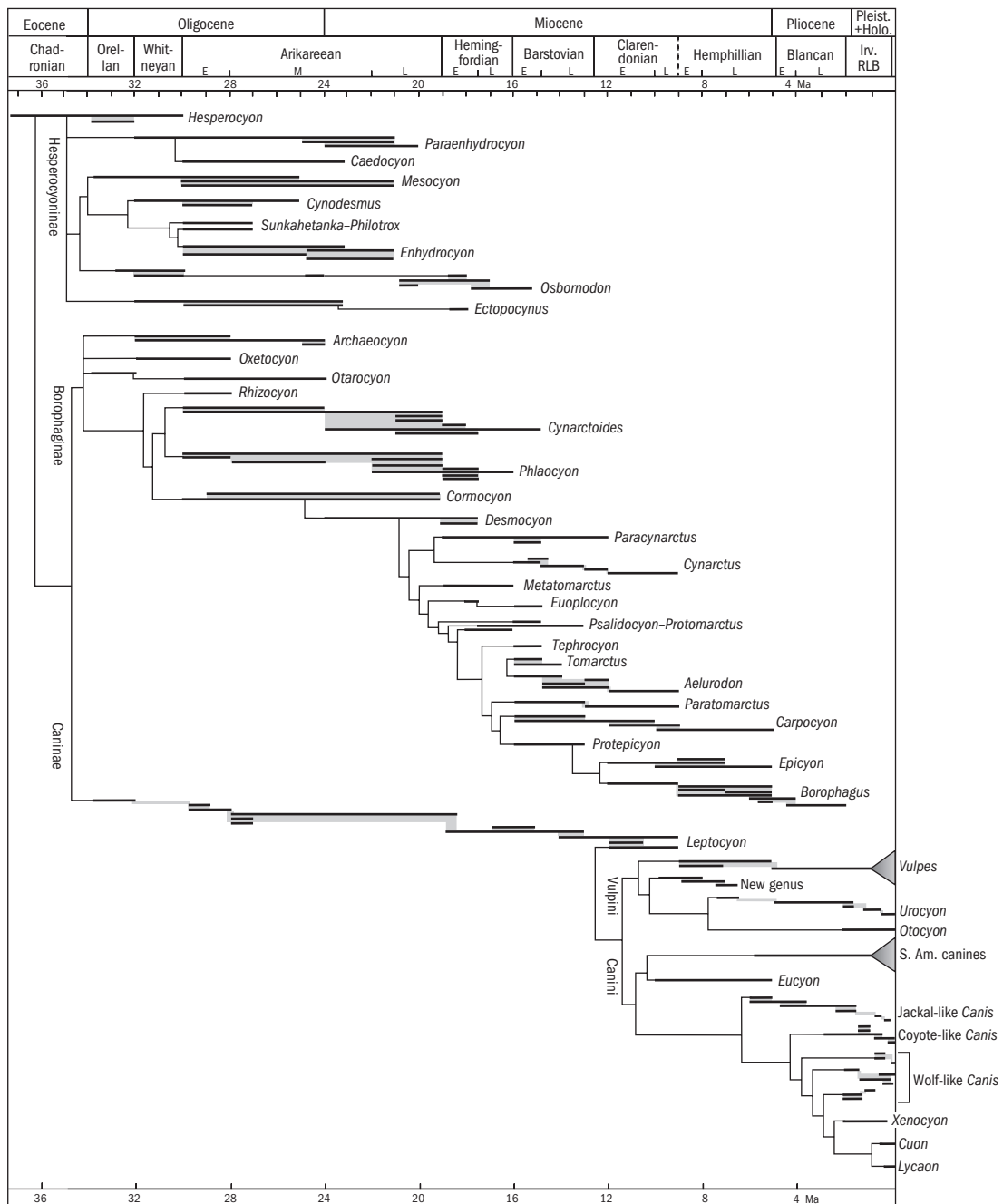
Here, in the context of this volume on the modern canids, we place more emphasis on the subfamily Caninae, the latest of the three successive radiations of the Canidae. We do not attempt to cite all of the references in canid palaeontology and systematics, most of which have been summarized in the papers that we cite at the end of each section. Certain phylogenetic relationships of the Caninae are controversial, as reflected in the different conclusions reached on the basis of evidence from palaeontological/morphological or molecular research as presented below.

### What is a canid?

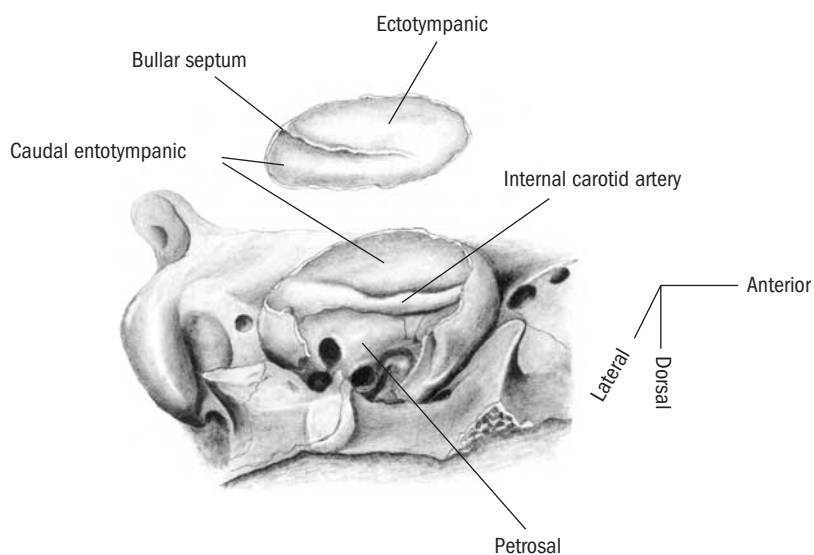
Canids possess a pair of carnassial teeth (the upper fourth premolar and lower first molar) in the form of a shearing device, and thus belong to the Order Carnivora. Within the Carnivora, canids fall into the Suborder Caniformia, or dog-like forms. The Caniformia are divided into two major groups that have a sister relationship: Superfamily Cynoidea, which includes Canidae, and Superfamily Arctoidea, which include the Ursidae, Ailuridae, Procyonidae, and Mustelidae, as well as the aquatic Pinnipedia and the extinct Amphicyonidae.

As a cohesive group of carnivorans, living canids are easily distinguished from other carnivoran families. Morphologically there is little difficulty in recognizing living canids with their relatively uniform and unspecialized dentitions. However, the canids as exemplified by the living forms are narrowly defined. Only a small fraction of a once diverse group has

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**Figure 2.1** Simplified phylogenetic relationships of canids at the generic level. Species ranges are indicated by individual bars enclosed within grey rectangles, detailed relationships among species in a genus is not shown. Relationships for the Hesperocyoninae is modified from Wang (1994, fig. 65), that for the Borophaginae from Wang *et al.* (1999, fig. 141), and that for the Caninae from unpublished data by Tedford *et al.*



**Figure 2.2** Ventrolateral view of basicranial morphology of a primitive canid, *Hesperocyon gregarius*, showing bullar composition and position of the internal carotid artery (see text for explanations). The ventral floor of the bulla is dissected away (isolated oval piece on top) to reveal the middle ear structures inside the bulla and the internal septum. Modified from Wang and Tedford (1994, fig. 1).

survived to the present day (Fig. 2.1). Canids in the past had departed from this conservative pattern sufficiently that paleontologists had misjudged some canids as procyonids. Similarly the extinct bear-dog Family Amphicyonidae, which belongs to the Arctoidea, is often placed within the Canidae, because of its unspecialized dentition.

