Chapter 15
Taxonomy, Morphology, and Genetics of Wolves in the Great Lakes Region

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15.1 Wolves: Characters and Relationships

Wolves are animals of the Class Mammalia, Order Carnivora, and Family Canidae. Their genus, *Canis*, comprises at least seven living wild species, including the North American coyote (*C. latrans*) and the Old World jackals. Some taxonomists have "lumped" wolves in a single circumpolar species, *C. lupus*, and some have "split" them among a number of species. The domestic dog sometimes is regarded as the subspecies *C. lupus familiaris* and sometimes as a fully separate species, *C. familiaris*. Wolves resemble certain large breeds of the domestic dog, but have a narrower body, a tail that does not curl, relatively larger teeth, and a flatter forehead (Nowak 1979).

In both the Old and New worlds, small kinds of wolves are present all along the southern fringe of the range of *C. lupus*. Whether they represent components of *C. lupus* or some other entity is the most persistent problem in the systematics of modern wolves. One of those forms occupied the three southern main islands of Japan. Extinct for a century, it has been variously considered a full species, *C. hodophilax* (Imaizumi 1970a,b), or a distinctive subspecies, *C. lupus hodophilax* (Nakamura 1998, 2004). Another small wolf, *pallipes*, still occurs from central Israel to eastern India. Nowak (1995) found nearly complete statistical separation between *pallipes* and more northerly wolves of Eurasia. Sharma et al. (2004) concluded that the Indian population of *pallipes* had diverged from northern wolves over 400,000 years ago, but that another population, occurring from eastern Nepal, across northern India, to eastern Kashmir, and hitherto assigned to the subspecies *C. lupus chanco*, probably had been distinct for over 800,000 years. Aggarwal et al. (2007) suggested that both Indian populations warrant full specific rank.

To the south of *pallipes*, in the Arabian Peninsula and the Israeli Negev Desert, the wolf is even smaller but generally recognized as the subspecies *C. lupus arabs* (Harrison and Bates 1991; Hefner and Geffen 1999). It has been suggested that the form *lupaster* of the Sinai Peninsula and northern Egypt and Libya represents a continuation of the range of *C. lupus* (Ferguson 1981), though *lupaster* usually is considered a large subspecies of *C. aureus*, the golden jackal (Kurten 1974; Spassov 1989). All wolves of the Middle East and India have declined sharply and are in danger of extinction (Mech and Boitani 2004).

Even farther south and more critically endangered is *C. simensis* of the Ethiopian highlands (Sillero-Zubiri and Marino 2004). Systematic studies have been somewhat contradictory, skull morphology suggesting it is the most distinctive species of *Canis* (Clutton-Brock et al. 1976), but molecular analysis indicating it is more closely related to *C. lupus* than are the African jackals, though not so closely as is *C. latrans* (Wayne and Vilà 2003).

Goldman (1937, 1944) assigned the wolves of North America to two species, *C. lupus* (gray wolf) in most of the continent and *C. rufus* (red wolf) in the southeastern United States. Many authorities have accepted that arrangement (Nowak 1979, 1999; Kurten and Anderson 1980; Hall 1981), though others hold *rufus* to be at most a subspecies of *C. lupus* (Lawrence and Bosssert 1967, 1975; Wozencraft 2005), or even a modern hybrid of *C. lupus* and *C. latrans* (Wayne and Jenks 1991; Wayne et al. 1992; Roy et al. 1994b, 1996; Reich et al. 1999). A more recent proposal is that *rufus* and some wolf populations of the Great Lakes region form an independent species, *C. lycaon* (Wilson et al. 2000, 2003; Kyle et al. 2006).

Wolves certainly once occurred all around the Great Lakes, from Minnesota to New York. For about 30 years, authorities usually followed Goldman (1937, 1944), who referred all populations in that region to the single species and subspecies, *C. lupus lycaon*. Jackson (1961) characterized the original Wisconsin population as follows: total length of adult, 1,490–1,650 mm; tail length, 390–480 mm; hind foot, 255–290 mm; adult weight, 30–45 kg; skull length, 230–268 mm; skull width, 120–142 mm; ears moderate and less conspicuous than in the coyote; coat moderately dense, somewhat coarse; in typical full fall and winter pelage, upper parts generally grayish, more or less overlaid with black from nape to rump, under parts whitish to pale buff, head mixed with ochraceous or cinnamon, ears cinnamon to tawny, outer parts of legs cinnamon buff to cinnamon, forelegs with a more or less conspicuous black line; tail grayish above, suffused with black, buffy below, the tip blackish; no seasonal change except for the fading and sometimes more reddish color of old pelage in spring and early summer; other color variations ranging from very pale gray to near blackish.

Goldman (1944) recognized some general differences between the wolves of the western Great Lakes region and those of southeastern Ontario and southern Quebec. He noted the usual smaller size, narrower proportions, and darker coloration of animals in the latter region. Pimlott et al. (1969) reported that in southeastern Ontario's Algonquin Provincial Park the wolves are usually gray to dark gray in winter and grizzled red in summer, and that they weigh 6.8–9.1 kg less than western wolves; averages for Algonquin adults were 24.5 kg in 33 females, 27.7 kg in 40 males.

