1 What makes a wolf

The zoological order Carnivora includes the canids. When discussing its members the term *carnivoran* is preferable to carnivore because it excludes unrelated predators.[1] Modern canids appeared about 10 million years before the present (years BP) and diverged into two branches, the dogs and the foxes.[2] Depending on how you divide them, living canids number about 35 species.[3] They have 78 *chromosomes*, and all are known to *admix*.[4] The golden jackal (*Canis aureus*) and gray wolf (*Canis lupus*) have been considered the domestic dog's possible ancestors,[5] and although all evidence points to the gray wolf,[6] some raise other possibilities, such as an extinct and unknown wolf-like canid.[7] Two of these are the dingo and a hypothetical and now extinct wild dog similar to the dingo.[8] The next closest relatives of gray wolves and domestic dogs are the coyote and Ethiopian wolf (*Canis simensis*), less accurately called the Simien jackal.[9] As later chapters should help clarify, implications of these relationships reach out from the past, affecting the behavior and social lives of all members of the genus *Canis*, including the domestic dogs we keep as pets.

1.1 Wolves in the beginning

The family Canidae (*Canis* means dog in Latin) evolved in North America, first appearing in the late *Miocene* 6 million years BP.[10] When North America and Asia formed a high-latitude connection in the late *Cenozoic* (3 million years BP) some canids migrated across, where they continued to evolve, and one returned later as the gray wolf.[11] The record infers that North American wolves and the coyote separated about 1–2 million years BP,[12] although genetic findings point to the gray wolf's origin being only 250 000 years BP.[13] According to a slightly different hypothesis, the gray wolf might have evolved in Asia and migrated to North America about 300 000 years BP across the Bering land bridge when sea levels were lower than today.[14]

At one time the gray wolf was the world's most widely distributed carnivoran,[15] ranging from Portugal to Siberia and throughout the Arctic, south into the Arabian peninsula and the rest of the Middle East, from the Himalayas to the Indian peninsular plains, and east into China.[16] Before Europeans arrived gray wolves could be found nearly everywhere in North America, from the Arctic deep into

Mexico. The exception was the southeastern US, thought by some to be occupied by an animal with relict descendants known today as the red wolf (*C. rufus*),[17] although this is doubtful (Section 1.4).

On the central plains modern ancestors of today's wolves preyed on American bison (*Bison bison*), toward the north and into Canada on moose (*Alces alces*), caribou (*Rangifer tarandus*), and elk (*Cervus canadensis*), and elsewhere on antelope, wild sheep and wild goats, and various species of deer. To European settlers wolves were vermin. Fur trappers, bounty hunters, farmers, government poisoning programs, and, it seems, any citizen with a gun, eventually killed them off,[18] sparing a few survivors in national parks and remote regions unsuited to human habitation or exploitation. The unfortunate experience of Old World wolves is similar and started much earlier.[19]

The opening of the North American landscape by European immigrants and their descendants altered ecosystems, making them better habitats for rodents, rabbits, and other small mammals, the principal prey of the coyote, which is indigenous to North America.[20] Before 1850 coyotes occupied an area west of the Mississippi River into the Sierra Nevada Mountains and California, south into Mexico, and north into Alberta.[21] Today their latitudinal range from Central America to northern Alaska exceeds that of any other terrestrial mammal.[22]

This rapid expansion began early in the twentieth century in conjunction with the sharp decline in wolf *populations* brought about by "predator control," clearing forests for timber and agriculture, and human competition for large game.[23] The coyote is smaller and less conspicuous than the wolf. It requires less space,[24] lives in flexible societies,[25] is comfortable near humans in urban and suburban areas,[26] scavenges efficiently,[27] and can exist on small prey[28] adapted to disturbed habitats.[29] Wolves often prefer forested areas, coyotes open spaces.[30] As the wolves and forests disappeared the coyotes moved in, and in the east they took up living in wooded areas too.[31]

Although fluid dispersal of a species is not a guarantee of rapid gene flow, mobility heightens the likelihood of genetic exchange.[32] The consequence can be surprisingly small genetic variations among broadly dispersed populations. Coyotes have a more diverse *genotype* than wolves[33] brought about by an astonishing capacity to disperse and high gene flow through their populations. A survey of 327 coyotes revealed 32 genotypes and a gene flow so rapid that today's coyotes are moving quickly toward homogenization.[34] The same genotypes, for example, have been recovered from animals as widely dispersed as California and Florida.[35] Nonetheless, genetic evidence shows US coyotes to still cluster in three major groups: western, Midwest/southeast, and northeast.[36]