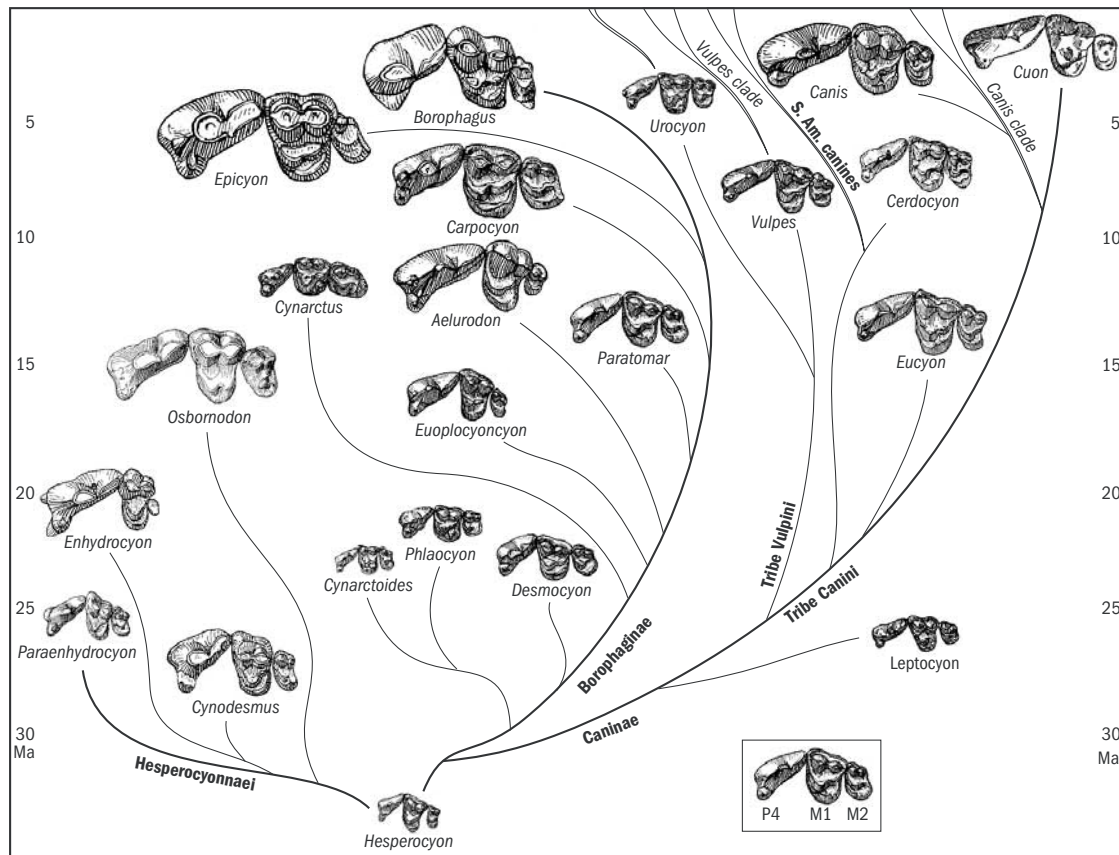
How do we know a canid when we see one? A key region of the anatomy used to define canids is the middle ear region, an area that distinguishes most families of carnivorans (Hunt 1974), perhaps as a result of a widespread trend of ossifying bullar elements in independent lineages. Canids are characterized by an inflated entotympanic bulla that is divided by a partial septum along the entotympanic and ectotympanic suture (Fig. 2.2). Other features characteristic of canids is the loss of a stapedial artery and the medial position of the internal carotid artery that is situated between the entotympanic and petrosal for most of its course and contained within the rostral entotympanic anteriorly (Wang and Tedford 1994). These basicranial characteristics have remained more or less stable throughout the history of canids, allowing easy identification in the fossil record when these structures are preserved.

## Evolutionary history

Among the living families within the Order Carnivora, the Canidae are the most ancient. The family arose in the late Eocene, when no other living families of carnivorans had yet emerged (two archaic families, Miacidae and Viverravidae, have a much older history but none survive to the present time). Furthermore, canids still maintain some features that are primitive among all carnivorans, to the extent that dog skulls are often used to illustrate a generalized mammal in zoological classrooms. Dentally, canids are closest to the ancestral morphotype of Carnivora. Canids have a relatively unreduced dental formula of 3142/3143 [numbers in sequence represent incisors, canines, premolars, and molars in the upper (left half before the oblique) and the lower (right half after the oblique) teeth] and relatively unmodified molars except for the morphology of the carnassials (P4, m1) typical of all carnivorans. In contrast, all other carnivoran families generally have a more reduced dental formula and highly modified cusp patterns.

From this mesocarnivorous (moderately carnivorous) conservative plan, canids generally evolve towards a hypercarnivorous (highly carnivorous) or hypocarnivorous (slightly carnivorous) dental pattern. In the hypercarnivorous pattern (Fig. 2.4(b,d))

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**Figure 2.3** Dental evolution of representative canids as shown in upper cheek teeth (P4–M2). Generally the most derived species in each genus is chosen to enhance a sense of dental diversity. Species in the Hesperocyoninae are: *Hesperocyon gregarius*; *Paraenhydrocyon josephi*; *Cynodesmus martini*; *Enhydrocyon crassidens*; and *Osbornodon fricki*. Species in the Borophaginae are: *Cynarctoides acridens*; *Phlaocyon marslandensis*; *Desmocyon thomsoni*; *Cynarctus crucidens*; *Euoplocyon brachygnathus*; *Aelurodon stirtoni*; *Paratomarctus temerarius*; *Carpocyon webbi*; *Epicyon haydeni*; and *Borophagus diversidens*. Species in the Caninae are: *Leptocyon gregorii*; *Vulpes stenognathus*; *Urocyon minicephalus*; *Cerdocyon thous*; *Eucyon davisii*; *Canis dirus*; and *Cuon alpinus*. All teeth are scaled to be proportional to their sizes.

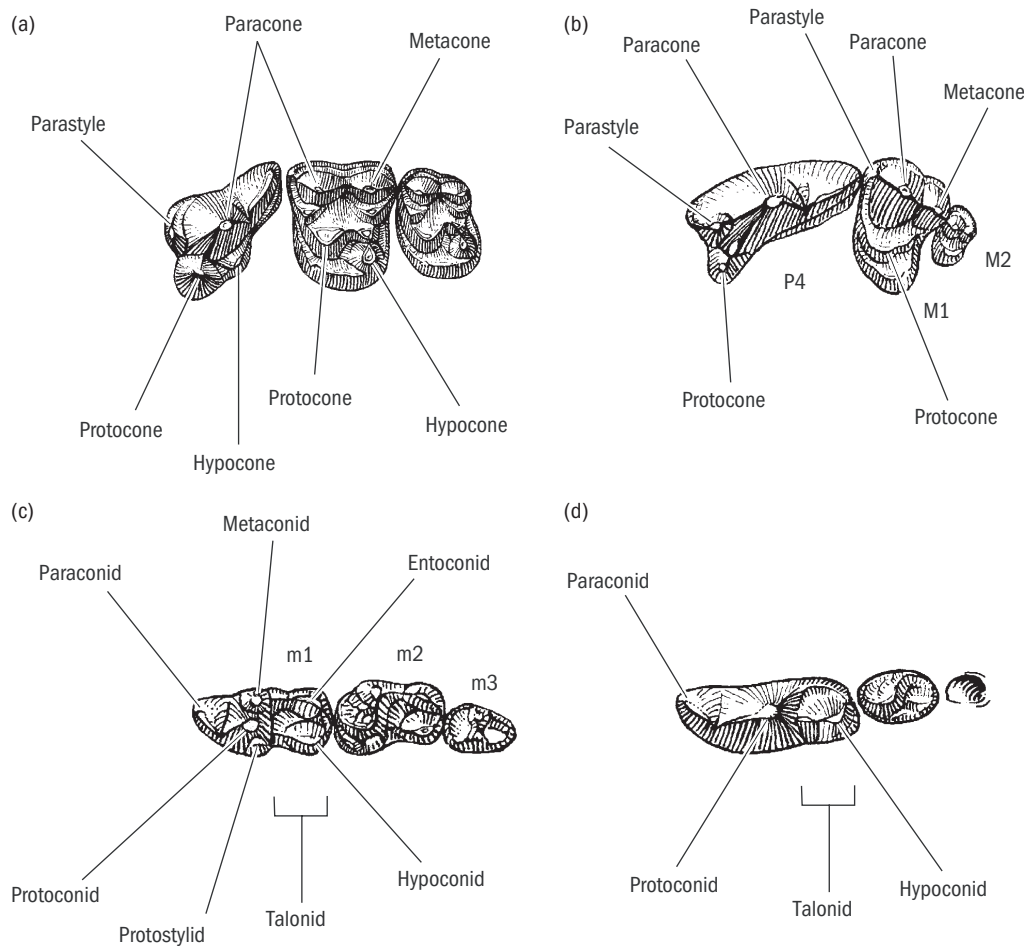
there is a general tendency to increase the size of the carnassial pair at the expense of the molars behind (see *Enhydrocyon*, *Aelurodon*, *Borophagus*, and *Cuon* in Fig. 2.3). This modification increases the efficiency of carnassial shear. A hypocarnivorous pattern (Fig. 2.4(a,c)) is the opposite, with development of the grinding part of the dentition (molars) at the expense of carnassial shear (see *Cynarctoides*, *Phlaocyon*, and *Cynarctus* in Fig. 2.3). This configuration was only possible in the sister-taxa Borophaginae and Caninae, which share a bicuspid m1 talonid (Fig. 2.4(c)). One of the major trends in canid evolution is the repeated

