

A review of selected features of the family Canidae with reference to its fundamental taxonomic status

Barnabas Pendragon

Dogs comprise 35 extant species in 14 genera. They belong to the order Carnivora, which has common morphological and karyotypic features. Within the order, member species can be grouped based on heterologous DNA melting temperatures. The family Canidae forms such a group. Selected features of the Canidae are reviewed here in order to examine the fundamental taxonomic status of this family. Hybrid relationships demonstrate that the family Canidae is a single, reproductively compatible group having the taxonomic status of basic type. As opposed to the various species in the family whose formation was accompanied by genetic change, establishment of the domestic dog was accompanied by almost no genetic change; genetically all domestic dogs are grey wolves. The remarkable variation observed among the various breeds of domestic dog reflects the potential for morphological change hard-wired into the canid genome. The basic type appears to be divided into two subfamilies in the Cenozoic strata; the extant Caninae and the extinct Borophaginae. The 'oldest' known canid species is *Prohesperocyon*, which is found in upper Eocene fossil deposits.

In 1870, George Vest, a Missouri lawyer gave us the adage "A dog is a man's best friend". More so than any other animal, dogs represent friendship and companionship. Nevertheless, dogs, the Canidae, are beasts of prey belonging to the order Carnivora. They have long slender heads with a prominent snout containing an extensive nasal cavity (dogs have a well-developed sense of smell). The ears are usually held erect and are quite large (they can be used to regulate body temperature). The legs are long and slender, since dogs tend to hunt their prey by chasing them and running them down. The front feet have five digits, the hind feet, four. The African wild dog is an exception, with four digits on all its feet, and some breeds of domestic dog have five digits on each foot. The tail of most dogs is well developed, characteristically so in the foxes, where it is referred to as the brush.

The order Carnivora

Canidae belong to the order Carnivora, which comprises nine families (or ten if the mongooses are considered a separate family; Herpestidae), grouped into two superfamilies, the Caniformia and the Feliformia. The aquatic carnivores, Otariidae (sea lions) and Phocidae (seals), are sometimes placed in a separate order, the Pinnipedia; however, the inclusion of these families within the Carnivora is usual (see table 1).

The main role of carnivores in nature is to keep in check the numbers of herbivores. They are primarily flesh eaters, and most are capable of running quickly. They have conspicuous long and sharp canine teeth for catching and killing prey. Most of them have the last upper premolar and the first lower molar transformed into the so-called carnassial teeth, which have a flattened, razor-like crown

for slicing muscle tissue. However, in the omnivorous carnivores such as the bears, true carnassial teeth do not develop.

Interestingly, the carnivore order has a largely conservative karyotype. The chromosome morphologies and G-banding patterns of several of the families are highly conserved. The Felidae is the prototype family. The domestic cat has 19 chromosomes, 16 of which are invariant in all 38 species of felids. Of these 16 chromosomes, 15 are present in several other carnivore families (Procyonidae, Mustelidae, Viverridae, Hyaenidae). In two families, however, the Canidae and Ursidae, there is a dramatic reorganization of this basic carnivore karyotype. Still, the overall picture is of a comparable group of animals with various features in common. Bennetzen and Freeling suggest the order Carnivora may represent a common 'genetic system' because of these karyotypic similarities.³

Homologies between the single-copy genes, recognized by evaluating the thermal stability of DNA duplexes, can be used to distinguish many of the families within the order.⁴ The technique estimates the difference in melting temperatures between homologous DNA duplexes (both DNA strands from one species) and heterologous DNA duplexes (one strand from each of two species). Species within the Canidae vary by less than 4°C from each other, but by more than 18°C from species in other carnivore families. Similarly, species within the Felidae vary by less than 4°C from each other but by more than 14°C from other carnivores; and this is also true of the Hyaenidae.⁵ All three families, Canidae, Felidae and Hyaenidae, may represent fundamental taxonomic units equivalent to basic types.

The family Canidae

Subdivision of the canids has been a field rich in conflicting hypotheses. Langguth² described a reasonable three partition subgrouping, which, with subsequent isolation of the grey foxes, now includes four lineages (see table 1).

A complete listing of recent canids is given in the appendix. The analysis of Wayne and O'Brien⁶, based on allozyme genetic distance and chromosome morphology, indicated that the genera *Urocyon*, *Otocyon* and *Nyctereutes* form separate monotypic lineages (see figure 1). Previously, placement of *Otocyon* within the *Vulpes*-like canids (see table 1) followed the recommendation of Berta.⁷ The only canid which did not readily fit into the earlier schemes was *Nyctereutes procyonoides* (raccoon dog). As the name raccoon dog suggests, due to its face mask, it remotely resembles a raccoon. It is the only canid which hibernates. Limb morphology suggested a wolf-like relationship.⁸ Based on masticatory characteristics, Berta⁷ had proposed that *Cerdocyon* (crab-eating fox) and *Nyctereutes* might share a common ancestor, which would have placed *Nyctereutes* among the South American canids, despite it being indigenous to the Far East. However, thermal stability of *Nyctereutes procyonoides*' unique sequence DNA varies by just 1.3°C from *Vulpes vulpes* (red fox), clearly placing it among the fox-like canids;⁴ and more recent sequencing data has confirmed placement of both *Nyctereutes* and *Otocyon* in the *Vulpes*-like clade.⁹