1.2 Modern wolves

The gray wolf's extensive range gave rise to regional variations in morphology. Dozens of scientific names (many of them synonyms) have been ascribed historically based on coat color, size, skull morphology, geographic distribution, and

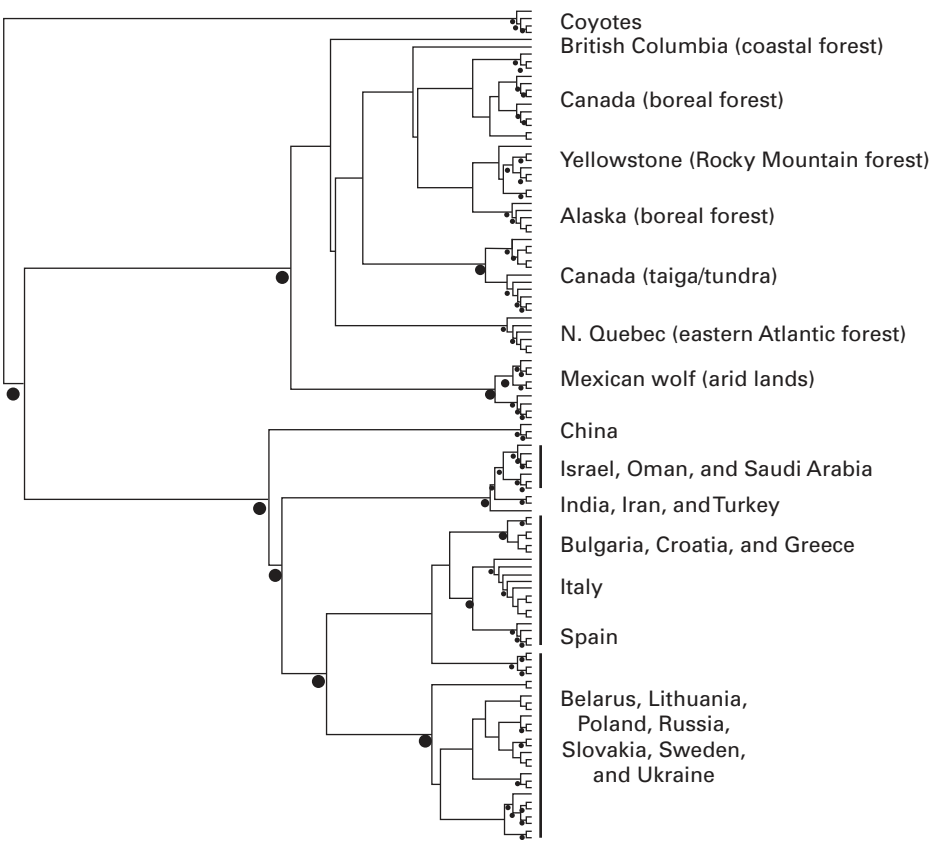

Figure 1.1 Neighbor-joining cladogram for non-admixed wolf populations using a 48 000 SNP data set. Dots show >95% bootstrap support of 1000 replicates. *Source*: vonHoldt *et al*. (2011).

other aspects of natural history and physical appearance.[37] Until recently the high tendencies of wolves to disperse have called into question any notion of long-term restriction to particular localities and subsequent speciation. North American gray wolves have been known to disperse hundreds of kilometers in a few months.[38] Identical genotypes appear in specimens from northeastern Minnesota and Inuvik in Canada's Northwest Territories (3100 km), and from Montana to Nome, Alaska (3600 km).[39] Dispersal distances of Old World wolves are equally impressive (Chapter 5).[40]

Nonetheless, as demonstrated by Bridgett M. vonHoldt and co-authors, gray wolves worldwide, like coyotes in North America, cluster regionally (Fig. 1.1) as assessed using *single-nucleotide polymorphisms* (*SNPs*).[41] Partial explanations include habitat-biased dispersal (Chapter 6) and *genetic drift* caused by habitat fragmentation, forcing of wolves into isolated pockets over centuries of persecution.[42] Genetic variability, which is essential for healthy populations, is reduced by discontinuous habitats and low population numbers.[43]