15.2   Changing Concepts of Taxonomy of Great Lakes Wolves

15.2.1   *The Varying Concept of* Lycaon

As explained by Goldman (1944), "*Canis lycaon*" was first used in a 1775 work by Von Schreber for an illustration he copied from a 1761 book by Buffon. The picture is of an animal regarded as a "black fox" by Von Schreber, though described as a "black wolf" by

Buffon, who indicated that it had been captured in Canada when very young and taken alive to Paris. Regarding that animal as the type specimen, Miller (1912a) designated *lycaon* the appropriate name for the wolf of eastern Canada and the northeastern United States. Goldman (1937) fixed the type locality of *lycaon* as the vicinity of Quebec City. Goldman (1944) observed that the skin of a dark-colored wolf, taken 80 km north of Quebec City in 1916, might resemble the type.

However, while *lycaon* sometimes is considered a relatively dark kind of wolf, fully black specimens are not well known (Mech and Frenzel 1971; Kolenosky and Standfield 1975). In contrast, melanistic examples of *C. rufus* were common; those seen in Florida by Bartram (1791) were the basis for his name *niger*, which formerly was applied to the red wolf. Audubon and Bachman (1851) reported black wolves from Texas to Indiana and the Carolinas, and Gregory (1935) photographed them in northeastern Louisiana. Partly on the basis of a skull collected in 1863 at Moosehead Lake, Maine, about 160 km southeast of Quebec City, Nowak (2002) thought that the range of *C. rufus* originally extended as far north as the St. Lawrence River. Therefore, it seems possible the type specimen of *lycaon* was taken from a population of the red wolf.

Whether scientific names of wolves have been applied at a specific or subspecific level seems for many years to have depended more on fashion than on careful study. Audubon and Bachman (1851) listed *lycaon*, *rufus*, *nubilus*, and all other named kinds of North American wolves (but not *latrans*) as varieties of *C. lupus*. Authorities of the late nineteenth and early twentieth centuries (e.g., Miller 1912a,b), generally treated *lycaon* and most other named kinds as full species. However, as noted by Kyle et al. (2006), it may be pertinent that Pocock (1935), who again united most of the world's wolves under the name *C. lupus*, did maintain *C. lycaon* as a separate species. Shortly thereafter, Goldman (1937, 1944) reduced *lycaon* to subspecific rank.

Goldman was a taxonomic splitter at the subspecies level, and named 11 of the 27 subspecies of Recent North American wolves listed by Hall (1981). He lumped into *lycaon* all wolves of the western and eastern Great Lakes regions, together with other populations extending as far south as Florida. That designated subspecies, then the most widespread in North America, comprised groups that now seem much more variable than do the seven subspecies of the western conterminous United States that Goldman (1944) accepted. He did acknowledge that in the western Great Lakes region, *lycaon* graded physically toward the neighboring subspecies, *C. lupus nubilus* of the Great Plains, while other specimens of *lycaon* showed close resemblance to *C. rufus* of the Southeast. Nonetheless, his arrangement was generally accepted and became fixed in United States law in 1967, when *C. lupus lycaon* was classified pursuant to the Endangered Species Protection Act and assigned a range from Minnesota to eastern Canada (United States Department of the Interior 1973).

Additional conservation interest may have been responsible for some initial challenge to Goldman's position. Mech and Frenzel (1971) pointed out that the Minnesota population might actually represent what was thought to be the otherwise extirpated subspecies *nubilus*. Their view centered primarily on observations of black or white pelage in Minnesota wolves, traits reportedly common for *nubilus* but supposedly not for *lycaon* in southeastern Ontario. Subsequently, based on color, size, and ecology, Van Ballenberghe (1977) concluded that *nubilus*, the wolf population of Minneosta, and the population farther north in western Ontario resembled each

other and, to some extent, had been genetically isolated by the Great Lakes from *lycaon* of southeastern Ontario. Skeel and Carbyn (1977) also suggested morphological affinity between the population of northwestern Ontario (just north of Minnesota), the subspecies *nubilus* and *irreomtus* of the western conterminous United States, and possibly the subspecies *hudsonicus* of the region just west of Hudson Bay.

Meanwhile, Standfield (1970) and Kolenosky and Standfield (1975), citing examination of a large new collection of specimens, reported two "morphologically distinct types" of wolves in the Great Lakes region of Ontario. The "Boreal type," found from the Minnesota border in the west to about 47°N on the east side of Lake Superior, was said to be generally larger, to have a more massive skull, and to vary from pure white to jet black. The "Algonquin type," occurring east of Lake Superior from about 48°N to the vicinity of Algonquin Provincial Park (45°N), was relatively small and slender, had a narrow rostrum, and was invariably gray-fawn in color. Notably, no cline between the two types was recognized, and, while the two overlapped geographically (in the region between 47° and 48°N), there reportedly was "no conclusive evidence of their interbreeding." Such findings are practically suggestive of specific distinction, though a multiple discriminant analysis of skulls did show some statistical overlap. Further analyses by Schmitz and Kolenosky (1985) did indicate clinal variation of Algonquin and Boreal wolves, and that the two were more closely related to one another than either was to the Minnesota population or to *nubilus*; those conclusions seem incongruous with most other recent morphological study (*see* Nowak 1995), though might be assessed for compatibility with molecular approaches (*see* Kyle et al. 2006).