South America canids form their own lineage; geographically, morphologically and genetically. Many are locally referred to as *zorros*, and sometimes the whole lineage is referred to by this name. They live on the mainland of South America and its neighboring islands. Various species were studied by Charles Darwin during his famous voyage on the HMS Beagle. South American

canids sometimes exhibit the peculiar behavior of remaining perfectly motionless on being approached by humans.¹⁰ Darwin actually killed one by simply walking up to it and hitting it on the head with his geological hammer.¹¹ The specimen accompanied him back to England. It belongs to a unique species of canid, the most recently recognized, and is named Darwin's fox (*Pseudalopex fulvipes*) in his honor. Sadly, it is in grave danger of extinction, listed as critically endangered by the World Conservation Union. During that same voyage, Darwin reported that another South American canid, the Falkland Island wolf (*Dusicyon australis*), was the only indigenous mammal on the Falkland Islands. By the end of the 1800s the species had been exterminated by fur traders.^{10,11} These are stark reminders of how fragile many species of wild canid have become.¹²

Hybrid relationships

An important question to clarify concerning the canids is whether they belong to a single, fundamental taxonomic unit.¹³ Do foxes, zorros and wolf-like canids all belong to a common genetic clade? In this respect, the concept of the basic type as a group of interfertile species is very useful.¹⁴ Ernst Mayr's influential definition of the term 'species' emphasized 'ability to hybridize'.¹⁵ Only those animals capable of hybridization belong to the same species. However, many examples of hybridization between species are now known. Clearly, it is more appropriate to use 'ability to hybridize' to define a higher taxon. Because hybridizations occur even between species from separate genera, 'ability to hybridize' seems to define groups of organisms at an even higher taxon; tending towards the taxonomic level of family. Until such definitions can be clarified, the useful term 'basic type' is employed. It should be born in mind, however, that 'ability to hybridize' can be a capricious definition. As a group of organisms changes via recombination and natural selection, its karyotype does not always remain static. Karyotype incompatibility can lead to prenatal mortality, or at best hybrid sterility, and prevent the production of fertile offspring. Various other mechanisms of reproductive incompatibility also exist. This should not detract from the fundamental genetic and phenotypic commonalities shared by species within a basic type. Organisms are still considered to belong to the same basic type if inability to hybridize results from secondary causes. With these limitations in mind, it is felt sufficient to demonstrate that hybridization between the major dog lineages occurs and that at least some hybridization also occurs within these lineages. If this can be done, then the hypothesis 'all extant canids belong to a single basic type', has been reasonably proven.

Table 1. Taxonomy of the order Carnivora. Families after Wozencraft¹, canid subgroups (clades) after Langguth².

Feliformia (Cats and cat allies)

- Herpestidae (mongooses, sometimes included in the Viverridae)
- Viverridae (civets)
- Felidae (cats)
- Hyaenidae (hyaenas)

Caniformia (Dogs and dog allies)

- Ursidae (bears)
- Otariidae (sea lions, and sometimes the walrus)
- Procyonidae (raccoons)
- Mustelidae (weasels)
- Phocidae (seals)
- Canidae (dogs)
- Wolf-like canids: *Canis*, *Cuon*, *Lycaon*
- South American canids: *Atelocynus*, *Cerdocyon*, *Chrysocyon*, *Pseudalopex*, *Speothos*
- Red fox-like canids: *Alopex*, *Otocyon*, *Nyctereutes*, *Vulpes*
- Grey fox-like canids: *Urocyon*

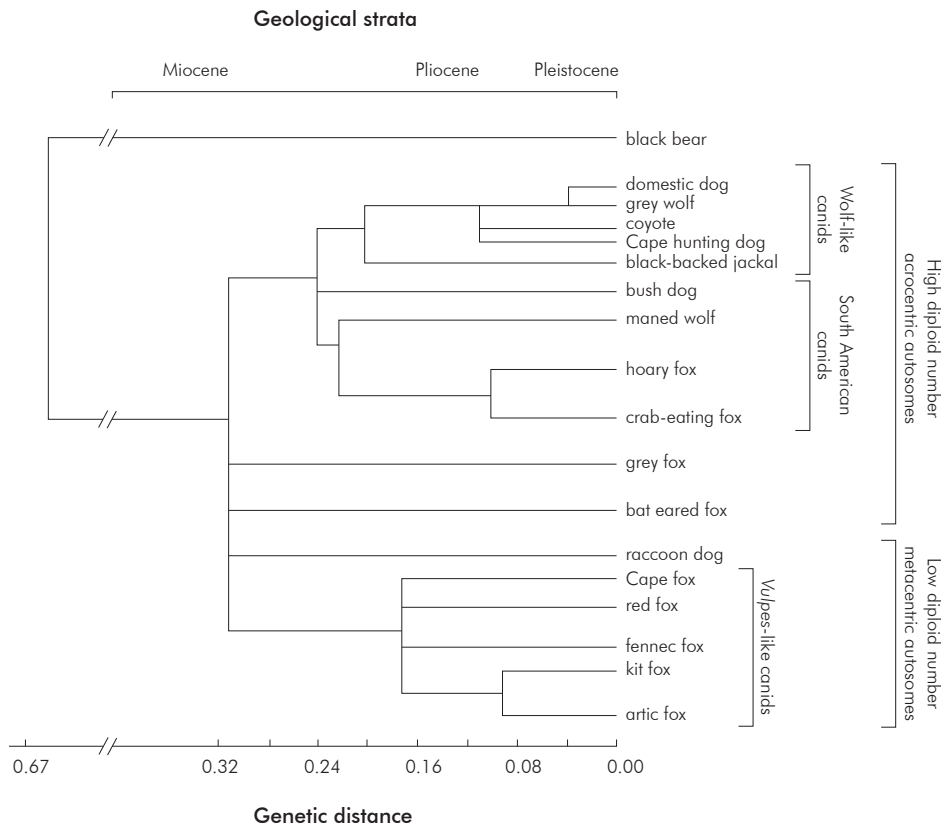


Figure 1. Consensus relationship tree of the canids based on allozyme genetic distance and chromosome morphology (after WAYNE and O'Brien⁶).