development of hyper- and hypocarnivorous forms (see below).

### Hesperocyoninae

The Subfamily Hesperocyoninae is the first major clade with a total of 28 species. Its earliest members are species of the small fox-like form, *Hesperocyon*, that first appears in the late Eocene (Duchesnean, 37–40 Ma) (Bryant 1992) and became abundant in the latest Eocene (Chadronian). By Oligocene time





**Figure 2.4** Hypercarnivorous (b, *Aelurodon* and d, *Euoplocyon*) and hypocarnivorous (a, *Phlaocyon* and c, *Cynarctus*) dentitions. In hypercarnivorous forms, the upper cheek teeth (b) tend to emphasize the shearing part of the dentition with an elongated and narrow P4, an enlarged parastyle on a transversely elongated M1, and a reduced M2. On the lower teeth (d), hypercarnivory is exemplified by a trenchant talonid due to the increased size and height of the hypoconid at the expense of the entoconid (reduced to a narrow and low ridge), accompanied by the enlargement of the protoconid at the expense of the metaconid (completely lost in *Euoplocyon*) and the elongation of the trigonid at the expense of the talonid. In hypocarnivorous forms, on the other hand, the upper teeth (a) emphasize the grinding part of the dentition with a shortened and broadened P4 (sometimes with a hypocone along the lingual border), a reduced parastyle on a quadrate M1 that has additional cusps (e.g. a conical hypocone along the internal cingulum) and cuspules, and an enlarged M2. The lower teeth (c) in hypocarnivorous forms possess a basined (bicuspid) talonid on m1 enclosed on either side by the hypoconid and entoconid that are approximately equal in size. Other signs of hypocarnivory on the lower teeth include widened lower molars, enlarged metaconids, and additional cuspules such as a protostylid.

(Orellan and Whitney, 34–30 Ma), early members of four small clades of the hesperocyonines had emerged: *Paraenhydrocyon*, *Enhydrocyon*, *Osbornodon*, and *Ectopocynus*. Hesperocyonines experienced their maximum diversity of 14 species during the late Oligocene (early Arikarean in 30–28 Ma), and

reached their peak predatory adaptations (hypercarnivory) in the earliest Miocene (late Arikarean) with advanced species of *Enhydrocyon* and *Paraenhydrocyon*. The last species of the subfamily, *Osbornodon fricki*, became extinct in the early Barstovian (15 Ma), reaching the size of a small wolf.

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With the exception of the *Osbornodon* clade, which acquired a bicuspid m1 talonid, hesperocyonines are primitively hypercarnivorous in dental adaptations with tendencies towards reduced last molars and trenchant (single cusped) talonid heels on the lower first molar. Although never reaching the extremes seen in the borophagines, hesperocyonines had modest development of bone cracking adaptations in their strong premolars. At least three lineages, in all species of *Enhydrocyon* and in terminal species of *Osbornodon* and *Ectopocynus*, have independently evolved their own unique array of bone cracking teeth. Hesperocyonines did not experiment with hypocarnivory.

Members of this subfamily were the topic of a monograph by Wang (1994). Two additional species of *Osbornodon* have since been added to the subfamily (Hayes 2000; Wang in press). The evolutionary transition from plantigrade to digitigrade standing posture in early canids was explored by Wang (1993). A hereditary condition, osteochondroma, in the postcrania of early canids was documented by Wang and Rothschild (1992).

### Borophaginae

From the primitive condition of a trenchant talonid heel on the lower first molar seen in the hesperocyonines, borophagines, and canines shared a basined (bicuspid) talonid acquired at the very beginning of their common ancestry (Fig. 2.4(c)). Along with a more quadrate upper first molar with its hypocone, the basined talonid establishes an ancestral state from which all subsequent forms were derived. Such a dental pattern proved to be very versatile and can readily be adapted towards either a hyper- or hypocarnivorous type of dentition, both of which were repeatedly employed by both borophagines and canines (Fig. 2.3).

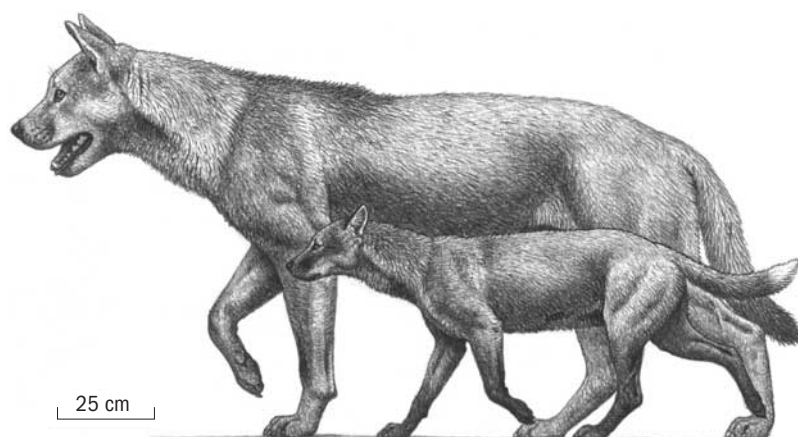
The history of the borophagines also begins with a small fox-like form, *Archaeocyon*, in the late Oligocene. Contemporaneous with larger and more predatory hesperocyonines, these early borophagines in the late Oligocene and early Miocene (Arikareean) tended to be more omnivorous (hypocarnivorous) in their dental adaptations, such as *Oxetocyon*, *Otarocyon*, and *Phlaocyon*. One extreme case, *Cynarctoides* evolved

selenodont-like molars as in modern artiodactyles, a rare occurrence of herbivory among carnivorans. These early borophagines are generally no larger than a raccoon, which is probably a good ecological model for some borophagines at a time when procyonids had yet to diversify.

After some transitional forms in the early Miocene (Hemingfordian), such as *Cormocyon* and *Desmocyon*, borophagines achieved their maximum ecological and numerical (i.e. species) diversity in the middle Miocene (Barstovian), with highly omnivorous forms, such as *Cynarctus*, that were almost ursid-like as well as highly predatory forms, such as *Aelurodon*, that were a larger version of the living African Hunting Dog *Lycaon*. By then, borophagines had acquired their unique characteristics of a broad muzzle, a bony contact between premaxillary and frontal, multicuspoid incisors, and an enlarged parastyle on the upper carnassials (modified from an enlargement of the anterior cingulum).

By the end of the Miocene, borophagines had evolved another lineage of omnivory, although only modestly in that direction, in the form of *Carpocyon*. Species of *Carpocyon* are mostly the size of jackals to small wolves. At the same time, the emergence of the genus *Epicyon* from a *Carpocyon*-like ancestor marked another major clade of hypercarnivorous borophagines. The terminal species of *Epicyon*, *E. haydeni*, reached the size of a large bear and holds record as the largest canid ever to have lived (Fig. 2.5). Closely related to *Epicyon* is *Borophagus*, the terminal genus of the Borophaginae. Both *Epicyon* and *Borophagus* are best known for their massive P4 and p4 in contrast to the diminutive premolars in front. This pair of enlarged premolars is designed for cracking bones, mirroring similar adaptations by hyaenids in the Old World. Advanced species of *Borophagus* survived the Pliocene but became extinct near the beginning of the Pleistocene.