The two populations of wolves in India appear to be genetically unique.[44] A group of about 350 individuals (called here the Indian Himalayan wolf) inhabits the Trans-Himalayan region spanning India's two northernmost states.[45] The other, numbering about 1500 (here called the Indian plains wolf), is found on the arid and semi-arid plains of peninsular India. Both show strong within-group *homogeneity* in having unique *haplotypes* and clustering separately from all other gray wolves including the nearest geographic populations. The Indian Himalayan wolf clustered separately from so-called Tibetan wolves; the Indian plains wolf formed a separate cluster from the so-called Middle Eastern wolf.[46] They appear to be distinct with no overlap in haplotypes with other gray wolves around the world.[47] This population "was found always to be basal to the other major clade comprising all other wolf haplotypes and closest to the jackal, one of the closest ancestral canid species, suggesting them to be the derivatives of a more ancient independent wolf radiation."[48] By this assessment, Indian wolves are the most divergent of the gray wolves, representing a relic ancestral lineage long isolated.[49] If so, their genetic composition could be evidence that wolf-like canids first evolved in Asia. The authors of this study proposed giving them full species status, *Canis himalayensis*[50] and *C. indica*.

1.3 Great Lakes wolf

The heritage of wolves in southeastern Canada and the northcentral and northeastern United States, already complicated, got moreso in the early 1900s shortly after most wolves had been exterminated and coyotes began expanding east through the Great Lakes states into Ontario.[51] Coyotes were historically restricted to the US south and southwest. Their simultaneous movement into other western regions appears not to have affected the genetics of western gray wolves (see below).[52] Relationships among the canids discussed here and in the next two sections are summarized diagrammatically in Fig. 1.2.

By 1975, before availability of modern molecular techniques, researchers recognized four "races," or "types," of Ontario wolves based on skull morphology: (1) a large, conventional-looking gray wolf (*Canis lupus hudsonicus*) in the northern reaches occupying subarctic *tundra*; (2) a similar animal (*Canis lupus lycaon*) in the boreal forest around Hudson Bay and called the "Ontario type;" (3) a wolf resembling (2) from deciduous forests of the upper Great Lakes (also designated *Canis lupus lycaon*) and called the "Algonquin type"; and (4) a purported *admixture* between the "Algonquin type" and western coyotes called the *Tweed wolf*.[53]

North American wolves had undergone several prior taxonomic revisions based on morphology,[54] but this one stood up well to later genetic testing.[55] An animal from Québec described originally by Johann Christian Daniel von Schreber in 1775 as a separate species (*Canis lycaon*)[56] and later by others as a subspecies of gray wolf (*C. lupus lycaon*)[57] was thought to be synonymous with the "Algonquin type," which supposedly evolved in North America. If true, this

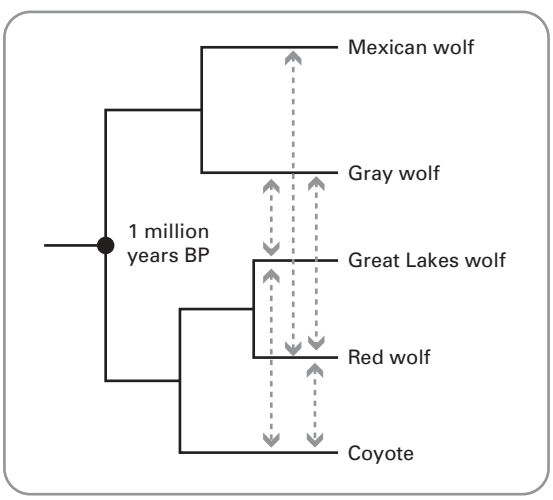

Figure 1.2 Joining tree showing hypothetical admixing (dashed lines) among North American canids.
Source: vonHoldt *et al*. (2011).

would make it North America's only endemic wolf, the ancestors of all others having immigrated from Eurasia. Applicable synonyms are *eastern wolf*, *eastern timber wolf*, and *eastern Canadian wolf*. Its descendants today, remnants of a unique population in existence before the arrival of Europeans, reside in *Algonquin Provincial Park*, Ontario, and the immediate surrounding area[58] separated by its unique C1 *mitochondrial DNA* (*mtDNA*) haplotype[59] and an apparent shared ancestry with western coyotes.[60] Return of this population to full species status as *C. lycaon* has been advocated.[61] Whether or not it happens remains to be seen. I doubt whether any admixed canid can properly be labeled a species, the obvious gradation in genomic composition making even the use of "coyote" and "wolf" problematical. Meanwhile, I use *Algonquin wolf* when referring specifically to descendants of the extinct lineage.