Gray's checklist of mammalian hybrids¹⁶ provides an excellent starting point. Many crosses have been attempted or observed between the domestic dog (*Canis lupus familiaris*) and wild dogs, including animals from all four major dog clades (see table 1).

As *Canis lupus familiaris* is descended from *Canis lupus*, it is perhaps not surprising that hybrids have been reported between these animals. Of more specific interest are its ability to hybridize with *Cerdocyon thous* and *Pseudalopex gymnocercus*, both of which belong to the South American canids, and its ability to hybridize with two *Vulpes* (fox) species. *Vulpes vulpes* also hybridizes with *Urocyon cinereoargenteus*, linking the red fox-like canids and the grey fox-like canids. These crosses demonstrate that hybridizations among all four major dog clades are possible. Hybrids within the wolf-like canids are expected to be fertile; they all have 78 chromosomes. Nevertheless, attempts to cross *Canis lupus familiaris* with *Cuon alpinus* have so far been unsuccessful. Successful intra-*Canis* crosses have been reported. Among the fox-like canids, two intergeneric crosses have been reported (see table 2).

No hybrids with 'non-canid' carnivores have been reported, at least none which can be taken seriously.¹⁶ The hybrid list presented here is based primarily on Gray's work. It is not meant to be an exhaustive listing. It is, however, sufficient to demonstrate that all extant canids belong to

a reproductively compatible or single genetic family based on their ability to form hybrids, and as such the extant members of the Canidae represent a single basic type.

Karyotype relationships

Although some trends are observed with respect to chromosome number and type, and the development of the canid karyotypes is a fascinating field of study, karyotypes *per se* are poorly indicative of fundamental canid taxonomy. Excellent studies of the canid G-banded karyotype have been published.^{5,17,18} All of the wolf-like canids have 78 chromosomes, the autosomes of which are usually acrocentric. The chromosome morphology of these species is always similar. The karyotype of *Canis lupus* and *Canis lupus familiaris* appear completely homoeologous (i.e. genetically essentially identical). The South American canids studied also have high numbers

of acrocentric chromosomes. *Chrysocyon brachyurus* (maned wolf) (figure 2) has a diploid complement of 76, having lost chromosome 28. *Speothos venaticus* (bush dog) and *Cerdocyon thous* (crab-eating dog) have a diploid complement of 74, having lost chromosomes 28 and 22. The closely related *Pseudalopex vetulus* (hoary fox) also has 74 chromosomes. *Cerdocyonthous* has a high number of metacentrics: 34 out of 74.

The fox-like canids and *Nyctereutes procyonoides* (raccoon dog) have chromosome numbers ranging from 72 in *Otocyon megalotis* (bat-eared fox) to 36 in *Vulpes vulpes* (red fox). The primary changes include chromosome loss and chromosome fusion. Interestingly, seven fox species possess chromosome 40, which is absent in all the wolf-like and South American canids tested. *Alopex lagopus* (arctic fox) and *Vulpes macrotis* (kit fox) both have 50 chromosomes identical in morphology and banding pattern, and all 48 autosomes are metacentric. *Vulpes vulpes* has 36 chromosomes (32 metacentrics, 2 acrocentrics, and the 2 sex chromosomes). None of these are entirely homoeologous to *Alopex lagopus* chromosomes, although extensive regions of homoeology do exist. *Otocyon megalotis*, *Urocyon cinereoargenteus* (grey fox) and *Vulpes zerda* (fennec) have 72, 66 and 64 mostly acrocentric chromosomes, respectively. All three lack chromosome 34 as does *Nyctereutes procyonoides*. *Nyctereutes* has a range of diploid numbers due to the presence of varying numbers of B chromosomes.

Table 2. Interspecific hybrids within the family Canidae, according to Gray¹⁶ and Alderton¹⁷.

Intragenetic hybrids:	
<i>Canis lupus familiaris</i> x <i>Canis lupus dingo</i> (dingo)	
<i>Canis lupus familiaris</i> x <i>Canis lupus</i> (grey wolf)	
<i>Canis lupus familiaris</i> x <i>Canis latrans</i> (coyote)	
<i>Canis lupus familiaris</i> x <i>Canis aureus</i> (golden jackal)	
<i>Canis lupus</i> x <i>Canis latrans</i> (fertile)	
<i>Canis rufus</i> x <i>Canis latrans</i>	
<i>Canis aureus</i> x <i>Canis latrans</i> (fertile)	
Intergeneric hybrids:	
<i>Canis lupus familiaris</i> x <i>Cerdocyon thous</i> (crab-eating fox)	
<i>Canis lupus familiaris</i> x <i>Pseudalopex gymnocercus</i> (pampas fox)	
<i>Canis lupus familiaris</i> x <i>Vulpes bengalensis</i> (Bengal fox)	
* <i>Canis lupus familiaris</i> x <i>Vulpes vulpes</i> (red fox)	
<i>Vulpes vulpes</i> x <i>Alopex lagopus</i> (arctic fox)	
<i>Vulpes vulpes</i> x <i>Urocyon cinereoargenteus</i> (grey fox)	

* A dog x fox hybrid is on display at 'Haus der Natur', Salzburg, Austria.

The chromosomes of *Nyctereutes* share arm homoeology to chromosomes of canids in each of the major branches of the Canidae. The karyotype is homoeologous to approximately 85% of the *Canis lupus* karyotype.