The phylogeny and systematics of the Borophaginae were recently revised by Wang *et al.* (1999), which is the basis of above summary. Munthe (1979, 1989, 1998) analysed the functional morphology of borophagine limb bones and found a diverse array of postcranial adaptations, in contrast to the more stereotypical view that the hyaenoid dogs were non-cursorial scavengers only. Werdelin (1989) compared



**Figure 2.5** Reconstruction of *Epicyon saevus* (small individual, based on AMNH 8305) and *Epicyon haydeni* (large individual, composite figure, based on specimens from Jack Swayze Quarry). These two species co-occur extensively during the late Clarendonian and early Hemphillian of Western North America. Illustration by Mauricio Antón. (From Wang *et al.* 1999.)

the bone-cracking adaptations of borophagine canids and hyaenids in terms of evolutionary constraints within their prospective lineages.

### Caninae

As in the hesperocyonines and borophagines, a small fox-sized species of *Leptocyon* is the earliest recognized member of the subfamily Caninae. Besides sharing a bicuspid talonid of m1 and a quadrate M1 with the borophagines, *Leptocyon* is also characterized by a slender rostrum and elongated lower jaw, and correspondingly narrow and slim premolars, features that are inherited in all subsequent canines. It first appeared in the early Oligocene (Orellan) and persisted through the late Miocene (Clarendonian). Throughout its long existence (no other canid genus had as long a duration), facing intense competition from the larger and diverse hesperocyonines and borophagines, *Leptocyon* generally remains small and inconspicuous, never having more than two or three species at a time.

By the latest Miocene (Hemphillian), fox-sized niches are widely available in North America, left open by extinctions of all small borophagines. The true fox clade, Tribe Vulpini, emerges at this time and undergoes a modest diversification to initiate primitive species of both *Vulpes* and *Urocyon* (and their extinct relatives). The North American Pliocene record of *Vulpes* is quite poor. Fragmentary materials

from early Blancan indicate the presence of a Swift Fox-like form in the Great Plains. *Vulpes* species were widespread and diverse in Eurasia during the Pliocene (see Qiu and Tedford 1990), resulting from an immigration event independent from that of the *Canis* clade. Red Fox (*Vulpes vulpes*) and Arctic Fox (*Vulpes lagopus*) appeared in North America only in the late Pleistocene, evidently as a result of an immigration back to the New World.

Preferring more wooded areas, the grey fox *Urocyon* has remained in southern North America and Middle America. Records of the grey fox clade have a more or less continuous presence in North America throughout its existence, with intermediate forms leading to the living species *Urocyon cinereoargenteus*. Morphologically, the living African Bat-eared Fox *Otocyon* is closest to the *Urocyon* clade, although molecular evidence suggests that the Bat-eared Fox lies at the base of the fox clade or even lower (Geffen *et al.* 1992d; Wayne *et al.* 1997). If the morphological evidence has been correctly interpreted, then the Bat-eared fox must represent a Pliocene immigration event to the Old World independent of other foxes. A transitional form, *Protocyon*, occurs in southern Asia and Africa in the early Pleistocene.

Advanced members of the Caninae, Tribe Canini, first occur in the medial Miocene (Clarendonian, 9–12 Ma) in the form of a transitional taxon *Eucyon*. As a jackal-sized canid, *Eucyon* is mostly distinguished from the Vulpini in an expanded paroccipital process and enlarged mastoid process, and in the



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consistent presence of a frontal sinus. The latter character initiates a series of transformations in the Tribe Canini culminating in the elaborate development of the sinuses and a domed skull in *C. lupus*. By latest Miocene time, species of *Eucyon* have appeared in Europe (Rook 1992) and by the early Pliocene in Asia (Tedford and Qiu 1996). The North American records all predate the European ones, suggesting a westward dispersal of this form.

Arising from about the same phylogenetic level as *Eucyon* is the South American clade. Morphological and molecular evidence generally agrees that living South American canids, the most diverse group of canids on a single continent, belong to a natural group of their own. The South American canids are united by morphological characters such as a long palate, a large angular process of the jaw with a widened scar for attachment of the inferior branch of the medial pterygoid muscle, and a relatively long base of the coronoid process (Tedford *et al.* 1995). By the close of the Miocene, certain fragmentary materials from southern United States and Mexico indicate that taxa assignable to *Cerdocyon* (Torres and Ferrusquía-Villafraña 1981) and *Chrysocyon* occur in North America. The presence of these derived taxa in the North American late Miocene predicts that ancestral stocks of many of the South American canids may have been present in southern North America or Middle America. They appear in the South American fossil record shortly after the formation of the Isthmus of Panama in the Pliocene, around 3 Ma (Berta 1987). The earliest records are *Pseudalopex* and its close relative *Protocyon*, an extinct large hypercarnivore, from the Pliocene (Uquian, around 2.5–1.5 Ma) of Argentina. By the latest Pleistocene (Lujanian, 300,000–10,000 years ago), most living species or their close relatives have emerged, along with the extinct North American Dire Wolf, *Canis dirus*. By the end of the Pleistocene, all large, hypercarnivorous canids of South America (*Protocyon*, *Theriodictis*) as well as *C. dirus* had become extinct.

The *Canis* clade within the Tribe Canini, the most derived group in terms of large size and hypercarnivory, arises near the Miocene–Pliocene boundary between 5 and 6 Ma in North America. A series of jackal-sized ancestral species of *Canis* thrived in the early Pliocene (early Blancan), such as *Canis ferox*, *Canis lepophagus*, and other undescribed species. At

about the same time, first records of canids begin to appear in the European late Neogene: '*Canis*' *cipio* in the late Miocene of Spain (Crusafont-Pairó 1950), *Eucyon monticinensis* in the latest Miocene of Italy (Rook 1992), the earliest raccoon-dog *Nyctereutes donnezani*, and the jackal-sized *Canis adoxus* in the early Pliocene of France (Martin 1973; Ginsburg 1999). The enigmatic '*Canis*' *cipio*, only represented by parts of the upper and lower dentition, may pertain to a form at the *Eucyon* level of differentiation rather than truly a species of *Canis*.

The next phase of *Canis* evolution is difficult to track. The newly arrived *Canis* in Eurasia underwent an extensive radiation and range expansion in the late Pliocene and Pleistocene, resulting in multiple, closely related species in Europe, Africa, and Asia. To compound this problem, the highly cursorial wolf-like *Canis* species apparently belong to a circum-arctic fauna that undergoes expansions and contractions with the fluctuating climate. Hypercarnivorous adaptations are common in the crown-group of species especially in the Eurasian middle latitudes and Africa. For the first time in canid history, phylogenetic studies cannot be satisfactorily performed on forms from any single continent because of their Holarctic distribution and faunal intermingling between the new and old worlds. Nevertheless some clades were localized in different parts of Holarctica. The vulpines' major centre of radiation was in the Old World. For the canines, North America remained a centre through the Pliocene producing the Coyote as an endemic form. A larger radiation yielding the wolves, dhole, African hunting dog, and fossil relatives took place on the Eurasian and African continents. During the Pleistocene elements of the larger canid fauna invaded mid-latitude North America—the last invasion of which was the appearance of the Grey wolf south of the glacial ice sheets in the latest Pleistocene (about 100 Ka).