The historical range of wolves in central and eastern regions of the US and Canada included Québec, Ontario, parts of Manitoba, the western Great Lakes states (Minnesota, Wisconsin, Michigan), New York, Pennsylvania, New Hampshire, and Vermont.[62] Those occupying the Great Lakes region today (including Algonquin Provincial Park) form a genetically admixed[63] population of western gray wolves, coyotes, and traces of the extinct endemic wolf,[64] and collectively called *Great Lakes wolves*. This heritage separates them from gray wolves occupying the American and Canadian west and Eurasia.

Great Lakes wolves diverge noticeably in appearance from gray wolves, distinguished by: (1) smaller size, (2) darker color (generally gray with dark back and pale undersides grading into fawn-gray), (3) slender rostrum, and (4) long ears relative to body size.[65] In his 1944 review, Edward A. Goldman noted presciently, "Specimens from the Great Lakes region represent a wide range of individual

variation in size and cranial details, and grade toward the more robust plains [gray] wolf."[66] Morphology and modern genetics validate his statement: today's admixture, as just noted, carries a heritage of western gray wolves and descendants of historical (i.e. endemic) wolves from the east that retain a coyote heritage.[67] It represents a genotypic/phenotypic cline, coyote-like toward its eastern limit (to about 50%) and increasingly wolf-like (to nearly 100% gray wolf) toward the west.[68] The *genomes* of Great Lakes wolves average about 15% coyote ancestry and >84% wolf, but the Algonquin wolves are 42% coyote, the most of any in the Great Lakes population.[69]

The Great Lakes wolf's smaller size probably explains both its history of breeding with coyotes[70] and confusion about its origin. Through the years it has been considered: (1) a distinct and valid species,[71] (2) a subspecies of gray wolf,[72] (3) a gray wolf × red wolf admixture,[73] (4) a gray wolf × coyote admixture,[74] (5) an admixture of coyote × Algonquin wolf,[75] (6) an admixture of gray wolf × coyote × Algonquin wolf,[76] (7) a smaller gray wolf *ecotype*,[77] (8) *conspecific* with the red wolf (Section 1.4) and both derived from a coyote-like ancestor,[78] (9) a wolf admixture of unknown heritage,[79] and (10) a gray wolf × Algonquin wolf admixture.[80] Hypotheses (6) and (10) are little different because a large part of the Algonquin wolf's genome is coyote. The large wolf component relative to coyote in Great Lakes wolves toward the west suggests extensive crossing back of offspring with wolves but not coyotes.

Admixing between coyotes and gray wolves around the Great Lakes is not entirely a result of coyote encroachment starting early in the twentieth century.[81] Genetic evidence shows the process occurring 546–963 years BP, prior to when Europeans arrived and disturbed the landscape.[82] Pre-Columbian remnants of coyotes have been found in Ontario, Maryland, and Pennsylvania;[83] as mentioned, ancient coyote mtDNA is still detectable in Great Lakes wolf haplotypes.[84] Remains of an extinct coyote-like canid from Québec (400–500 years BP) demonstrates earlier eastern occupation and overlap with wolves now extinct.[85] Coyotes later disappeared from these areas,[86] their descendants not moving north and east again until humans cut down the forests and killed the resident wolves.