While the karyotypes of felids, mustelids, ursids and pinnipeds remained relatively stable as these families underwent speciation and adaptive radiations, the karyotypes of canids displayed extensive genome rearrangement.¹⁹ Graphodatsky and his colleagues¹⁹ noted that chromosome variation in carnivores is an excellent example of species, and families, belonging to the same mammalian order but with contrasting genomic organizations, i.e. highly conserved versus highly rearranged. These studies highlight the fact that within an order some families can share very similar karyotypes (even though they may be separate basic types) whereas other families can display significant karyotypic variation. Nevertheless, despite numerous phenotypic traits shared with members of other carnivore families, the postulated canine ancestral karyotype differs by at least 42 fission events and 25 fusion events from the postulated ancestral carnivore karyotype.¹⁹

Using chromosome painting methods, it has been possible to track the karyotype changes that have occurred within the canids, and to determine a consensus canid phylogeny.¹⁹ This phylogeny corroborates the one previously published by Lindblad-Toh and colleagues based on 15 kb of exon and intron sequencing data.⁹ These studies demonstrate that extensive phenotypic variation, even associated with speciation, does not require karyotypic change; for example, as evidenced by the Dhole and domestic dogs. The studies also demonstrate the converse, that phenotypic variation is not necessarily caused by extensive karyotypic change; for example, as evidenced in the raccoon dog, where eight centric fusions distinguish the nominate (Chinese) subspecies' *Nyctereutes procyonoides*

procyonoides, from the phenotypically similar Japanese subspecies, *N. p. viverrinus*.¹⁹ Can underlying genetic causes of speciation be brought to light using such model karyotype systems? Studies of 103 different species of picture-wing *Drosophila* in Hawaii showed the speciation events were accompanied by 214 chromosomal inversion events. The associated karyotypic changes permitted tracking of the species phylogeny. However, there was little to suggest the inversion events were in any way causative of the phenotypic changes.²⁰ Nevertheless, an attempt is currently underway to map and eventually sequence the actual sites of canid chromosome rearrangements.²¹ The hope is that some genetic causes of speciation will be revealed.

Fossil dogs

Basic type taxonomy is based upon hybridization criteria between extant species of organisms. This approach does more than define simple linear relationships between closely related species. The approach tacitly assumes natural limits exist to the morphogenetic (phenotypic) potential of a basic type. Therefore, organisms are placed within polyphyletic or sylvan relationships rather than a single, all-embracing, monophyletic tree of life. Choice between these two models would be easy if intermediate forms were abundantly present in the 'fossil record'. This is not the case, and is a primary reason why punctuated equilibrium models of evolution have become more and more popular in mainstream biology.^{22,23} The unmistakable paucity of intermediate forms is clearly predicted in polyphyletic models of the 'fossil record'.

A second-best (least-worst), monophyletic default-interpretation is what remains. With few, only questionable intermediates to work from, 'default' evolutionary scenarios must suffice.¹⁵ Basal families are designated by default. Within an order, the family (or basic type) represented by the 'oldest' fossils must be the most primitive. The designation is not by proof but by default. It must change if 'older' fossils from another family are subsequently discovered. Always the 'oldest' family must necessarily be designated most primitive. Likewise, link fossils are designated by default. Among the various species in a 'most primitive' family, that species with the 'least-fewest' characters in common with the 'most primitive' (i.e. 'oldest') species from a sister family is necessarily the intermediate or link to that other family. Once again designation is not by proof but by default. Such model-driven interpretation leads to designation of link fossils, but usually in spite of unwieldy fit. Therefore, civet-like (*Proailurus*) or mustelid-like (Hesperocyoninae) species are required to give rise to cats and dogs, early tapir-like species (Hyracotheriinae) are required to give rise to horses, ungulate-like species (Mesonychids) are required to give rise to whales, and so on. The default-interpretation approach is the least-worst option available for interpreting a polyphyletic 'fossil record' within a monophyletic model. One is left with questionable link-fossils inserted into otherwise well-separated families (basic types) of organisms.

Obviously, the polyphyletic model does not require these unwieldy insertions.

Hybridizations observed within basic types provide a theoretical scaffold, which delimits and predicts morphogenetic potential of these groups. The hybridization criterion relates species not by a single or even a few characters but by the theoretical maximum available. It is a holistic rather than a simplistic approach. Biologists often use various cranial and dental characters to identify canids,²⁴ which have proven to be symptomatic, but are not considered causative, of the canid state. For example, if morphogenetic potential within the canids permitted the atypical development of the ‘feliform-characteristic’ bilaminar septum in the auditory bulla of the skull of a particular animal, it would not cease to be a canid. Should more and more characters be found to be of a feliform type, at some stage placement of the animal within the Canidae would be questioned. In practice, characters are chosen which do not lead to inclusion or exclusion errors. If exceptions are found, the characters are replaced, or suites of characters are used to define tendencies. The holistic nature of hybridization is, in effect, a maximum character indicator for species inclusion. Furthermore, the reproductive nature of hybridization resolves at least two acknowledged weaknesses of character-dependent (phenetic) inclusion methods. First, degree of trait variability can be highly irregular, which can lead to ambiguous inclusion criteria in an unknown number of characters (Ernst Mayr’s ‘high variability’ characters¹⁵). Second, trait variability in different characters is interconnected by ill-defined genetic mechanisms, which leads to unknown bias in the importance of different traits (Ernst Mayr’s ‘redundant’ characters¹⁵). Hybridization naturally ensures it is all the characters, and

primarily those characters vital to ontogenetic success that define species inclusion.