Using statistical analysis of multiple skull measurements, Nowak (1979, 1983, 1995, 2002, 2003) progressively corroborated earlier suggestions that the wolves of Minnesota and the boreal region of Ontario are closely related and should be assigned to the subspecies *nubilus*, together with most other named subspecies of the western conterminous United States and the subspecies *hudsonicus* farther north. He restricted the original range of *lycaon* to a relatively small part of southeastern Ontario and southern Quebec, and proposed that it had been affected by long-ago hybridization with *C. rufus*, but did conclude that it is a subspecies of *C. lupus* and does statistically intergrade with other populations of the latter.

15.2.2 Reexamination of Great Lakes
and Great Plains Wolf Specimens

Nowak's (1979, 1983, 1995, 2002, 2003) previous work was part of a larger assessment of both intraspecific and interspecific relationships of living, historical, and fossil species and populations of *Canis* throughout North America and the world. Hence, a new analysis has been done, emphasizing roughly coeval series of Great Lakes wolves collected not long ago. This assessment involved subjecting ten cranial and dental measurements to canonical discriminant analysis using the Statistical Analysis System (SAS Institute 1987). The measure-

ments, weighted by their ability to distinguish designated groups, assign each specimen a total abstract numerical value—the first canonical variable. The next best distinguishing combination of measurements, uncorrelated with the first, provides a second variable, and so on. Commonly, a single graphical position is plotted based on the first two canonical variables arranged as perpendicular axes. The ten measurements (numbered as in Table 15.1) are (1) greatest length of skull, (2) zygomatic width, (3) alveolar length from P1 to M2, (4) maximum width of rostrum across outer sides of P4, (5) palatal width between alveoli of P1, (6) width of frontal shield, (7) height from alveolus of M1 to most ventral point of orbit, (8) depth of jugal, (9) crown length of P4, and (10) greatest crown width of M2 [*see* Nowak (1995) for illustrations of the measurements and a more detailed explanation of statistical procedures].

As in several previous studies (Nowak 1995, 2002, 2003), only the skulls of fully and normally developed males were used in the analysis. Females tend to occur less frequently than do males in series of *Canis*. Earlier work (Nowak 1979) indicated that analysis of either sex produces about the same result.

Three groups of specimens were used: (1) 27 *C. lupus nubilus* collected prior to 1930 in Idaho, Kansas, Montana, Nebraska, Oklahoma, North Dakota, South Dakota, and Wyoming (26 now at United States National Museum, 1 at American Museum of Natural History); (2) 23 collected 1970–1975 in northern Minnesota (15 now at United States National Museum, 8 at University of Minnesota Museum of Natural History); and (3) 20 *lycaon* collected 1964–1965 during an effort to totally remove wolves from Algonquin Provincial Park, southeastern Ontario (examined at Natural Resources DNA and Forensic Profiling Centre, Trent University, Peterborough, Ontario). In addition, the following specimens were tested against the three groups as individuals: 16 collected before 1966 from the original wolf population of the Upper Peninsula of Michigan (9 now at United States National Museum, 3 at Michigan State Museum, 4 at University of Michigan

Table 15.1 Means of skull measurements (in millimeters and numbered as in text) for male *Canis lupus nubilus* taken before 1930, Minnesota specimens taken 1970–1975, and Algonquin *lycaon* taken 1964–1965

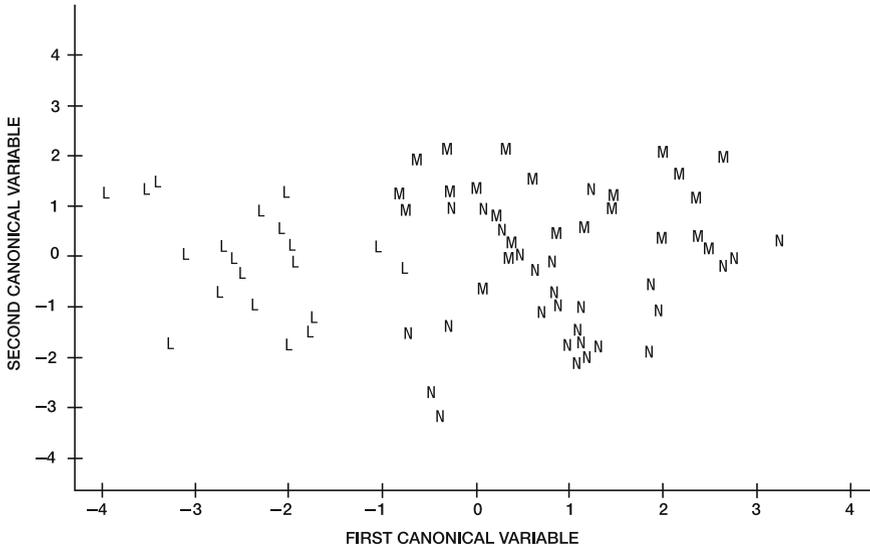|	*nubilus*	Minnesota	*lycaon*
	n = 27	n = 23	n = 20
1	256.85	256.30	245.10
2	139.59	140.13	132.05
3	86.24	86.25	82.53
4	82.35	81.82	76.16
5	31.89	31.97	27.05
6	64.57	64.69	60.69
7	39.95	39.67	37.27
8	19.73	20.00	17.20
9	25.70	25.09	24.51
10	13.39	14.20	14.34

