Canids: Foxes, Wolves, Jackals and Dogs

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IUCN/SSC Canid Specialist Group

IUCN – The World Conservation Union
2004
The family Canidae belongs to the order Carnivora, a large
group of mostly predatory mammals characterised by
their common possession of a pair of carnassial teeth
(upper fourth premolar and lower first molar) that are
modified to maximise efficiency for shearing skins, tendons,
and muscles in their preys. Canids are characterised by an
inflated entotympanic bulla (bony chamber enclosing the
middle ear region) that is divided by a partial septum along
the entotympanic and ectotympanic suture. Other features
characteristic of canids are 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.

2.1 Phylogeny from morphological
and palaeontological perspective

There are three major groups (subfamilies) in the family
Canidae: Hesperocyoninae, Borophaginae and Caninae
(Tedford 1978) (Figures 2.1, 2.2). Of these, two are
represented by fossil forms only. The Hesperocyoninae is
the most ancient group of all canids, and its basal member,
Hesperocyon, gave rise to the two more advanced
subfamilies, Borophaginae and Caninae (Wang 1994). A
major evolutionary transformation involves the
modification of the talonid heels on the lower carnassial
tooth (first lower molar), which changes from that of a
trenchant, blade-like condition in the Hesperocyoninae to
that of a basined condition enclosed by two cusps in the
Borophaginae and Caninae (Figure 2.3). Mainly due to
their common possession of this basined talonid, the
Borophaginae and Caninae are hypothesised to share a
common ancestry. Along with a more quadrate upper first
molar with a large hypocone on the inner corner of the
tooth, the basined talonid establishes an ancestral state
from which all subsequent forms were derived. Such a
dental pattern has proved to be very versatile and can
readily be adapted toward either a highly carnivorous or
a less carnivorous type of dentition, both of which were
repeatedly employed by both Borophaginae and Caninae.

The extinct Borophaginae was the first major group of
canids to demonstrate the viability of a basined talonid
and achieved the greatest morphological breadth and
taxonomical diversity within the North American
continent (Wang et al. 1999). Toward the less predaceous
end of the morphological spectrum, it sports highly
omnivorous forms that parallel similar adaptations by
living Procyonidae (the raccoon family). Toward the more
predaceous end, on the other hand, the Borophaginae is
well known for its tendencies to develop strong bone-
crushing dentitions that parallel the habits of living
Hyaenidae (the hyaena family).

The subfamily Caninae started with Leptocyon, an
ancestral species the size of a small fox. Besides sharing a
bicuspied talonid of M1 and a quadrate M1 with the
borophaginae, Leptocyon is also characterised 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, 34–32 million years before present
[BP]) and persisted through the late Miocene
(Clarendonian, 12–9 million years BP). Throughout its
long existence (no other canid genus had as long a duration),
facing intense competition from the larger and diverse
hesperocyonines and borophaginae, Leptocyon generally
remained small in size and low in diversity, never having
more than two or three species at a time.

By the latest Miocene (Hemphillian, 9–5 million years
BP), fox-sized niches are widely available in North
America, left open by extinctions of all small borophaginae.
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 (Vulpes velox) 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

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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, Wang, and Taylor.
Figure 2.2. 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 cricidens; Euoplocyon brachynathus; Aelurodon stirtoni; Paratomarctus temerarius; Carcocyon webbi; Epicyon haydeni; and Borophagus diversidens. Species in the Caninae are: Leptocyon gregorii; Vulpes stenognathus; Urocyon minicephalus; Cerdocyon thous; Eucyon davisi; Canis dirus; and Cuon alpinus. All teeth are scaled to be proportional to their sizes.

Figure 2.3. Hypercarnivorous (B, Aelurodon and D, Euoplocyon) and hypocarnivorous (A, Phlaocyon and C, Cynarctus) dentitions.
In hypercarnivorous forms, the upper cheek teeth (B) tend to emphasise 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) emphasise 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 (bicuspoid) 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.
that of the Canis clade. Red fox (Vulpes vulpes) and Arctic fox (Alopex lagopus) appeared in North America only in the late Pleistocene, evidently as a result of immigration back to the New World.

Preferring more wooded areas, the gray fox (Urocyon) has remained in southern North America and Central America. Records of the gray fox clade have a more or less continuous presence in North America throughout its existence, with intermediate forms leading to the living species U. cinereorargenteus. Morphologically, the living African bat-eared fox (Otocyon megalotis) 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. 1992; Wayne et al. 1997). If the morphological evidence is correct, then the bat-eared fox must represent a Pliocene immigration event to the Old World independent of other foxes.