The occurrence of hybridization in extinct species is almost impossible to assess. Therefore, basic type categorization of fossils must employ alternative approaches. Three versatile principles are listed below. If such principles cannot be applied, ‘unspecified basic type’ status is retained, even though classification into higher taxa may still be undertaken using various contemporary techniques.

If the phenotype of the fossil falls:

1. Within the holistic morphogenetic space of a basic type, as delineated by the documented hybridizations between species, inclusion within the basic type is considered appropriate.
2. Outside this holistic morphogenetic space, but within its reasonable morphogenetic potential, inclusion within the basic type is indicated.
3. Within the holistic morphogenetic potential of a basic type, but displaying a limited number of characters used to define organisms outside the basic type, inclusion within the basic type is indicated, and the reliability of the defining characters is questioned.

The holistic approach to phylogenetic categorization of fossils, based on the concept of basic types and ability to hybridize, avoids unnecessary multiplication of anachronistic or ‘chimeric’ forms at basal locations in otherwise monophyletic clades. It leads to clarification of a number of fossil relationships, and it indicates limits to morphogenetic potential which can be tested empirically.

Canids are typically recognized by three aspects of cranial anatomy: the type of auditory bulla, the location of the internal carotid artery, and specific features of dentition. The family Canidae, both extant and extinct, is currently recognized as comprising three major subfamilies; the Caninae, and two others known only from fossil specimens.^{25,26} The Caninae and the Borophaginae are considered sister groups. The third subfamily, Hesperocyoninae, appears to include a different kind, or type, of animal. Many Hesperocyoninae species are known only from cranial remains. They are placed within the Canidae based on the three characteristic aspects of cranial anatomy. However, the post-cranial skeleton (when available) emphasizes the separate nature of these animals. The skeleton displays a short muzzle (rather than an elongate snout), a long tail and a long, slender body shape.^{11,27,28} The features are far more reminiscent of various Mustelidae, whose auditory bulla can be very similar to those of the Canidae.^{29,30} From a holistic perspective, which takes into account both cranial and post-cranial characteristics, the Hesperocyoninae appear to belong to a basic type separate from the other two canid subfamilies; possibly a mustelid-like animal.²⁴

The Hesperocyoninae are considered forerunners of both the Borophaginae and the Caninae. An excellent and comprehensive review of the Hesperocyoninae, with many photographs of fossil skulls, is available from Wang.²⁸ Their dental pattern is I3/3, C1/1, P4/4, M2/2. This is



Photo courtesy of Sage Ross

Figure 2. *Chrysocyon brachyurus*, the maned wolf. Sometimes referred to as a fox on stilts, its long legs help it to see over the tall pampas grass. Its karyotype is very similar to that of the grey wolf but has 76 chromosomes instead of 78, having lost a single chromosome pair.

typical of canids and viverrids, and close to badger and wolverine dental patterns (both mustelids). The relatively prominent carnassials and the inflated auditory bullae are more indicative of canid and mustelid types than the viverrid type. Distinguishing between extant species of canid and mustelid is readily accomplished by examining the rostral part of the skull (see figure 3). This is drawn out into a prominent snout in canids, often accompanied by an excellent sense of smell. In mustelids the muzzle does not display this rostral extension; the infraorbital foramen (a hole through the skull just in front of, or below, the orbit) is not stretched and remains a prominent and characteristic hole. Viverrids display a somewhat intermediary state, very like the Hesperocyoninae; an abbreviated snout but with a prominent infraorbital foramen.

Specimens from the fossil record paint an intriguing picture. The basal canid species, *Prohesperocyon wilsoni*, has many cranial features typical of canids, including the extended snout. However, it is placed as *Canidae incertis cedis* ‘canid of uncertain status’.²⁸ This is because it is considered ancestral to the far less dog-like Hesperocyoninae. Therefore, *Prohesperocyon* is prematurely dog-like and so cannot be a dog. The subsequent canid fossils include skulls of the Hesperocyoninae. When available the post-cranial skeletons of the Hesperocyoninae are slender and long-tailed, similar to that of viverrids or mustelids,²⁷ and they possess a prominent baculum, typical of mustelids and occasional viverrids, but not like canids. In addition, the musteloid species *Mustelavus*, which is found in the same stratum as Hesperocyon, had an identical dental formula and similar skull and dental proportions; it was simply 25% smaller.²⁸ These many features strongly support placement of the Hesperocyoninae among mustelid (or perhaps viverrid) carnivores rather than among the canids. The fossils at least, if not the monophyletic interpretation, place *Prohesperocyon* as the ancestral dog.

Of the various clades of Borophaginae, members of the basal clade thought to link the Borophaginae to the Hesperocyonidae include *Archaeocyon*, *Oxetocyon*, and *Otarocyon*. They share much in common with *Hesperocyon*, and it has been acknowledged that cladistic analysis might fail to place these basal species in the monophyletic Borophaginae subfamily.³¹ It is submitted that the Hesperocyoninae and these closely similar basal Borophaginae belong to a separate mustelid-like (or viverrid-like) basic type. The more recent Borophaginae appear to be a sister clade of the Caninae. The enhanced dental features of the Borophaginae, in some cases for crushing bone, appear to lie reasonably within the morphogenetic potential of the canid basic type. If so, non-basal Borophaginae and Caninae may have arisen from a common basic type. To summarize, evaluation of extant and extinct Canidae suggests that current interpretation of the family actually encompasses a biphyletic clade: the Canidae and the Hesperocyoninae.