Fig. 15.1 Statistical distribution of three groups of North American male wolves (*Canis*), plotted on the first and second canonical variables. L's, *lycaon* collected 1964–1965 in Algonquin Provincial Park, southeastern Ontario; M's, specimens collected 1970–1975 in northern Minnesota; N's, *C. lupus nubilus* collected prior to 1930 in Idaho, Kansas, Montana, Nebraska, Oklahoma, North Dakota, South Dakota, and Wyoming

Museum of Zoology), and 6 collected 1958–1963, along an approximate east–west axis, between the Upper Peninsula of Michigan and Algonquin Provincial Park, at the Ontario towns of Sault Ste. Marie, Sudbury, and North Bay (examined at Natural Resources DNA and Forensic Profiling Centre, Trent University, Peterborough, Ontario).

15.2.3   Results of Recent Analysis

Western *C. lupus nubilus* and the Minnesota series show substantial statistical overlap, while each of those groups is completely distinct from *C. lupus lycaon* of Algonquin Provincial Park in southeastern Ontario (Fig. 15.1). The analysis thus supports assignment of the Minnesota wolf population to *nubilus*, not *lycaon*. However, individuals collected in the geographic region between Minnesota and Algonquin Park indicate morphological intergradation of *nubilus* and *lycaon* (Fig. 15.2). Hence, the analysis continues to support recognition of *lycaon* as a subspecies of *C. lupus*.
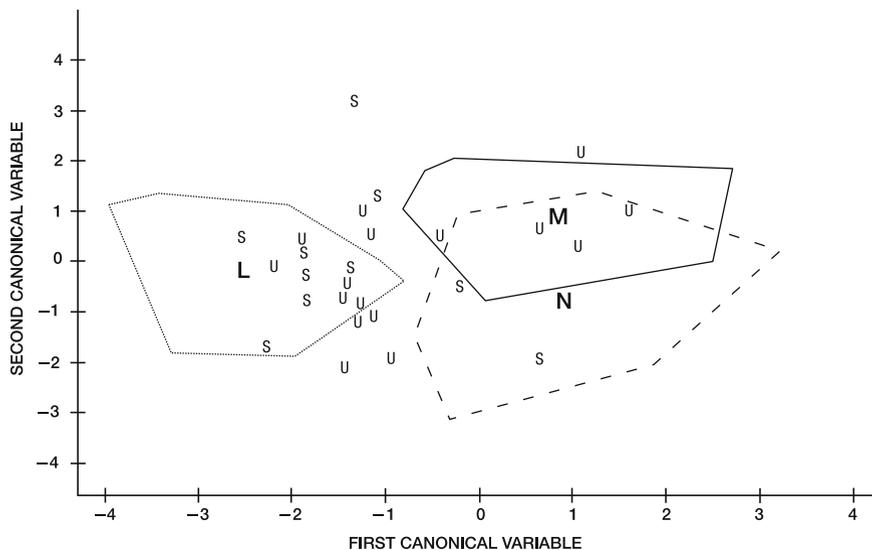
Fig. 15.2 Statistical distribution of three groups (the same depicted in Fig. 15.1) and certain individuals of North American male wolves (*Canis*), plotted on the first and second canonical variables. *Dotted lines*, limits of *lycaon* collected 1964–1965 in Algonquin Provincial Park, southeastern Ontario (letter L shows mean position); *solid lines*, limits of specimens collected 1970–1975 in northern Minnesota (letter M shows mean position); *dashed lines*, limits of *C. lupus nubilus* collected prior to 1930 in Idaho, Kansas, Montana, Nebraska, Oklahoma, North Dakota, South Dakota, and Wyoming (letter N shows mean position); U's, individuals collected before 1966 from the original wolf population of the Upper Peninsula of Michigan; S's, individuals collected 1958–1963, along an approximate east–west axis, between the Upper Peninsula of Michigan and Algonquin Provincial Park, at the Ontario towns of Sault Ste. Marie, Sudbury, and North Bay

15.3   The Molecular Recasting

Gray and red wolves, along with the domestic dog and coyote, have a diploid chromosome number of 78 (Wayne 1993). Molecular technology seeks to assess variation in the chromosomal (nuclear) DNA, or in the protein sequences that DNA specifies, to determine relationships of the individuals and populations involved. Such studies also sometimes use nucleotide variation in mitochondrial DNA, which is particularly applicable to phylogeny, as it has a very high mutation rate and, unlike nuclear DNA, is solely maternally inherited. Certain nuclear DNA loci, known as microsatellites, also have been found to have high mutation rates; their study has allowed broader evaluation of highly degraded DNA, as found in bones and old skins, and permitted identification of the two alleles inherited from the parents at each locus (Wayne and Vilà 2003).