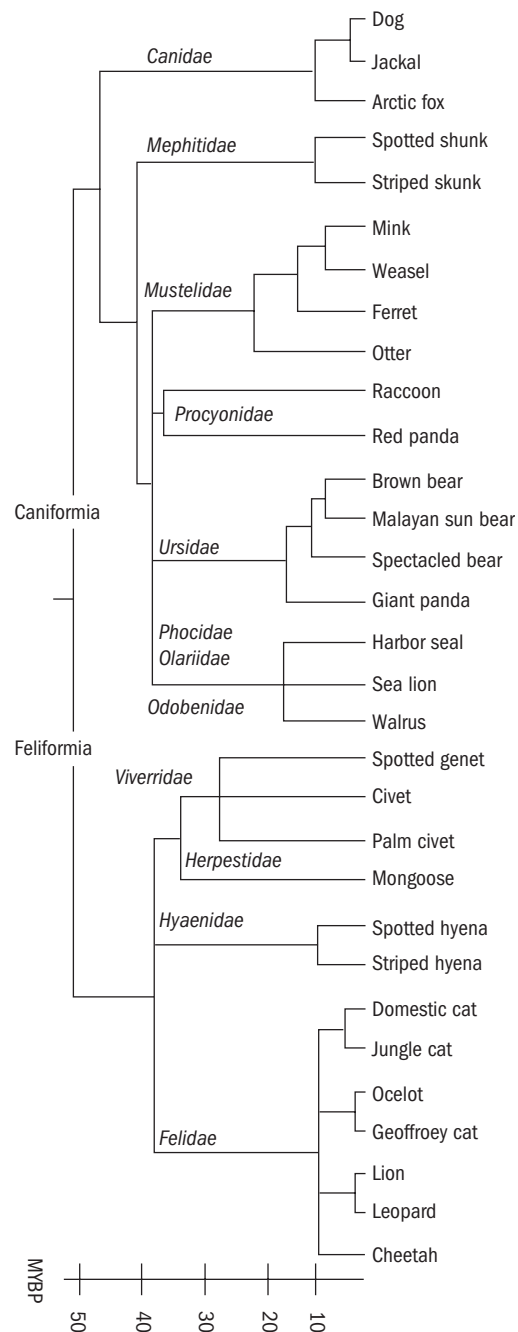
A comprehensive systematic revision of North American fossil canines by Tedford *et al.* (in preparation) forms the basis of much of the foregoing summary. As part of that revision, the phylogenetic framework as derived from living genera was published by Tedford *et al.* (1995). Nowak (1979) published a monograph on the Quaternary *Canis* of North America. Berta (1981, 1987, 1988) undertook the most recent phylogenetic analysis of the South

American canids. Rook (1992, 1994) and Rook and Torre (1996a,b) partially summarized the Eurasian canids. The African canid records are relatively poorly understood but recent discoveries promise to advance our knowledge in that continent (Werdelin, personal communication). See also citations below for recent molecular systematic studies.

## Molecular systematics

The ancient divergence of dogs from other carnivores is reaffirmed by molecular data. DNA-DNA hybridization of single copy DNA clearly shows them as the first divergence in the suborder Caniformia that includes seals, bears, weasel, and raccoon-like carnivores (Fig. 2.6). This basal placement is further supported by mitochondrial DNA sequence studies (Vrana *et al.* 1994; Slattery and Brien 1995; Flynn and Nedbal 1998), and recently studies of DNA sequences from nuclear genes (Murphy *et al.* 2001). Based on molecular clock calculations, the divergence time was estimated as 50 million years before present (Wayne *et al.* 1989). This value is consistent with the first appearance of the family in the Eocene, although it is somewhat more ancient than the date of 40 million years suggested by the fossil record (see above). Considering that first appearance dates generally post-date actual divergence dates because of the incompleteness of the record (e.g. Marshall 1977), the agreement between fossil and molecular dates is surprisingly good.

Evolutionary relationships within the family Canidae have been reconstructed using comparative karyology, allozyme electrophoresis, and mitochondrial DNA protein coding sequence data (Wayne and Brien 1987; Wayne *et al.* 1997, 1987a,b). Further, relationships at the genus level have been studied with mtDNA control region sequencing (a non-coding, hypervariable segment of about 1200 bp in the mitochondrial genome) and microsatellite loci (hypervariable single copy nuclear repeat loci) (Geffen *et al.* 1992; Bruford and Wayne 1993; Girman *et al.* 1993; Gottelli *et al.* 1994; Vilà *et al.* 1997, 1999). The protein-coding gene phylogeny, which is largely consistent with trees based on other genetic approaches, shows that the wolf genus *Canis* is a monophyletic group that also includes the Dhole or Asian Wild Dog (*Cuon alpinus*). The Grey wolf, coyote

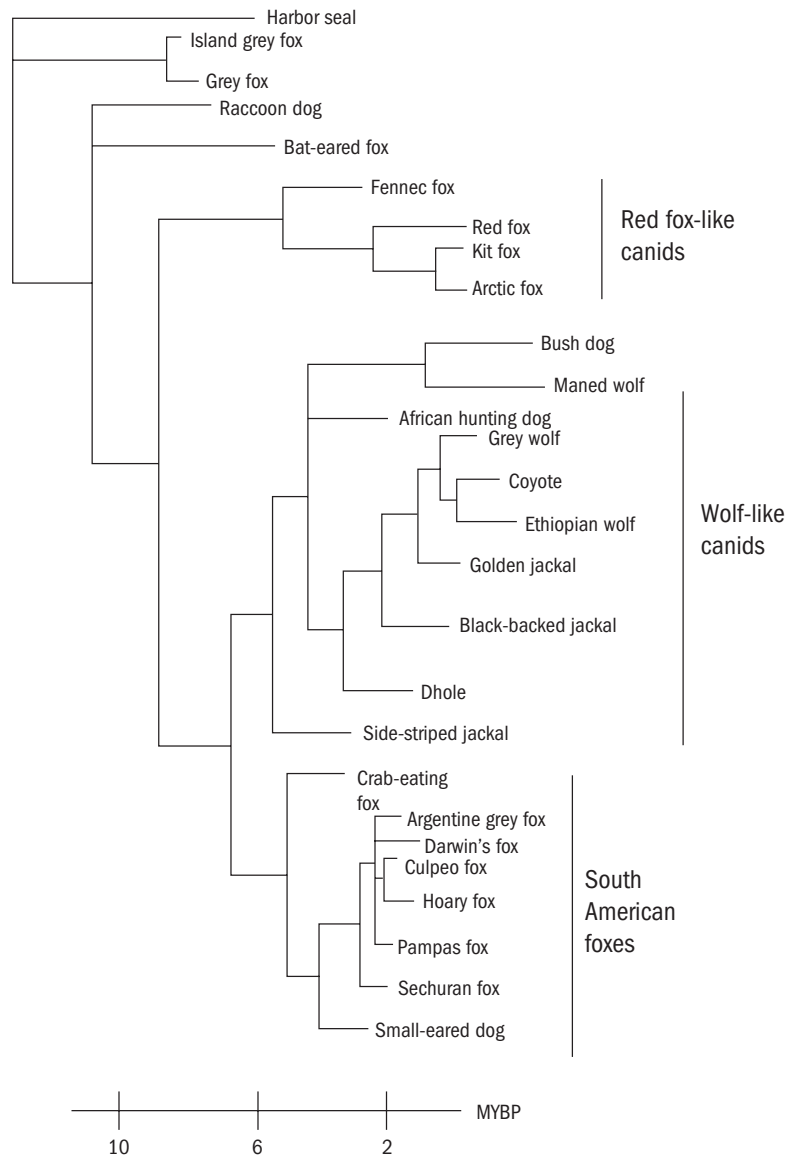


**Figure 2.6** Relationship of carnivores based on DNA hybridization data (Wayne *et al.* 1989). Family and suborder groupings are indicated. Time scale in millions of year before present (MYBP) is based on comparisons of DNA sequence divergence to first appearance times in the fossil record.