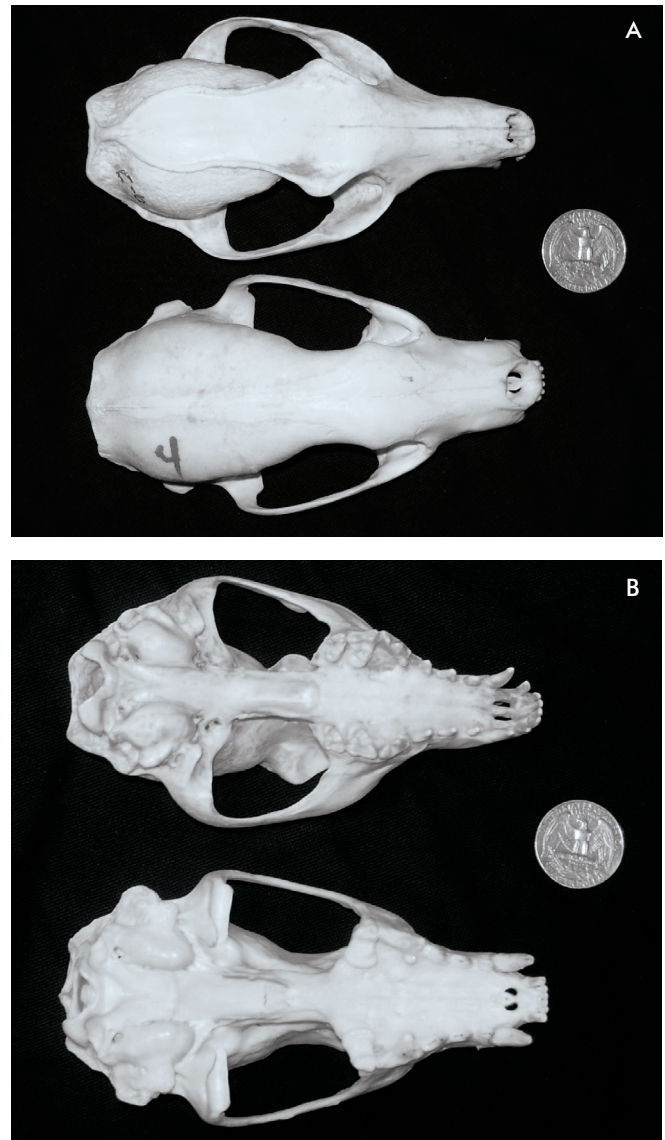


Figure 3. Crania of *Urocyon cinereoargenteus*, the grey fox (top), and *Martes pennanti*, the fisher (bottom). **A)** view from above; **B)** view from below. The rostrum of the grey fox (and all dogs) forms an extended snout, which results in the eyes being located approximately half-way along the skull, creating room for an extra set of molar teeth and the typically longer face of canids. The rostrum of the fisher is shorter, which results in the eyes being located less than 40% of the way along the skull, creating the typically shorter face of mustelids. Despite the similarity of the two crania, the two animals belong to separate families of carnivores. The grey fox is a small-sized species of canid. The fisher is a medium-sized species of mustelid. The cranium of the fisher is similar to that of the Hesperocyonidae. The dental formula of the fisher is: I3/3, C1/1, P4/4, M1/2; of the Hesperocyonidae is: I3/3, C1/1, P4/4, M2/2, and of the grey fox is: I3/3, C1/1, P4/4, M2/3.

The domestic dog: *Canis lupus familiaris*

The domestic dog, *Canis lupus familiaris*, is a grey wolf.^{5,33} Karyotypic and mitochondrial DNA sequence evidence clearly demonstrates this. Mitochondrial DNA sequences between the domestic dog and the grey wolf differ by at most 0.2%. This is to be compared with a 4%

difference between the grey wolf and the coyote (*C. latrans*) and a 4% difference even between some populations of grey wolf.⁵ Morphologically, however, the domestic dog displays an unsurpassed degree of variation. One clear example is size variation, which in the domestic dog surpasses that of all other living and extinct species of dog.³⁴ In many cases differences observed in the domestic dog are at least as great as differences observed between genera of wild canids. Before cytogenetic and DNA analyses were available, the morphological differences led to the erroneous assumption that dogs arose from a number of wild canids. Based on the diversity of breeds, on geographical and on other considerations Darwin thought it “highly probable that our domestic dogs have descended from several wild species”.^{35,36} This is not the case. The domestic dog is descended from the grey wolf only.

A number of recent genetic studies have pieced together the following history of domestication. During the Pleistocene, domesticated dogs began to appear in Asia and migrated with nomadic human groups both south to Africa and north to the Arctic, with subsequent migrations throughout Asia and via the Bering Strait into the Americas.³⁷⁻⁴¹ There are fascinating parallels between these hypothesized dog migrations and our contemporary understanding of human migrations, especially as evidenced by studies of human genetic haplotypes and the development of languages.⁴² Experimental evidence suggests that dog domestication may have been rapid. Recently, Trut and colleagues reported on extensive domestication studies in the silver fox.⁴³ Ten generations were sufficient to select for domestication. The study demonstrated both the rapidity of the process, under guided selection, and the simultaneous drop in glucocorticoid blood levels in the animals, which appears to provide a biochemical explanation for the alteration in behavior. A number of unique phenotype changes accompanied domestication in the foxes. The same changes are thought to have accompanied domestication of the dog.^{43,44} It is still unclear whether the unique form of dominant melanism observed in dogs, which is exceptional among mammals, arose before or after domestication occurred.⁴⁵