Gray wolf × coyote admixtures are notably absent from northern and western North America.[87] Because mtDNA is inherited only from the maternal lineage, the absence in coyotes of gray wolf mtDNA means that female gray wolf × male coyote crosses either do not occur or the progeny fail to integrate into coyote populations.[88] In addition, western gray wolves commonly kill coyotes where the two are *sympatric*, and any close interaction is likely to be tense and unfriendly (Chapter 6). Whereas gray wolves make war on coyotes (Chapter 6), Great Lakes wolves make love to them. Thus gray wolves rarely mate with coyotes, but Great Lakes wolves, by being admixtures, do. As one group of collaborators wrote: "The absence of a Canis [genetic] soup in western North America appears to be attributed to the absence of *C. lycaon* [the Great Lakes wolf], which easily hybridizes with coyotes and can hybridize with gray wolves, thus mediating

gene flow among the 3 species."[89] In contrast, coyote genes in Mexican gray wolves, which once ranged into the American southwest and were recently reintroduced there,[90] are barely detectable as genetic background noise.[91] The Mexican wolf is a gray wolf, and its historical reproductive isolation from coyotes is not surprising.

Goldman pointed out the slender muzzles of eastern specimens, their generally small size but grading toward the larger gray wolf, and a resemblance to the red wolf.[92] As mentioned, some authorities see the Great Lakes wolf simply as a gray wolf ecotype or admixture; others disagree and consider it unique. The longitudinal and latitudinal variety expressed by gray wolves inspired several subspecies descriptions. Such variation is common in wolves everywhere,[93] even regions of restricted space. Israel is slightly smaller than New Jersey, extending 418 km at its greatest length. Its northern climate is Mediterranean, and wolves there were historically larger and darker than those inhabiting the arid south.[94] The southern wolves, in adapting to desert conditions, have become smaller, pallid, and able to withstand dry conditions, having been sighted 50 km from the closest source of water.[95]

The Great Lakes wolf genome persists despite rigorous three-way gene flow with *eastern coyotes* (Section 1.5) in the eastern part of its range and gray wolves toward the west.[96] Where admixing with gray wolves it grows bigger.[97] As mentioned, Great Lakes wolves indigenous to Algonquin Provincial Park and vicinity differ genetically from other Great Lakes wolves, and to some authorities this warrants its return to species status as *C. lycaon*.[98] Proponents have argued that the lack of gray wolf mtDNA[99] in pelts of two 1880s wolves, one killed in New York State and the other in Maine, weakens the hypothesis of gray wolf × coyote crosses and strengthens the argument for a North American origin of the Great Lakes wolf (specifically the Algonquin wolf) and its place as a unique historical entity.[100] Whatever the case, the Great Lakes wolf's propensity to interbreed with coyotes is ancient, extensive, and admixing continues.[101]

The percentage of wolves (including gray wolves) carrying coyote genotypes increases from west to east, from zero in Alaska[102] to about 50% in Minnesota and 100% in Québec,[103] but the disparity narrows at latitudes north of central Ontario and Québec. As a result of admixing, the wolves in southern Québec are more similar genetically to Maine eastern coyotes than to other wolves, and gray wolves in northern Québec and Alaska's Kenai Peninsula (4000 km) are more closely related (the *genetic distance* is less) than wolves spanning northern and southern Québec (400 km) are to each other.[104]

Mechanisms perpetuating admixing in these populations are largely unknown. One could be disintegration of the "species recognition barrier" through long-term *introgression* of foreign genes.[105] Viewed from this perspective, the Great Lakes wolf has lost crucial behavioral tools that allowed its gray wolf ancestors to recognize their own kind and reject those unlike them.[106] With continued admixing came a blending and attenuation of species-specific behaviors leading eventually to familiarity.

1.4 Red wolf

Another North American canid, the so-called red wolf, now enters this confusing picture. Admixing with coyotes started 287–430 years BP,[107] well within the time of European occupation and raising the possibility that the red wolf might once have been a distinct genomic entity. Disturbance of the ecosystem that followed culminated in fewer gray wolves and more coyotes. Crossing back of offspring after the initial admixing was predominantly into the coyote population, perhaps because wolves became too scarce,[108] eventually diluting what wolf genes remained. The genome of today's red wolf is 75–80% coyote (Fig. 1.3),[109] calling for a name change to red coyote.