Advanced members of the Caninae, Tribe Canini, first occur in the medial Miocene (Clarendonian) 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 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 the grey wolf (Canis lupus). By the late Miocene, 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 palatine, 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 late Hemphillian and early Blancan, certain fragmentary materials from southern United States and Mexico indicate that the earliest taxa assignable to Cerdocyon (Torres and Ferrusquia-Villafranca 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 Central America. They appear in the South American fossil record shortly after the formation of the Isthmus of Panama in the Pliocene, around three million years BP (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 million years BP) of Argentina. By the late Pleistocene (Lujanian, 300,000–10,000 years BP), 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 Canis dirus had become extinct.

The Canis-Lycaon clade within the Tribe Canini, the most derived group in terms of large size and hypercarnivory, arose near the Miocene-Pliocene boundary between 6 and 5 million years BP in North America. A series of jackal-sized ancestral species of Canis thrived in the early Pliocene (early Blancan), such as C. ferox, C. leopaphus, 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 monticicneus in the late Miocene of Italy (Rook 1992), the earliest raccoon-dog (Nyctereutes domenzani), and the jackal-sized Canis adoxus in the early Pliocene of France (Martin 1973; Ginsburg 1999). The enigmatic C. cipio, only represented by parts of the upper and lower dentition at a single locality, may represent 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 compund this problem, the highly cursorial wolf-like Canis species apparently belong to a circum-arctic fauna that undergoes expansions and contractions with the fluctuating climates. 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 are localised in different parts of the Holarctic. 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 (Canis latrans) as an endemic form. The wolves, dhole (Cuon alpinus), African wild dog (Lycaon pictus) and fossil relatives are the products of 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 late Pleistocene (about 100,000 years BP).

A comprehensive systematic revision of North American fossil canines by Tedford et al. (in prep.) is near completion, which forms the basis of much of the above summary. As part of the above revision, the phylogenetic framework as derived from living genera was published by
Tedford et al. (1995). Nowak (1979) monographed the Quaternary Canis of North America; Berta (1981, 1987, 1988) did the most recent phylogenetic analysis of the South American canids; Rook (1992, 1994) and Rook and Torre (1996a, 1996b) partially summarised the Eurasian canids. The African canid records are relatively poorly understood and recent discoveries promise to significantly advance our knowledge in that continent (L. Werdelin pers. comm.).

### 2.2 Molecular phylogeny

The ancient divergence of dogs from other carnivores is reaffirmed by molecular data. DNA-DNA hybridisation of single copy DNA clearly shows them as the first divergence in the suborder Caniformia that includes pinnipeds, bears, weasel and raccoon-like carnivores (Figure 2.4). This basal placement is further supported by mitochondrial DNA (mtDNA) sequence studies (Vrana et al. 1994; Slattery and O’Brien 1995; Flynn and Nedbal 1998). Based on molecular clock calculations, the divergence time was estimated as 50 million years BP (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 postdate 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, mtDNA protein coding sequence data, and, most recently, supertree method (Wayne and O’Brien 1987; Wayne et al. 1987a, 1987b, 1997; Bininda-Emonds et al. 1999). Further, relationships at the genus level have been studied with mtDNA control region sequencing (a non-coding, hypervariable segment of about 1200 years 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. The grey wolf, coyote and Ethiopian Wolf or Simien Jackal (Canis simensis) form a monophyletic group, with the golden jackal (C. aureus) as the most likely sister taxon (Figure 2.5). The black-backed (C. mesomelas) and side-striped jackals (C. adustus) 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 wild dog and a clade consisting of two South American canids, the...
bush dog (*Speothos venaticus*) and the maned wolf (*Chrysocyon brachyurus*). Consequently, although the African wild dog preys on large game as does the grey wolf and dhole, it is not closely related to either 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 7–6 million years BP, well before the Panamanian land bridge formed about 3–2 million years BP. Thus, three canid invasions of South America are required to explain the phylogenetic distribution of the extant species. These invasions are today survived by the bush dog, maned wolf, and the South American foxes. Further, within the South American foxes, divergence values between crab-eating fox (*Cerdocyon thous*), the short-eared dog (*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).