Since domestication, dog breeding has been characterized by significant phenotypic diversity but little genetic diversity. Wayne provided interesting insights into dog diversification when he asked the question: “In what ways can morphology change in the absence of appreciable genetic change?”⁴⁶ Using the three-pronged approach of bivariate allometry, discriminate analysis, and allometric scaling to compare 21 dental and cranial measurements, Wayne concluded that most small breeds of domestic dog are paedomorphic with respect to certain morphologic characters, and that potential morphologic diversity depends on the spectrum of diversity expressed during development. In a second study of canid limbs identical conclusions were reached.⁴⁶ Limb proportions of adults of small dog breeds correspond to those of the juveniles of larger dog breeds. Although

the large domestic dog breeds are very similar to the grey wolf, all the small breeds are to some extent juvenilized or paedomorphic.⁸ Despite phenotypic change not requiring genetic change, the latter is an ongoing process, and in the case of length variations in tandemly repeated sequences, these have been shown to be a significant source of morphological variation within breeds.⁴⁷

Despite the large spectrum of diversity displayed among domesticated breeds, no fox-like dogs have been observed. It would appear that wolves no longer have the genetic potential to form a fox-like canid. Wayne studied cranial morphology.⁴⁶ Foxes have small, narrow skulls. Domestic breeds include those with small skulls (toy breeds) or with narrow skulls (Russian wolfhounds and Salukis) but of the breeds sampled, none displayed both features. If skull length was increased but overall growth rate reduced, small dogs with long, narrow skulls, not unlike foxes, would result. Similarly, the domestic dog displays an impressive diversity of limb sizes and proportions. Here, too, allometric analysis of the limb demonstrates close kinship with the wolf-like canids, but not with other wild canids such as the fox.⁸ The wolf/fox transition involves complex phenotypic changes. Modulation or activation of suites of genes is required for this process; no simple mutation event appears to suffice. The selective breeding of the domestic dog does not appear to be able to mimic this process and to produce a fox.⁴⁶ Mechanisms involving simply mutation and selection are unable to produce a fox. An alternative model, requiring creation of no new genetic information, is one where early dogs possessed combinations of alleles able to produce both wolf and fox phenotypes. In subsequent generations, due to loss of heterozygosity and reproductive isolation, wolf-like descendants lost the alleles critical for the fox phenotype. Because domestic dogs are descended from the grey wolf, they also lack these fox-alleles, which is why selective breeding in dogs has been unable to give rise to foxes. However, dogs and foxes belong to the same basic type, and dogs are able to hybridize with foxes. Under these circumstances fox-alleles can be reintroduced into the dog genome. The presence of chromosome 40 in many fox species and its absence in wolf-like and South American canids make it a candidate repository for at least some of the missing fox-alleles.

The behavioral studies of Trut and colleagues in Novosibirsk indicated that tameness (domestication) is dormant in foxes. Once selected for, and it required only 10 generations, the behavior greatly resembled tameness in wolves, i.e. domestic dogs, even though foxes and wolves are genetically well separated.^{48,49} Selection for tameness was accompanied by co-segregation of additional morphological traits, including floppy ears, rolled tails, and changes in skull shape.⁴⁸ Such studies indicate that although in some instances traits may be lost from populations, for instance by gene fixation, and can no longer be selected for, i.e. the fox phenotype in wolves; in other instances traits can lie dormant in genomes, perhaps suppressed by regulatory genes, and

these can be ‘reactivated’ upon artificial selection. Raccoon dog skulls greatly resemble those of South American foxes, particularly the crab-eating fox (*Cerdocyon thous*), even though these two species are genetically well separated.⁵⁰ Skull shape variation may be ‘hard-wired’ into the canid genome.

Activation of common, inherent genetic potential by carnivore species

An exception to the rule, ‘large domestic dogs are morphologically equivalent to grey wolves’, is seen in their dentition. Grey wolves usually have longer teeth than equally sized domestic breeds. In fact tooth dwarfism frequently accompanies animal domestication.⁴⁶ This observation probably reflects a general feature of the carnivore phenotype. The heart of the wolf pack is the breeding couple. It is invariably the only couple who mate. These individuals are the fittest, most aggressive animals. Any trait in their phenotype which promotes this type of dominance such as tooth length, body size, or assertive behavior, will be positively selected for. Domestication, however, will be accompanied by a relaxation of this strict selection pressure (unless the features are artificially selected for). Thus, the natural state of an animal biases selection towards particular extremes of its potential phenotypic diversity. This accounts for the phylogenetic inconsistency reported by Wayne⁴⁶ in the pattern of morphological similarity between breeds of domestic dog and the grey wolf. The placing of the grey wolf, although clearly the progenitor of the domestic breeds, is not intermediate within the range of the breeds but peripheral. The traits responsible for this inconsistency were the generally greater size and the longer teeth of the grey wolf, which are precisely those traits predicted to be at their extremes due to natural selection pressure.

Another interesting aspect of canine dental adaptation is the development of a trenchant heel on the carnassial teeth of three canid species: *Cuon alpinus* (Dhole), *Lycaon pictus* (African wild dog), and *Speothos venaticus* (bush dog). The carnassials are composed of an anterior cutting blade (trigonid) and a posterior grinding basin (talonid). In canids with a trenchant heel, the talonid basin is reduced and altered to form a second blade. A reduction of the post-carnassial molars occurs parallel with this. It is similar to the carnivorous dentition observed in felids. Because there is a wide biological distance between *Speothos* and the other two canid species, it has been proposed that the trenchant heel developed independently at least twice.⁶ However, this dental pattern is observed in a number of carnivore families. It seems more likely that it reflects activation of common genetic potential among the carnivores, rather than the repeated development of new genetic information and novel phenotypic traits. Activation of common genetic potential could also be responsible for the presence of additional teeth in *Otocyon megalotis* (bat-eared fox), reflecting its more omnivorous diet. Similarly, activation of common genetic potential could also cause change in toe number in various

dogs: from five to four on the front limbs of *Lycaon pictus* (African wild dog), and from four to five on the hind limbs of some breeds of *Canis lupus familiaris* (domestic dog).