Molecular genetic studies of *Canis* have proliferated, becoming far more common than systematic investigations using traditional morphological techniques. Wayne and

Vilà (2003) listed 35 such studies of *C. lupus* and related canids. Kyle et al. (2006) cited 11 more, particularly those applying to wolves in eastern North America.

An initial objective of this new methodology was a better means of identifying specimens of *C. rufus*. Wayne and Jenks (1991), however, reported the species to lack a unique identifying mitochondrial DNA genotype. Instead, it had only genotypes of *C. lupus* or *C. latrans* and thus was considered to have originated as a hybrid of those two species. Subsequent study of both mitochondrial and nuclear DNA supported that conclusion (Wayne 1992; Roy et al. 1994a,b, 1996; Wayne and Gittleman 1995; Wayne et al. 1995). Most recently, Reich et al. (1999: 143) reported that their comparison of microsatellite allele length distributions supported "the hypothesis of a recent hybridization between coyotes and grey wolves that may have been associated with the extensive agricultural cultivation of the southern United States by European settlers beginning around 250 years ago."

Meanwhile, Lehman et al. (1991) carried out a study of mitochondrial DNA of gray wolves and coyotes from localities throughout North America. They found all wolves within the presumed range of the "Algonquin type" of *lycaon* in southeastern Ontario and southern Quebec to have coyote genotypes. The wolves of Isle Royale, Michigan, and a majority of those in Minnesota and the adjacent part of western Ontario also were found to have coyote genotypes. This situation was seen to have led to formation of a "hybrid zone," paralleling the process with the red wolf, but not to be so far advanced. Essentially the same conclusions were reached by Roy et al. (1994a) using analysis of microsatellite loci.

The molecular genetic studies cited above, all associated with work initiated at the University of California, Los Angeles [except that of Kyle et al. (2006)], have not been universally accepted. Although wolf–coyote hybridization is known to have occurred in southeastern Canada (Kolenosky and Standfield 1975; Nowak 1979; Kyle et al. 2006), observations by field personnel in Minnesota and on Isle Royale indicate no change in the morphological, behavioral, or ecological characteristics and hence no evidence that introgression from *C. latrans* has spread to those areas (Nowak et al. 1995:413). Likewise, hybridization with coyotes long has been recognized as a factor in the *demise* of the red wolf (McCarley 1962; Nowak 1979), but hybrid *origin* of *rufus* has not been supported by morphometric analysis (Nowak 1979, 1992, 1995, 2002), by observation of living animals (Phillips and Henry 1992; Nowak et al. 1995), by several recent molecular studies (Bertorelle and Excoffier 1998; Hedrick et al. 2002; Mech and Federoff 2002), or by some other geneticists who have reviewed the issue (Dowling et al. 1992a,b; Cronin 1993).

Wilson et al. (2000), as amplified by Kyle et al. (2006), provided a completely new assessment and interpretation of molecular data relevant to all eastern wolves. Using both mitochondrial DNA and nuclear microsatellite loci, a close genetic relationship between *rufus* and *lycaon* was identified. That affinity was not caused by common introgression from *latrans*; hybrid origin for *C. rufus* was rejected. In addition, many of the genes found in both kinds of eastern wolves were not found in either western coyote or gray wolf populations, though seemed more closely

associated with *latrans*. Genetic structure suggested *rufus* and *lycaon* were components of a single species, which, because of nomenclatural priority, would take the name *C. lycaon*. Previously reported molecular evidence of wolf–coyote hybridization in the western Great Lakes region now was considered to show presence of *C. lycaon*. That species would have diverged from *C. latrans* well after their common ancestor split from the line leading to *C. lupus*. On the basis of molecular analysis, the current range of *C. lycaon* was thought to include southern Quebec and the vicinity of Algonquin Provincial Park in southeastern Ontario. The species also occurred, together with *C. lupus*, around the north of Lake Superior to western Ontario and possibly southern Manitoba.

Wilson et al. (2003) examined genetic material from two wolf skins collected in the northeastern United States long before *C. latrans* had spread to the region. One was taken in northern New York around 1890, the other in Penobscot County, Maine in the 1880s. Neither specimen was identified as *C. lupus*. The Maine sample was found to have a genotype of the kind previously found in *lycaon* and *rufus*, while the New York sample was like that of western coyote populations. Those results were interpreted to be conducive to designation of original eastern wolves as an independent species, with affinity to *C. latrans*.