**Figure 2.5.** Consensus tree of 26 canid species based on analysis of 2,001 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 years before present (MYBP) is based on comparisons of DNA sequence divergence to first appearance times in the fossil record.
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 (6–3 million years BP) (Berta 1984, 1987, see above). Consequently, only the foxes of the genus *Pseudalopex*, *Lycalopex* and perhaps *Atelocynus*, appear to 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 *Alopex* and *Vulpes* (here considered to include the fennec fox, *Vulpes zerda*, sometimes included in the genus *Fenmecus*) (Figure 2.5) (Geffen et al. 1992; Mercure et al. 1993; Wayne et al. 1997). The Arctic fox is a close sister to the kit fox (*Vulpes macrotis*) and both share the same unique karyotype (Wayne et al. 1987a). 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 gray fox (*U. cinereoargenteus*). The three genera diverged early in the history of the family, approximately 12–8 million years BP 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, Ethiopian wolf, jackals, dhole and African wild 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* and *Vulpes* (including the fennec fox). Finally, three lineages have long distinct evolutionary histories and are survived today by the raccoon dog, bat-eared fox and island and gray fox. Assuming an approximate molecular
clock, the origin of the modern Canidae begins about 12–10 million years BP and is followed by the divergence of wolf and fox-like canids about 6 million years BP. 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 that diverged from each other about 6–3 million years BP.

2.3 Evolutionary ecology

2.3.1 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). Hypercarnivory 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 (Figures 2.1, 2.2, 2.6) and the most advanced forms appear in the early Miocene (about 24–20 million years BP) 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 Hyaeodonta, a group of somewhat dog-like predators included in the extinct order Creodonta. The nimravids and hyaeodontids dominated the North American guild of large, predatory mammals in the late Eocene to mid-Oligocene (37–29 million years BP), but faded rapidly in the late Oligocene, and were extinct in North America by about 25 million years BP (Van Valkenburgh 1991, 1994). During most of their reign, hesperocyonines existed at low diversity and small (fox-size) body size, but as the hyaeodontids 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 10kg), with only the last surviving species, Osbornodon fricki, reaching the size of a small wolf (Wang 1994). In the early Miocene, large hypercarnivores emigrated 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 (Figures 2.1, 2.6). As was true of the hesperocyonine example, the South American radiation of large hypercarnivorous canids occurred at a time (2.5–0.01 million years BP) when cat-like predators were rare or absent. It followed the elevation of the Panamanian land bridge around 3–2 million years BP that allowed immigration between the previously separated continents. The canids that first entered South America found a

Figure 2.6. Iterative evolution of large hypercarnivores.

Number (N) of hypocarnivorous (white), mesocarnivorous (grey), and large (>20kg) 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 20kg 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 five 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).
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 specialised hypercarnivore. Between 2.5 million and 10,000 years BP, 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, C. gezi, C. nehringi, and C. 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 canids of South America went extinct at the end of the Pleistocene (Van Valkenburgh 1991). The sole survivor, the bush dog, is rarely sighted.

In the Old World, the evolution of hypercarnivorous canines occurred within the last four million years and did not coincide with an absence of cats. Large cats, both the 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 million years BP, but then declining dramatically to just five species by about 4 million years BP (Werdelin and Turner 1996). Their decline may have opened up ecospace for the large canids and favoured the evolution of hypercarnivory.

The remaining episode of hypercarnivory in canids occurred in the Borophaginae between 15 and 4 million years BP (Van Valkenburgh et al. 2003). 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 to late Miocene; Figures 2.1, 2.6). 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 10 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 (Figure 2.6). Even in the Hesperocyoninae, where hypercarnivory evolves very early, large species with the most specialised meat-eating dentitions appear later (Wang 1994). This directional trend toward 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 sizeable quantity of food that is worthy of stealing and defending. Competition appears to be a motive for 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 21kg 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 as, 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 21kg but it seems relatively rare. It has occurred in the Canidae as evidenced by the hesperocyonines and the extant Arctic fox and kit fox. However, the two extant foxes do not have trenchant-heeled carnassials despite their highly carnivorous diets (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 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).
2.3.2 The last one million years

All of the canids that are extant today evolved prior to the late Pleistocene extinction event approximately 11,000 years BP. 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 BP (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 the Holarctic, but it has only held this position for the last 10,000–11,000 years. For hundreds of thousands of years prior to that time, the wolf coexisted with 11 species of predator as large as, or larger than, itself (Figure 2.7). Now only the puma (Puma concolor), American or Asiatic black bears (Ursus americanus and U. thibetanus) and grizzly bear (U. arctos) remain, 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 utilisation 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 North America by the late Pleistocene was the dire wolf. 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 (Figure 2.7). By examining the ‘winners’ and ‘losers’ in the late Pleistocene we are able to learn about the causes of current predator declines. Examination of the loser species reveals that they tended to be the more specialised members of their clades, they were larger (Figure 2.7) and tended to be more dentally specialised 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. This suggests that the dire wolf and sabertooth cat were dominant predators at this time, comparable to the numerically dominant African lion (Panthera leo) and spotted hyaena (Crocuta crocuta) 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 suggests that large prey biomass dropped to extremely low levels. Supporting this are the parallel extinctions of ten 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. Looking at the case today, of the three large hypercarnivorous canids, the dhole, grey wolf and African wild dog, both the dhole and the wild dog are Endangered. Among living canids in general, species that appear to be most at risk tend to be insular (Darwin’s fox, island fox) or restricted to limited habitats (Ethiopian wolf), or just very poorly known species (e.g., short-eared dog, bush dog). Indeed, it is a bit difficult to answer the question of which of the living species are most threatened because we have so little information on many of the smaller taxa. Nevertheless, it does seem that by the Late Pleistocene extinction is not a good analog for what is happening at present, at least in terms of who 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 late 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 and the black-backed jackal.