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(*Canis latrans*) and Ethiopian wolf (*Canis simensis*) form a monophyletic group, with the Golden Jackal (*C. aureus*) as the most likely sister taxon (Fig. 2.7). The Black-backed and Side-striped jackals are sister taxa, but they do not form a monophyletic group with the Golden jackal and Ethiopian wolf. Basal to *Canis* and

*Cuon* are the African hunting dog (*Lycaon pictus*) and a clade consisting of two South American canids, the bush dog (*Speothos venaticus*) and the maned wolf (*Chrysocyon brachyurus*). Consequently, although the African hunting dog preys on large game as does the Grey wolf and dhole, it is not closely related to either



**Figure 2.7** Consensus tree of 26 canid species based on analysis of 2001 bp of DNA sequence from mitochondrial protein coding genes (Wayne *et al.* 1997). See Geffen *et al.* (1992) for a more detailed analysis of the Red-fox like canids. Time scale in millions of year before present (MYBP) is based on comparisons of DNA sequence divergence to first appearance times in the fossil record.

species but is sister to the clade containing these species. This phylogeny implies that the trenchant heeled carnassial now found only in *Speothos*, *Cuon*, and *Lycaon*, evolved at least twice or was primitive and lost in other wolf-like canids and the maned wolf.

The South American canids do not form a monophyletic group. *Speothos* and *Chrysocyon* are sister taxa that group with the wolf-like canids rather than the South American foxes. The large sequence divergence between the bush dog and maned wolf and between these taxa and the South American foxes suggests that they diverged from each other 6–7 Ma, well before the Panamanian land bridge formed about 2–3 Ma. Thus, three canid invasions of South America are required to explain the phylogenetic distribution of the extant species. These invasions are today survived by (1) the bush dog, (2) the maned wolf, and (3) the South American foxes. Further, within the South American foxes, divergence values between crab-eating fox (*Cerdocyon thous*), the Short-eared fox (*Atelocynus microtis*), and other South American foxes, suggest they may have diverged before the opening of the Panamanian land bridge as well (Wayne *et al.* 1997). The fossil record supports the hypothesis that the crab-eating fox had its origin outside of South America, as the genus has been described from late Miocene deposits of North America (3–6 Ma) (Berta 1984, 1987, see above). Consequently, only the foxes of the genus *Pseudalopex*, *Lycalopex*, and perhaps *Atelocynus*, might have a South American origin. Further, the generic distinction given to *Pseudalopex* and *Lycalopex* does not reflect much genetic differentiation, and in the absence of appreciable morphologic differences, the genetic data suggest these species should be assigned to a single genus.

A fourth grouping in the tree consists of other fox-like taxa, including *Vulpes*, *Alopex*, and *Fennecus* (Fig. 2.7) (Geffen *et al.* 1992; Mercure *et al.* 1993; Wayne *et al.* 1997). The Arctic Fox, *Alopex*, is a close sister to the Kit Fox, *Vulpes macrotis* and both share the same unique karyotype (Wayne *et al.* 1987a). Basal to *Vulpes* is *Fennecus*, suggesting an early divergence of that lineage. Finally, *Otocyon*, *Nyctereutes*, and *Urocyon* appear basal to other canids in all molecular and karyological trees (Wayne *et al.* 1987a). The first two taxa are monospecific whereas the third includes the Island Fox, *Urocyon littoralis* and the grey fox,

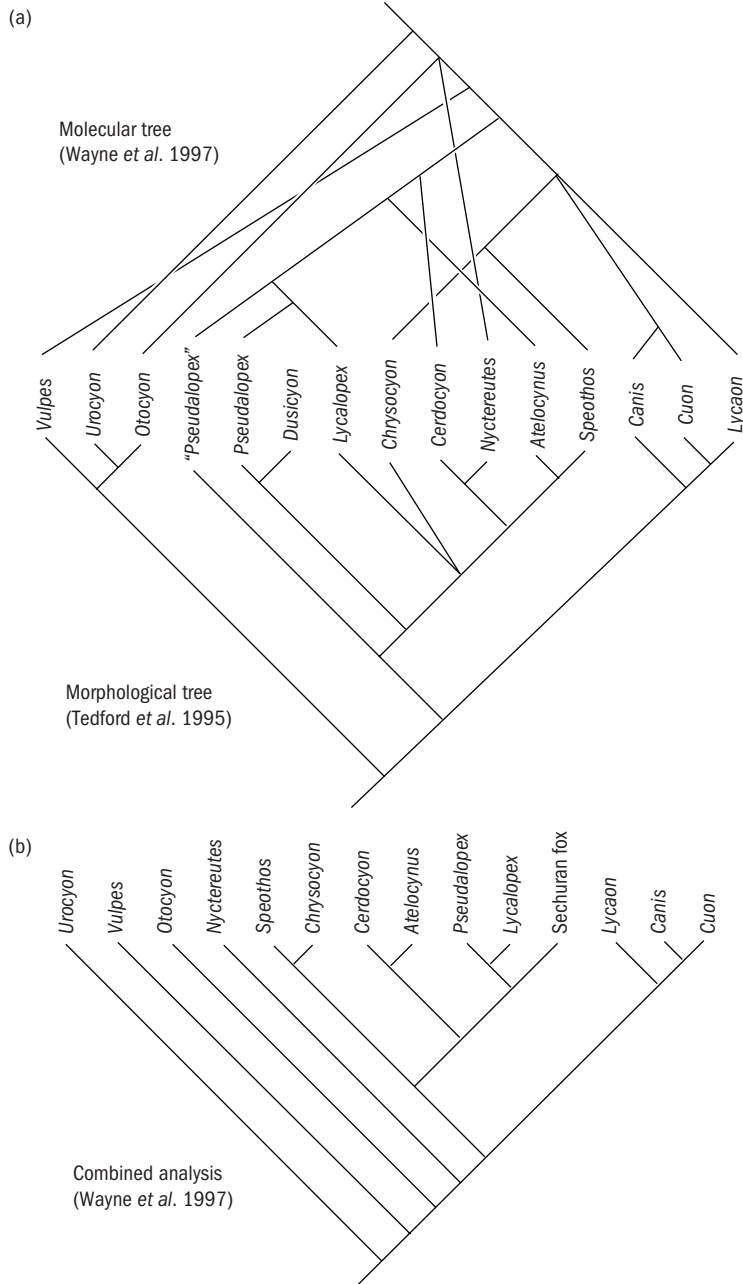
*U. cinereoargenteus*. The three genera diverged early in the history of the family, approximately 8–12 Ma as suggested by molecular clock extrapolations.

In sum, the living Canidae is divided into five distinct groupings. These include the wolf-like canids, which consists of the Coyote, Grey wolf, Jackals, dhole, and African hunting dog. This clade is associated with a group containing bush dog and maned wolf in some trees and further, this larger grouping is associated with the South American foxes (Wayne *et al.* 1997). The Red Fox group is a fourth independent clade containing *Alopex*, *Vulpes*, and *Fennecus*. Finally, three lineages have long distinct evolutionary histories and are survived today by the Raccoon Dog, Bat-eared Fox, and grey fox. Assuming an approximate molecular clock, the origin of the modern Canidae begins about 10–12 Ma and is followed by the divergence of wolf and fox-like canids about 6 Ma. The South American canids are not a monophyletic group and likely owe their origin to three separate invasions. This group included the maned wolf, bush dog, crab-eating fox, and the other South American canids, which diverged from each other about 3–6 Ma.

## Morphological and molecular phylogenies

Tedford *et al.* (1995) performed a cladistic analysis of living canids on morphological grounds. The result is a nearly fully resolved relationship based on an 18 taxa by 57 characters matrix at the generic level. This relationship recognizes three monophyletic clades in the canines: the fox group (tribe Vulpini), the South American canine group, and the wolf group containing hypercarnivorous forms (the latter two form the tribe Canini). Recent molecular studies (presented above), on the other hand, contradict some of these arrangements while maintaining other parts in the morphological tree (Fig. 2.8(a)).

Trees derived from 2001 bp of mitochondrial DNA (Wayne 1997, p. 239 and Fig. 2.7 of this chapter) tend to place the foxes near the basal part, the South American canines in the middle, and the wolves and hunting dogs towards the terminal branches, a pattern that is consistent with the morphological tree.

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**Figure 2.8** (a) Contrasting canine relationships from recent morphological (Tedford *et al.* 1995) and molecular studies (Wayne *et al.* 1997 and Fig. 2.7); (b) combined analysis of 2001 bp of canid mtDNA and 57 morphological characters (Wayne *et al.* 1997, fig. 7).