Such an assessment of eastern wolves has been supported with the assertion that *C. latrans* seems to readily hybridize with *lycaon* and *rufus*, at least during times of environmental disruption and when numbers of the latter two forms have been depleted, whereas hybridization between western *C. lupus* and *C. latrans* is unknown (Kyle et al. 2006). Actually, Nowak (1979) reported three specimens that statistically appeared to be possible hybrids of *C. latrans* and the small Mexican wolf *C. lupus baileyi*. A subsequent multivariate analysis by Bogan and Mehlhop (1983) suggested that the smallest and most coyote-like of the three did represent *baileyi*. That specimen was collected, probably in the 1800s, at Orizaba, Veracruz, far to the south of any substantive series of known *C. lupus*; the other two specimens also date back over a century and could be small examples of *baileyi*. Wayne and Vilà (2003) considered *baileyi* to be the most highly differentiated North American gray wolf taxon and was the only nominal subspecies of *C. lupus* they recognized based on their molecular studies.

In any case, even if the Mexican wolf did cross with the coyote on rare occasion, there is no morphological evidence of introgression from the latter in series of *baileyi* taken during intensive control operations in the twentieth century (Nowak 1979, 1995), or molecular evidence of such in the living population of *baileyi* (Wayne and Vilà 2003). There also is no sign of coyote introgression in the large series of *C. lupus* collected throughout the western United States in the early 1900s, when the wolf populations of that region were rapidly being fragmented and eliminated (Nowak 1979), or in the population of *C. lupus* that recently was introduced from western Canada to the northwestern United States (Pilgrim et al. 1998). Therefore, the molecular case for uniting *rufus* and Algonquin *lycaon* in a species separate from *C. lupus*, based on their readiness to hybridize with *C. latrans*, seems compelling.
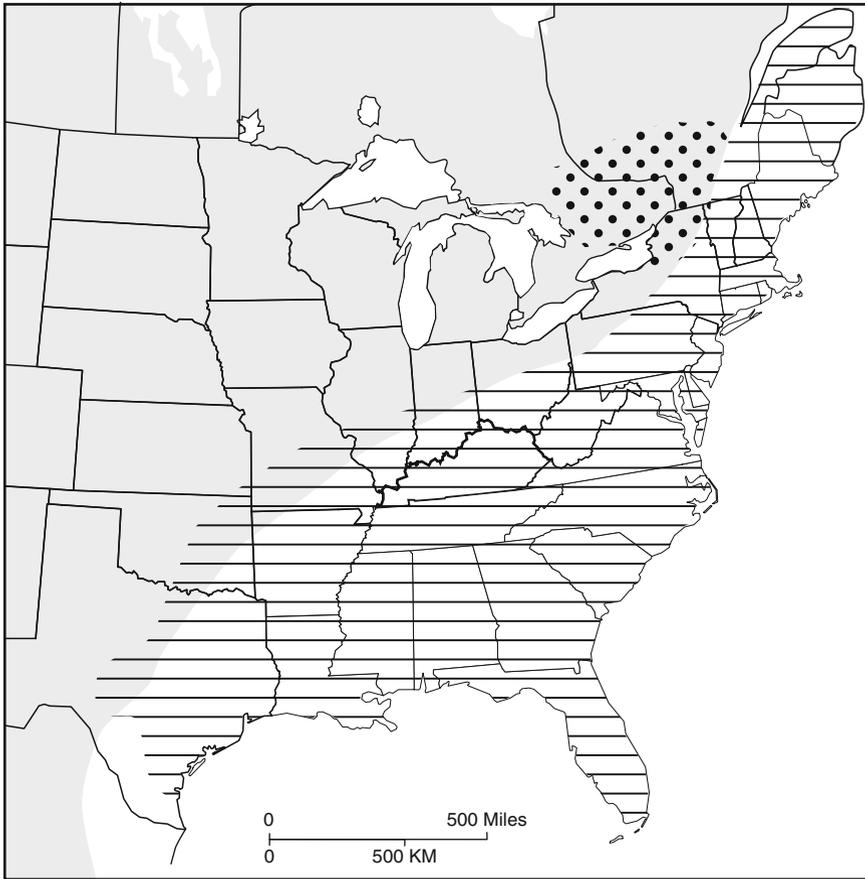
Fig. 15.3 Geographical distribution of wolves (*Canis*) in eastern North America, based primarily on morphological evidence (Nowak 2002, 2003). *Shading*, original range of *C. lupus*; *horizontal hatching*, original range of *C. rufus*; *stippling*, zone of possible hybridization between *C. lupus* and *C. rufus*, which may have contributed to development of the subspecies *C. lupus lycaon*