2.4 History of canid classification

Caroli Linnaeus (1758) listed four genera, Canis, Hyaena, Vulpes, and Alopex, under the heading Canis, an informal category between genus and order (family level classification was not used then). Besides the misplaced Hyaena, Linnaeus’s basic concept of canids has endured to the present time. By the late 1800s, the family Canidae had stabilised to include most of what are presently regarded as species of canids (e.g., Mivart 1890a, 1890b). The late 1800s and early 1900s was also a time of explosive growth of the number of fossil canids. However, the fragmentary nature of most of the fossil forms became a major source of confusion in canid classification. As a result, a much broader concept of the Caninae was still adopted to accommodate a wide range of forms that do not neatly fit into existing categories. Thus, fossil forms such as amphicyonid bear-dogs, certain basal arctoids, and hyaenoid ‘dogs’ frequently became mixed with real canids (e.g., Zittel 1893; Trouessart 1897; Matthew 1930). This is primarily caused by an over reliance on the evolutionarily highly repetitive dental patterns, i.e., dental morphologies that evolved multiple times in independent lineages. Such a broadened concept of Caninae was still seen in Simpson’s classification of mammals (Simpson 1945), in which numerous primitive arctoids as well as whole groups of amphicyonids were still considered canid. Simpson, however, was keenly aware that the rich fossil records only serve to compound the problems and much remained to be done to sort out the complexity. The legacy of Simpson’s classification was still felt in the 1970s, when one of his peculiar group, the subfamily Simocyoninae (a mixed bag of highly predaceous carnivorans), was still being circulated (Stains 1974).

Shortly after Simpson’s influential classification, students of Carnivora began to gain increasing appreciation of the importance of morphologies in the middle ear region (bones around and behind the ear drums) (Hough 1948; Hunt 1974). The recognition that different groups of carnivores tend to have a unique pattern of middle ear region greatly enhanced our ability to discriminate members of various families of Carnivora. Focusing on the ear bones, many of the forms previously considered canid have now been allocated to other groups. The Canidae thus defined attains a greater degree of uniformity in morphology and consistency with phylogeny (Wang and Tedford 1994). McKenna and Bell’s (1997) latest revision of Simpson’s (1945) classification largely reflects these results. Throughout this period of waxing and waning of the scope of fossil canids during the past 100 years, the content of living species of canids, however, has remained largely stable.

Recent advances in the last 30 years in systematic practices favour approaches that evaluate characters in a historical perspective to guard against rampant parallelisms in evolution, in contrast to phenetic approaches that evaluate overall similarities only. Numerical taxonomic analysis of living canids by Clutton-Brock et al. (1976) was based on a large number (666 characters) of quantitative measurements of skull and body proportions, skin colours, and a few dental characters. The few qualitative characters were also treated in a phenetic way (i.e., lacking polarity determination) and were easily overwhelmed by a large number of other phenotypic characters. Not surprisingly, the dendrograms derived from their cluster analysis (Clutton-Brock et al. 1976; Figure 8) bear little resemblance to those derived from phylogenetic analyses (both morphological and molecular) discussed above and are inappropriate to be the basis for classification. Similar caution should be exercised regarding attempts to introduce hybridisation data into the canid classification by Van Gelder (1978), a result that also lacks a phylogenetic basis.

2.5 Classification of the living Canidae

As discussed above, the classification of living Canidae amounts to the classification of a subset of the subfamily Caninae since two ancient subfamilies, the Hesperocyoninae and Borophaginae, were long extinct (see Wang and Tedford 1994; Wang et al. 1999 for their classifications). Within the Caninae, genera and species that are exclusively in the fossil record are not discussed here. At the generic level, at least six genera are represented by extinct forms only and are not further discussed: Leptocyon, Eucyon, Thrioidictis, Norcyon, and Xenocyon. At the species level, many fossil species are included under common generic names that may or may not be ancestral to living species. For example, large numbers of fossil species of Canis are recognised throughout Eurasia and North America. While these extinct forms may shed light in the history of modern species, they are not further discussed here since we are dealing with classification of living forms without attempt to elucidate detailed relationships between species.