The detailed arrangements, however, differ in a number of ways. The foxes are generally in a paraphyletic arrangement in contrast to a monophyletic clade in the morphological tree. The grey fox and bat-eared fox are placed at the base despite their highly derived dental morphology compared with other foxes.

Similarly, South American canines are no longer monophyletic under molecular analysis but form at least two paraphyletic branches. A glaring discrepancy is the Asiatic raccoon dog being allied to the foxes in the molecular analysis despite its numerous morphological characters shared with some South



American forms. Finally, molecular data suggest independent origins for the Asiatic and African hunting dogs in contrast to a sister relationship in the morphological tree supported by a large number of characters related to hypercarnivory.

Not surprisingly, there are increased agreements between the molecular and morphological results when the two data sets are combined in a total evidence analysis (Fig. 2.8(b)). Under such conditions, the South American canines (except *Nyctereutes*) become monophyletic, as does the clade including the wolf, dhole, and African hunting dog.

## Evolutionary ecology

### Iterative evolution of hypercarnivory

One of the most remarkable features of canid history is their repeated tendency to evolve both hypocarnivorous and hypercarnivorous forms. As noted above, hypercarnivorous species evolved within each subfamily, and hypocarnivorous species evolved within two of the three (all but the Hesperocyoninae). Hypocarnivory was most fully expressed in the Borophaginae, where at least 15 species showed a tendency towards a dentition similar to that of living raccoons (Wang *et al.* 1999). Among the Caninae, the tendency has not been quite as strong, with only a single lineage, *Nyctereutes*, developing a markedly hypocarnivorous dentition. However, all three subfamilies include multiple species of apparent hypercarnivores with enhanced cutting blades on their carnassials, reduced grinding molars, and enlarged canines and lateral incisors. When and why did hypercarnivory evolve within each subfamily?

In two of the three subfamilies, Hesperocyoninae and Caninae, the evolution of hypercarnivory appears to have occurred at least partly in response to a reduced diversity of other hypercarnivorous taxa. The Hesperocyoninae evolved hypercarnivory early in their history (Figs 2.1 and 2.7) and the most advanced forms appear in the early Miocene (about 24–20 Ma) at a time when the two previously dominant carnivorous families had vanished. These two families were the Nimravidae, an extinct group of saber-tooth cat-like forms, and the Hyaenodontidae, a group of somewhat dog-like predators included in the extinct order Creodonta. The nimravids

and hyaenodontids dominated the North American guild of large, predatory mammals in the late Eocene to mid-Oligocene (37–29 Ma), but faded rapidly in the late Oligocene, and were extinct in North America by about 25 Ma (Van Valkenburgh 1991, 1994). During most of their reign, hesperocyonines existed at low diversity and small (fox-size) body size, but as the hyaenodontids and nimravids declined in the late Oligocene, the early canids seem to have radiated to replace them. Most of these hypercarnivorous canids were jackal-size (less than 10 kg), with only the last surviving species, *Osbornodon fricki*, reaching the size of a small wolf (Wang 1994). In the early Miocene, large hypercarnivores immigrated from the Old World in the form of hemicyonine bears (Ursidae) and temnocyonine bear-dogs (Amphicyonidae). The subsequent decline to extinction of the hesperocyonines might have been a result of competition with these new predators (Van Valkenburgh 1991, 2001).

Hypercarnivory appears late in the history of the Caninae and represents at least several independent radiations in South America, North America, and the Old World (Figs 2.1 and 2.7). As was true of the hesperocyonine example, the South American radiation of large hypercarnivorous canids occurred at a time (2.5–0.01 Ma) when cat-like predators were rare or absent. It followed the elevation of the Panamanian land bridge around 2–3 Ma that allowed immigration between the previously separated continents. The canids that first entered South America found a depauperate predator community, consisting 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. Between 2.5 Ma and 10,000 years ago, 16 new species of canids appeared in South America, at least seven of which had trenchant heeled carnassials and clearly were adapted for hypercarnivory (Berta 1988; Van Valkenburgh 1991). They represent three different endemic genera, *Theriodictis*, *Protocyon*, and *Speothos*. In addition, there were three large wolf-like species of *Canis* in South America, *Canis gezi*, *Canis nehringi*, and *Canis dirus*, all of which were probably hypercarnivorous but retained a bicuspid heel on their carnassials. Of these only the Dire Wolf, *C. dirus*, evolved in North America. All but one of these ten hypercarnivorous

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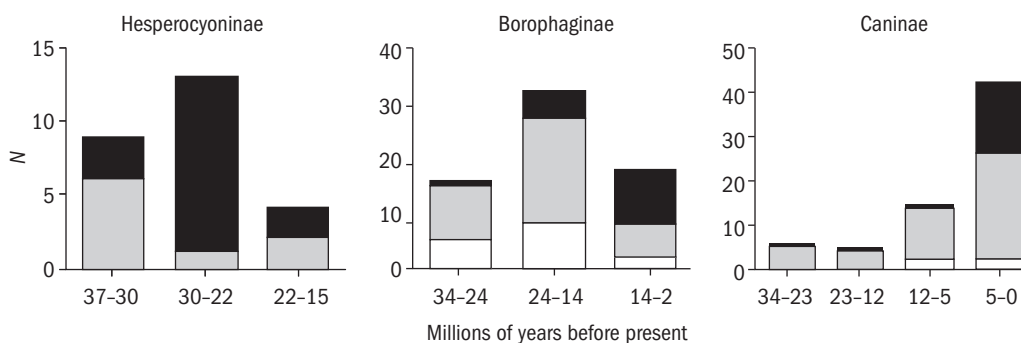
canids of South America went extinct at the end of the Pleistocene (Van Valkenburgh 1991). The sole survivor, the bush dog (*Speothos*) is rarely sighted.

In the Old World, the evolution of hypercarnivorous canines occurred within the last 4 million years and did not coincide with an absence of cats. Large cats, both sabertooth and conical tooth forms, are present throughout the Plio-Pleistocene when the highly carnivorous species of *Canis*, *Cuon*, *Lycaon*, and *Xenocyon* appear (Turner and Antón 1996). However, their evolution might be a response to the decline of another group of hypercarnivores, wolf-like hyaenids. Hyaenids were the dominant dog-like predators of the Old World Miocene, reaching a diversity of 22 species between 9 and 5 Ma, but then declining dramatically to just five species by about 4 Ma (Werdelin and Turner 1996). Their decline may have opened up ecospace for the large canids and favored the evolution of hypercarnivory.

The remaining episode of hypercarnivory in canids occurred in the Borophaginae between 15 and 4 Ma (Van Valkenburgh *et al.* in press). As was true of the Caninae, the hypercarnivorous species do not evolve early in the subfamily's history. Instead, they appear in the latter half of the subfamily's lifespan and only become prevalent in the last third (mid-late Miocene; Figs 2.1 and 2.7). In the late Miocene,

borophagine canids were the dominant dog-like predators of North America, having replaced the amphicyonids and hemicyonine bears that had themselves replaced the hesperocyonines some ten million years earlier (Van Valkenburgh 1999). In the case of the Borophaginae, the evolution of hypercarnivory appears more gradual than in the other two subfamilies, and is not easily ascribed to opportunistic and rapid evolution into empty ecospace.

In all three subfamilies, there is a pattern of greater hypercarnivory and increasing body size with time (Fig. 2.9). Even in the Hesperocyoninae, where hypercarnivory evolves very early, large species with the most specialized meat-eating dentitions appear later (Wang 1994). This directional trend towards the evolution of large, hypercarnivorous forms is apparent in other groups of dog-like carnivores, such as the amphicyonids (Viranta 1996) and hyaenids (Werdelin and Solounias 1991; Werdelin and Turner 1996), and may be a fundamental feature of carnivore evolution. The likely cause is the prevalence of interspecific competition among large, sympatric predators. 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. Competition appears to be a motive for



**Figure 2.9** Iterative evolution of large hypercarnivores. Number ( $N$ ) of hypocarnivorous (white), mesocarnivorous (grey), and large (>20 kg) hypercarnivorous (black) species over time in each of the three subfamilies. The few hesperocyonine species with trenchant-heeled carnassials estimated to have been less than 20 kg in mass were assigned to the mesocarnivorous category because they are assumed not have taken prey as large or larger than themselves. For the Hesperocyoninae and Borophaginae, their stratigraphic ranges were broken into thirds; for the Caninae, four time divisions were used because of the large number of species appearing in the past 5 million years. Species were assigned to dietary categories and body mass was estimated on the basis of dental morphology as described in Van Valkenburgh (1991) and Wang *et al.* (1999).