Remarkably, if the views of Wilson et al. (2000, 2003) and Kyle et al. (2006) are accepted, the original geographic range of *lycaon* will be restored to much the same as that assigned by Goldman (1944), effectively undoing the reductions resulting from subsequent morphological assessment (Standfield 1970; Mech and Frenzel 1971; Kolenosky and Standfield 1975; Skeel and Carbyn 1977; Van Ballenberghe 1977; Nowak 1979, 1983, 1995, 2002, 2003). Not only would *lycaon* again be a name applicable throughout the Great Lakes region, it also would extend as far south as Miami, Florida, where a specimen was collected in 1854 that Goldman (1944) did indeed refer to *lycaon*, though Nowak (2002) included it within *C. rufus*. Figures 15.3 and 15.4 compare the overall distributions of eastern wolves suggested by the contending evidence.
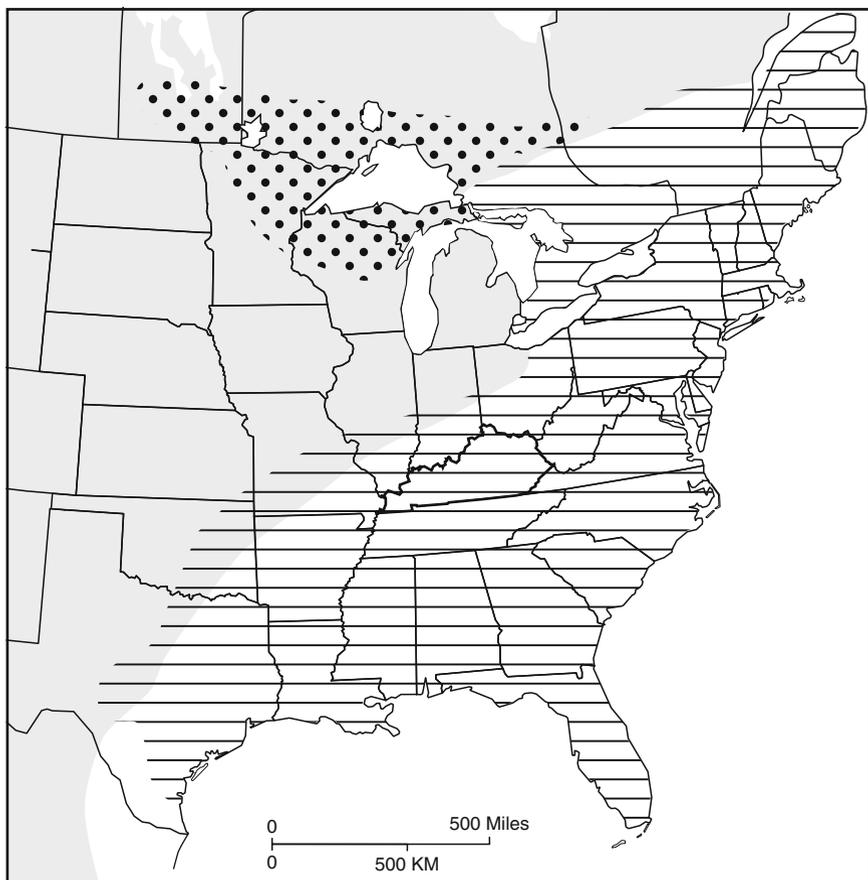
Fig. 15.4 Geographical distribution of wolves (*Canis*) in eastern North America, based primarily on molecular evidence (Wilson et al. 2000, 2003; Wayne and Vilà 2003; Kyle et al. 2006). *Shading*, original range of *C. lupus*; *horizontal hatching*, original range of *C. lycaon*; *stippling*, zone of possible hybridization between *C. lupus* and *C. lycaon*

15.4   Resolution?

As explained above, and in detail by Kyle et al. (2006), there are three rival systematic positions on eastern wolves. The most divergent are the two based on molecular studies, one designating the red wolf part of an ancient and distinct species, the other holding that the red wolf originated as a modern hybrid. However, as indicated by the advocates of the former view (Kyle et al. 2006), the advocates of the latter view (Wayne and Vilà 2003) now have acknowledged that there might have been a distinct red wolf-like species that migrated into Canada after the last glaciation and interbred with the gray wolf, which is exactly what was proposed by the advocate

of the third, morphologically based, view (Nowak 2002). Wayne and Vilà (2003) used the name *C. lycaon* for that species, which would indeed have priority over *rufus*, if the animal named by Von Schreber in 1775 (see above) represented the red wolf, and/or if *rufus* and *lycaon* are accepted as conspecific.

While there thus has been a start to resolution, obstacles remain, one being the reported genotypes of *C. lupus* found in studies of both mitochondrial DNA and microsatellite loci of the red wolf (Wayne and Jenks 1991; Roy et al. 1994a,b, 1996). Wilson et al. (2000) suggested that the involved genetic samples were from actual specimens of *C. lupus nubilus*, *C. l. baileyi*, or *C. l. familiaris*. Such seems unlikely, as the samples were taken from specimens geographically and temporally well removed from then existing populations of *C. lupus*, and there is no evidence of introgression from the domestic dog into the wild canid populations of the involved region (Nowak 1979, 1995). A more plausible explanation for the presence of genotypes of *C. lupus* in specimens of red wolves taken in the south-central United States in the early twentieth century might be that the two species underwent limited hybridization when they were still in contact but coming under intense pressure from hunting and ecological disturbance. Such interaction would be closely comparable to what may have occurred more recently between *C. lupus* and *lycaon* in the western Great Lakes region.

There may be no trenchant disagreement between the assessments set forth by Nowak (2002) and Kyle et al. (2006). They concur that there was a distinct species of wolf in the east, though they have applied different names to it. Nowak also thought that its original range was primarily south of the St. Lawrence River, and that it underwent hybridization with *C. lupus* just to the north, in the Algonquin vicinity (Fig. 15.3). Kyle et al. (2006) believed the historical range to extend at least through southeastern Ontario and that hybridization with *C. lupus* occurred farther to the north and west (Fig. 15.4). Both sides might agree that genetic material of the eastern wolf, and perhaps the wolf itself, is spreading into the western Great Lakes region, possibly beyond, and that there could also be some opposite movement from *C. lupus*.