As can be seen from the above sections, there are parts of phylogenetic hypotheses that are consistent between morphological and molecular evidences, and there are parts that are not. Such conflicts are the results of our inability to unambiguously discriminate noise from true signal. In other words, true genealogical relationships can be overshadowed by superficial similarities due to evolutionary tendencies of parallelism. Such conflicts are likely to continue for a long time and our classification (Table 2.1) largely follows that of Wozencraft (1993). See Ginsberg and Macdonald (1990) for a list of subspecies.
2.5.1 Genus or species of controversial taxonomic status

The following discussions of selected taxa involve controversial cases of taxonomy that were discussed during the Canid Biology and Conservation Conference held in the Department of Zoology at Oxford University during September 2001.

Canis rufus Audubon and Bachman, 1851

The systematic status of the red wolf in the south-eastern United States has become increasingly contentious. Current theories of origin range from it being a small distinct wolf species with an ancient ancestry going back to the Pleistocene or a more recent hybrid between the grey wolf and coyote. Additionally, other alternative scenarios have been suggested. The wide-ranging issues cannot be adequately explored in this chapter, although they mainly involve evidence from a palaeontological, morphological, morphometric, molecular, and conservation perspective (Paradiso and Nowak 1971; Wayne and Jenks 1991; Nowak 1992; Phillips and Henry 1992; Roy et al. 1994; Wilson et al. 2000; Nowak 2002). Palaeontological and morphological approaches suffer from a poor fossil record, especially those from the high latitudes of Eurasia and North America where wolves were presumed to have radiated from, and of recent samples of confidently identified museum specimens. Additional difficulties are encountered in attempts to resolve relationships among the early members of Canis (Tedford et al. in prep.). Yet, Nowak (2002) reaffirmed his earlier conviction that a distinct red wolf-like form can be traced back to the late Pleistocene based on multivariate analysis. The debate in the last ten years has not brought about a convergence, and it is not wise to legislate the debate at this time.

Lycalopex vs. Pseudalopex

Debate about the proper usage of Lycalopex vs. Pseudalopex for certain South American foxes, particularly regarding the hoary fox (vetulus), has been going on for many years (e.g., Cabrera 1931; Osgood 1934; Langguth 1975; Berta 1987, 1988; Tedford et al. 1995). The controversy focuses on the question of whether or not vetulus should be placed under the monotypic Lycalopex or included under Pseudalopex, along with various other small foxes. The ultimate solution lies in the determination of whether vetulus represents a unique lineage distinct from other species of Pseudalopex. However, the primitive morphology of the small foxes is a major hindrance to a clear resolution of their relationships. The key to resolving this problem may lie in a detailed species-level phylogenetic analysis. Until that is done, it is still a matter of opinion which generic name is the most appropriate.

Pseudalopex fulvipes Martin, 1837

Osgood (1943) argued that the dark-coloured fox from southern Chiloé Island off the southern coast of Chile (and first collected by Charles Darwin) is morphologically distinct. Cabrera (1957) followed Osgood’s conclusion,
whereas Langguth (1969) presented data for its inclusion in *Pseudalopex griseus*, its mainland counterpart in Chile and Argentina, a conclusion also followed by Wozencraft (1993). However, mtDNA sequencing studies clearly established that the taxon has a mainland distribution, reaffirming earlier reports, and showed that sequences from the Darwin’s fox defined a distinct clade (Yahnke *et al*. 1996). Consequently, rather than representing an island form of *griseus*, Darwin’s fox is genetically distinct from the South American gray fox and was, until recently, sympatric with this species at one or more mainland localities. Hence, it should be considered a separate species, *Pseudalopex fulvipes*.

**New Guinea singing dog**

Preliminary sequencing studies showed that the New Guinea singing dog has mtDNA sequences identical to the dingo (*Canis lupus dingo*), which is classified within a clade of dog sequences distinct from grey wolves (Vilà *et al*. 1997; Wayne *et al*. 1997; Leonard *et al*. 2002). Contrary to one report (Koler-Matznick *et al*. 2003), sequencing studies rule out an ancestry with dholes and the African wild dog, and clearly assign it to the domestic dog, which is sister to the grey wolf (Vilà *et al*. 1997; Wayne *et al*. 1997; Leonard *et al*. 2002). Given the current evidence, we feel there is little justification for assigning specific or subspecific status.