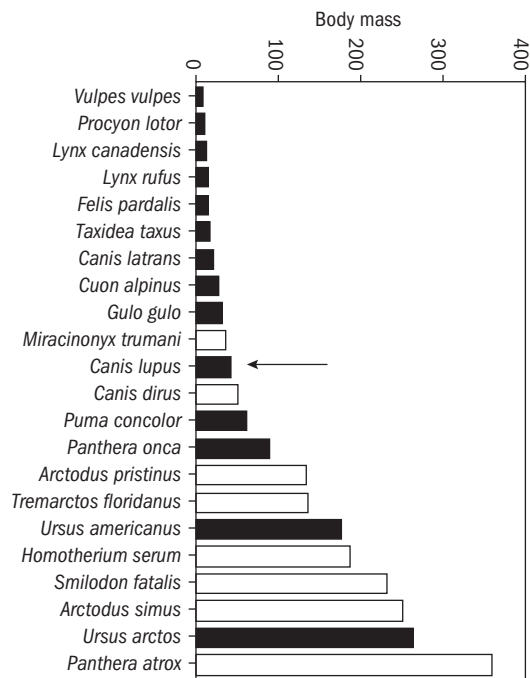
much intraguild predation because the victim often is not eaten (Johnson *et al.* 1996; Palomares and Caro 1999; Van Valkenburgh 2001). Larger carnivores tend to dominate smaller ones and so selection should favour the evolution of large body size. Large body size in turn selects for a highly carnivorous diet because of energetic considerations. As shown by Carbone *et al.* (1999), almost all extant carnivores that weigh more than 21 kg take prey as large or larger than themselves. Using an energetic model, they demonstrated that large body size brings with it constraints on foraging time and energetic return. Large carnivores cannot sustain themselves on relatively small prey because they would expend more energy in hunting than they would acquire. By taking prey as large or larger than themselves, they achieve a greater return for a given foraging bout. Killing and consuming large prey is best done with a hypercarnivorous dentition and so the evolution of large body size and hypercarnivory are linked. Of course, this does not preclude the evolution of hypercarnivory at sizes less than 21 kg, but it seems relatively rare. It has occurred in the Canidae as evidenced by the hesperocyonines and the extant Arctic Fox, *V. lagopus*, and Kit Fox, *V. macrotis*. However, the two extant foxes do not have trenchant-heeled carnassials despite their tendency towards a highly carnivorous diet, and this may reflect regular, opportunistic consumption of fruits and invertebrates (Van Valkenburgh and Koepfli 1993).

Returning to the questions of when and why hypercarnivory evolves among canids, it seems that when and why are intertwined. That is, because of intraguild competition and predation, selection favours the evolution of larger size in canids and as a consequence, hypercarnivory. However, *when* this occurs it is largely a function of other members of the predator guild. In the case of the Hesperocyoninae, it occurred relatively early in their history because previously dominant large hypercarnivores were in decline or already extinct. In the case of the Borophaginae and Caninae, it did not occur until much later because other clades held the large hypercarnivorous roles for much of the Miocene. In all these examples, it appears as though the rise of large hypercarnivorous canids reflects opportunistic replacement rather than competitive displacement of formerly dominant taxa (Van Valkenburgh 1999).

### The last one million years

All of the canids that are extant today evolved well prior to the late Pleistocene extinction event approximately 11,000 years ago. The same could be said of most, if not all, extant carnivores. In the New World, the end-Pleistocene event removed numerous large mammals, including both herbivores (e.g. camels, horses, proboscideans) and carnivores (e.g. Sabertooth Cat, Dire Wolf, Short-faced Bear). In the Old World, many of the ecological equivalents of these species disappeared earlier, around 500,000 years ago (Turner and Antón 1996). Consequently, all extant carnivore species evolved under very different ecological circumstances than exist at present. For example, the Grey wolf today is considered the top predator in much of Holarctica, but it has only held this position for the last ten to eleven thousand years. For hundreds of thousands of years prior to that time, the wolf coexisted with 11 species of predator as large or larger than itself (Fig. 2.10). Now there are but three, the Puma, Black Bear, and Grizzly Bear, and wolves are usually dominant over the first two species at least (Van Valkenburgh 2001). Thus, for most of its existence, the Grey wolf was a mesopredator rather than a top predator, and so its morphology and behaviour should be viewed from that perspective. Given the greater diversity and probable greater abundance of predators in the past, interspecific competition was likely more intense than at present. Higher tooth fracture frequencies in late Pleistocene North American predators provide indirect evidence of heavy carcass utilization and strong food competition at that time (Van Valkenburgh and Hertel 1993). Intense food competition would favour group defence of kills and higher levels of interspecific aggression. Perhaps the sociality of the wolf and the tendency of some carnivores to kill but not eat smaller predators are remnant behaviours from a more turbulent past.

The only canid to go extinct in the North American end Pleistocene was the Dire Wolf, *C. dirus*. The Grey wolf, Coyote, and several foxes survived. In addition to the Dire Wolf, two bears and three cats went extinct, all of which were very large (Fig. 2.10). Can we learn something about the causes of current predator declines by examining the winners and losers in the late Pleistocene? Examination of the

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**Figure 2.10** North American Pleistocene carnivorans arranged by body mass. Black bars represent extant species, and white bars represent extinct species. Arrow indicates the Grey wolf (*Canis lupus*). Data from Van Valkenburgh and Hertel (1998).

loser species reveals that they tended to be the more specialized members of their clades; they were larger (Fig. 2.10) and tended to be more dentally specialized for hypercarnivory (Van Valkenburgh and Hertel 1998). Remarkably, two of the species that went extinct, the Dire Wolf and Sabertooth Cat (*Smilodon fatalis*), are five times more common in the Rancho La Brea tar pit deposits than the next most common carnivore, the Coyote (*C. latrans*). This suggests that the Dire Wolf and Sabertooth Cat were dominant predators at this time, comparable to the numerically dominant African Lion and Spotted hyena of extant African ecosystems. The extinction of the apparently successful Dire Wolf and Sabertooth

Cat implies there was a major perturbation to the ecosystem in the late Pleistocene. Their demise and that of the other large hypercarnivores suggest that large prey biomass dropped to extremely low levels. Supporting this are the parallel extinctions of 10 of the 27 species of raptors and vultures (Van Valkenburgh and Hertel 1998).

In the late Pleistocene, the largest meat-eaters, both avian and mammalian, were the most vulnerable. Is this the case today for canids? Of the three large hypercarnivorous canids, the dhole, Grey wolf, and African hunting dog, only the hunting dog is highly endangered. Among living canids in general, species that appear to be most at risk tend to be insular (Darwin's Fox, Channel Islands Fox) or restricted to limited habitats (Ethiopian Wolf), or just very poorly known species (e.g. Short-eared Zorro, bush dog). Indeed, it is a bit difficult to answer the question of which of the living species are most endangered because we have so little information on many of the smaller taxa. Nevertheless, it does seem that the end Pleistocene extinction is not a good analogue for what is happening at present, at least in terms of which is most vulnerable. Then, it was the largest, most abundant, and most carnivorous. Now it seems more often to be smaller mesocarnivores that are at risk due to small population size exacerbated by habitat loss. In both the end-Pleistocene and at present, the hand of humanity looms large as a cause of predator declines. Initially, the damage was largely due to overhunting of both prey and predator, and to this we have added significant habitat loss. Survivors of the current crisis are likely to be both dietary and habitat generalists, such as the Coyote.

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