By 1975 admixtures known as red wolves had reached near extinction from interbreeding with coyotes, their range contracted to a few contiguous counties in Louisiana and Texas.[110] The remaining animals were captured in the mid-1970s, and 14 appearing to match the red wolf phenotype – as judged by looking at them – were selected for captive breeding as a "founder" population. Genetic testing was not available at the time, and looks can be deceiving. Twelve of 77 animals captured for the project from 1974 to 1976 and tested years later contained a gray wolf mtDNA haplotype. Of these, one had been identified originally as a red wolf, four as coyotes, and six as admixtures.[111] The initial selection process turned out to be irrelevant. Examination of museum skins of red wolves killed between 1905

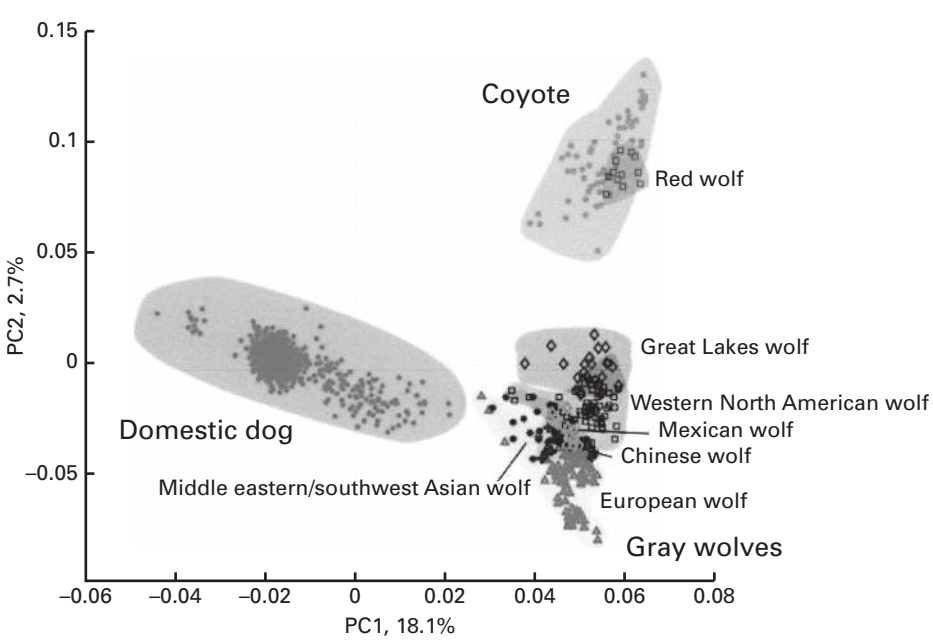

Figure 1.3 Principal component analysis using 710 SNPs ascertained by comparing the dog genome sequence (vonHoldt *et al*. 2010) with that of wolves and the coyote. *Source*: vonHoldt *et al*. (2011).

and 1930 revealed only coyote and gray wolf genotypes.[112] As a result, "captive bred animals are a faithful genetic representation of animals that once lived in the wild and can justifiably be used as a source for reintroduction."[113] That the red wolf was ever a separate species is doubtful. There are now about 100 of them in the wild and many more in captivity across the US. Progeny of the 14 founders were released into eastern North Carolina in 1987,[114] and to the dismay of government biologists they quickly started mating with the local coyotes.[115]

Few would dispute that red wolves carry both wolf and coyote genes or that extant red wolves and coyotes continue to admix.[116] Red wolf vocalizations are apparently distinctive, neither wolf nor coyote but somewhere between,[117] although closer to the coyote's.[118] Red wolves eat like coyotes, focusing on small prey and neither animal declining any known food group. Stomach analyses of specimens killed in the 1930s included rodents, rabbits, birds, carrion, bird eggs, insects, spiders, crayfish, and plant material (e.g. mesquite beans, cactus fruits, persimmons).[119] A list of coyote diets at Lava Beds National Monument (northern California) in the 1930s was similar: rodents, rabbits, birds of more than a dozen species (including domestic turkeys), carrion, bird eggs, insects, badgers, domestic cats (*Felis catus*), reptiles (lizards and snakes), and plant material (grass, apples, wild cherries, gooseberries).[120]