Not only dentition but also coat color schemes are shared among carnivores, and mammals in general.^{51,52} *Alopex lagopus* (arctic fox) displays two coat colors, the winter pelage being snow white. This trait is shared by the Corsac fox (*Vulpes corsac*), though it is less pronounced. The unrelated mustelid, *Mustela erminea* (stoat/ermine), similarly shares this trait. Although white coat color may have arisen independently in foxes and stoats, the trait probably results from simple activation of common genetic potential within at least the order Carnivora; certainly a number of other species display white coat-color variants. Another example of a shared trait is the face-mask of *Nyctereutes*. In its bushy summer coat with its black eye-cheek patches, white snout, and white forehead, it looks like a raccoon, at least at first glance. This face-mask is also shared with *Otocyon megalotis* (bat-eared fox) among the dogs, with *Procyon* (the raccoons), *Ailurus fulgens* (lesser panda), *Ailuropoda melanoleuca* (giant panda), *Tremarctos ornatus* (spectacled bear), *Mustela putorius* (common polecat), *Mustela eversmanni* (Steppe polecat), *Viverra civetta* (African civet) and *Paradoxurus hermaphroditus* (palm civet). It appears unlikely that the face-mask is under such strong selective pressure that it would develop independently in all these species. It is more likely that the trait is caused by activation of common genetic potential within the order. A further example of common genetic potential involves the long-legged, narrow-bodied, large-eared phenotype typical of the grassland carnivore ecomorph, which both the maned wolf (*Chrysocyon brachyurus*) among the canids, and the serval (*Felis serval*) among the felids, so clearly exemplify. Therefore, although the canid basic type is unique, it appears to use genetic potential common to various basic types of carnivore.

Conclusion

The primary requirement of belonging to a single basic type, ability to hybridize, is fulfilled by the canids. In addition to this, on the basis of their single gene sequence homologies and the thermal stability of DNA duplexes, the canids clearly belong to a unique group, and karyotype data also supports this. Canid karyotypes have far more in common with each other than with other members of the Carnivora. Therefore, the extant canids form a recognizable and fundamental taxonomic unit with the status of basic type. Currently recognized extinct canids, however, appear to include animals from at least one other basic type.

The Canidae are a part of the order Carnivora, and have various traits in common with members of other carnivore families. These include features of karyotype, morphology, dentition, and coat colour. This suggests that the various carnivore families have much genetics in common. The term ‘common genetic system’ could be applied here.³ The canid pattern adopts the common carnivore ‘phenotype’ as a base

from which to express its unique set of characters. However, boundaries defined by natural hybridization potential ensure that, although the Canidae are a part of the order Carnivora, they represent a unique basic type with a recognizable and separate identity. Defining the extent and nature of such boundaries is a significant goal of future studies in basic-type research.

Appendix

The 36 recent Canidae, after Sillero-Zubiri *et al.*⁵³ and Lindblad-Toh *et al.*⁹

Wolf-like canids (9)

<i>Canis lupus</i>	grey wolf (incl. dog & dingo)
<i>Canis rufus</i>	red wolf
<i>Canis latrans</i>	coyote
<i>Canis aureus</i>	golden jackal
<i>Canis simensis</i>	Ethiopian wolf
<i>Cuon alpinus</i>	dhole
<i>Lycaon pictus</i>	African wild dog
<i>Canis adustus</i>	side-striped jackal
<i>Canis mesomelas</i>	black-backed jackal

South American canids/ Zorros (11)

<i>Chrysocyon brachyurus</i>	maned wolf
<i>Speothos venaticus</i>	bush dog
<i>Atelocynus microtis</i>	short-eared dog
<i>Cerdocyon thous</i>	crab-eating fox
<i>Pseudalopex culpaeus</i>	culpeo
<i>Pseudalopex fulvipes</i>	Darwin's fox
<i>Pseudalopex griseus</i>	chilla
<i>Pseudalopex gymnocercus</i>	pampas fox
<i>Pseudalopex sechurae</i>	Sechuran fox
<i>Pseudalopex vetulus</i>	hoary fox
<i>Dusicyon australis</i>	Falkland Island wolf (†)

Red fox-like canids (14)

<i>Nyctereutes procyonoides</i>	raccoon dog
<i>Otocyon megalotis</i>	bat-eared fox
<i>Vulpes bengalensis</i>	Indian fox
<i>Vulpes cana</i>	Blanford's fox
<i>Vulpes chama</i>	Cape fox
<i>Vulpes corsac</i>	corsac fox
<i>Vulpes ferrilata</i>	Tibetan fox
<i>Vulpes macrostis</i>	kit fox
<i>Vulpes pallida</i>	pale/pallid fox
<i>Vulpes rueppelli</i>	Rueppell's fox
<i>Vulpes velox</i>	swift fox
<i>Vulpes vulpes</i>	red fox
<i>Vulpes zerda</i>	fennec fox
<i>Alopex lagopus</i>	arctic fox

Grey fox-like canids (2)

<i>Urocyon cinereoargenteus</i>	rey fox
<i>Urocyon littoralis</i>	island fox

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Barnabas Pendragon holds a B.Sc. (hons.) (1980) and an M.Sc. (1982) from the faculty of science at Manchester University, England, a Ph.D. (1987) from the faculty of science at the Justus Liebig University, Giessen, Germany, and a D.Sc. (1998) from the faculty of medicine at Zurich University, Switzerland. He has published almost 100 scientific papers and is a referee for ten international science journals. He has taught and held consultancy positions throughout Europe, USA and Asia.