Eight hypotheses have purported to explain the red wolf's origin and status as: (1) a distinct and valid species,[121] (2) a coyote × gray wolf admixture[122] of mostly coyote heritage,[123] (3) a valid species prior to its genome having been diluted by coyotes in recent history,[124] (4) a descendant of a now extinct species of gray wolf,[125] (5) descended along with coyotes from a common ancestor without admixture with gray wolves,[126] (6) a subspecies of gray wolf,[127] (7) the original ancestor of the gray wolf and coyote,[128] and (8) conspecific with the Great Lakes wolf and both derived from a coyote-like ancestor.[129] We now know that (2) is valid, and the red wolf is now – and probably always has been – a coyote × gray wolf admixture without unique genetic components.[130]

A report favoring (8) argued that eastern wolves and red wolves diverged from the coyote line about 150 000–300 000 years BP.[131] The authors proposed synonymy of red and Great Lakes wolves (specifically the Algonquin wolf) and granting the merged entity full species status as *C. lycaon*, this name having taxonomic priority over *C. rufus*.[132] Thus a case was made for the Algonquin wolf and red wolf being the same animal.[133] Additional indirect support of a common origin comes from possible intersecting or overlapping historical ranges.[134] More recent research demonstrates that Great Lakes and red wolves are genetically distinct and unlikely to have shared a common origin: red wolves show close affinity with coyotes, Great Lakes and Mexican wolves more closely resemble North American gray wolves.[135] As mentioned, the genomes of Great Lakes wolves average about 15% coyote ancestry; in red wolves ancestral coyote averages more than three-quarters of the genome.

A major problem for the red wolf as a stand-alone species has been that unlike the gray wolf, Mexican gray wolf, and coyote it has no separate *genetic markers*,

no ancient remnant suggesting it was ever unique.[136] If it is now – or ever had been – a separate species there should be genetic material in its lineages distinct from former or current sympatric canids, but none has so far been found.[137] All 14 red wolf "founders," for example, contained a genotype identical to that occurring in Louisiana coyotes.[138]

As mentioned, the red wolf's lineage reveals no history prior to the arrival of Europeans, making it so young that evident mutations have not accumulated since admixing commenced.[139] Nor could the red wolf be a subspecies of the gray wolf. By definition, a subspecies shares special character traits, which red wolves do not.[140] Moreover, the high gene flow that seems standard among canids probably would have engulfed emerging red wolves in a sea of gray wolf and coyote genotypes.[141] Signs of reproductive isolation based on behavioral recognition disappeared long ago, if they ever existed.

The red wolf's convenient size might make breeding easier with both coyotes and gray wolves, thus abetting admixture.[142] Skull comparisons show many putative red wolves to be intermediate between gray wolves and coyotes.[143] Accepting this as indirect evidence of genetic separation requires circular reasoning, because the morphologies of admixtures are typically intermediate.[144] Poor correlation between morphological and mtDNA findings is additional evidence of a muddled inheritance.[145] The red wolf, in other words, is more a mongrel than its nearest relatives, its heritage a blend of genes, a situation that in no way lessens its importance as a top predator in southeastern US ecosystems.[146] However, whether its use of space and other resources differs significantly from the coyote's has not been assessed. If coyotes and red wolves turn out to be ecological synonyms then the red wolf's protected status as a unique biological entity must be questioned.

For its part, the coyote's genes have been barely affected by other canids, indicating sex-biased introgression. Because mtDNA is maternally inherited the coyote genotype has been transferred to Great Lakes wolves but seldom vice versa, evidence of female coyotes mating with male wolves.[147] The offspring might cross back into either species, although genetic evidence favors admixtures later breeding with wolves.[148] If so it means that adult female coyotes could be accepted by wolf packs and allowed to rear young. This would seem to be a rare occurrence among gray wolves, but coyotes are obviously tolerated by Great Lakes wolves.[149] More likely, female coyotes occasionally mated with lone male wolves, either forming pair bonds or rearing their offspring alone.

Wolves and coyotes can easily traverse plains, mountains, and deserts. The lack of historical geographic barriers suggests other reasons why they evidently did not interbreed everywhere. As stated before, some authorities posit that their smaller size makes Great Lakes and red wolves more likely than gray wolves to mate with coyotes.[150] However, the Mexican gray wolf is smaller than other western and northern gray wolves, has coexisted with coyotes throughout its history, and evidence of admixing is barely detectable in its genome.[151]

Environmental barriers that might ordinarily prevent interbreeding are thought to break down during conditions favoring coyotes over wolves. Wolves are