A more difficult problem involves evolutionary history. On the basis of divergence of genetic sequences, Wilson et al. (2000) concluded that the eastern wolf is a close relative of *C. latrans*, the two species separating only 150,000–300,000 years ago, while their common ancestor would have split from the line leading to *C. lupus* 1–2 million years ago. Nowak (1979) initially did postulate division of the ancestral stock of *rufus* and *lupus* at about that same time. Subsequently, however, Nowak (2002, 2003) noted that small wolves disappeared entirely from eastern North America for a period of about a million years, from the middle Irvingtonian to the late Rancholabrean. He suggested that the species *C. priscolatrans* (=*C. edwardii*) of the early Irvingtonian, previously thought to be the ancestor of *rufus*, actually gave rise to an archaic line of large New World wolves, culminating in *C. dirus* of the late Rancholabrean. He thought that *rufus* had arisen in the Old World from the same ancestral stock as *C. lupus*. Meanwhile, *C. latrans* had a separate history in North America since the early Irvingtonian.

An alternative was offered by Kurten (1974), who considered *C. priscolatrans* not a small wolf but part of a Holarctic group of coyotes that sometimes attained

substantial size and preceded modern *C. latrans*. *C. priscolatrans* disappeared well before the division of *C. latrans* and *lycaon/rufus* hypothesized by Wilson et al. (2000), but a small Eurasian wolf, *C. mosbachensis*, may have persisted from the early Irvingtonian to the early Rancholabrean (Nowak 2003). Sotnikova (2001) suggested affinity among *mosbachensis*, *latrans*, *pallipes*, and *rufus*. However, while *mosbachensis* or *priscolatrans* might not be an unreasonable progenitor of a *lycaon/rufus* group, we still are left with the million-year gap in the fossil history of small wolves in eastern North America (Nowak 2002).

15.5 Conclusions and Conservation Implications

Notwithstanding debate on identity of *rufus* and *lycaon*, there is agreement that both hybridized with *C. latrans* as the latter species invaded the natural range of eastern wolves (Nowak 1979; Schmitz and Kolenosky 1985; Reich et al. 1999; Sears et al. 2003; Wayne and Vilà 2003; Kyle et al. 2006). That process was a critical factor in near extinction of the red wolf and remains a serious problem to the reintroduced population in North Carolina (Phillips et al. 2003; Fredrickson and Hedrick 2006). Hybridization also is a growing threat to surviving wolf populations from southern Quebec and southeastern Ontario to Minnesota (Lehman et al. 1991; Roy et al. 1994a). However, Kyle et al. (2006) suggested that presence of coyote-like genotypes in wolves of that region is partly reflective of some of those wolves representing a species (*C. lycaon*) that is closely related to *C. latrans*.

If Kyle et al. (2006) are correct, the extent of coyote introgression in Great Lakes wolves may be less imminent a threat than previously suggested, at least to more westerly populations. However, presence of a second species of wolf in the region would introduce entirely new issues of environmental usurpation and hybridization. Kyle et al. (2006) reported that the genotypic composition of wolves in that part of Ontario around Lake Superior represents both *C. lycaon* and *C. lupus*, thus indicating interbreeding between the two species. It may be that logging and other ecological changes have produced a habitat more favorable to a smaller, predominantly deer-eating wolf, *C. lycaon*, which is displacing and genetically swamping the larger *C. lupus*, which originally preyed mainly on moose. Interestingly, a remnant pocket of *C. lupus*, free of genetic material from *C. lycaon* or *C. latrans*, was found on the north shore of Lake Superior in Pukaskwa National Park, an area where boreal forest and moose still prevail.

It still seems uncertain as to whether and to what extent western (or boreal) *C. lupus* and eastern (or Algonquin) *lycaon* are intergrading as subspecies, interbreeding as distinct species, and/or behaving as sympatric entities. Kyle et al. (2006) suggested that *lycaon* is either phenotypically or genetically present throughout the involved region, perhaps essentially in its original form in the vicinity of Algonquin Park, but having extensively interbred with *C. lupus* to the north and west, and having crossed with *C. latrans* to the south to form a hybrid population sometimes designated the "Tweed wolf." Kyle et al. (2006) cautioned that presence of *lycaon* not only may

threaten the integrity of *C. lupus* but may lead to overestimating the latter's population and thus to unwise mitigation of conservation measures. On the other hand, Kyle et al. (2006) believed that current hybridization should not always be viewed as negative, and that management policies should deemphasize preserving the phenotype of *lycaon* to allow continued adaptation to its anthropogenically modified environment.

That last suggestion is debatable. If *lycaon* is an ancient species, or even if it represents post-Pleistocene hybridization, its dissolution through human-induced ecological disruption and accelerated interbreeding would seem contrary to any program seeking to conserve examples of populations present before European colonization. *Lycaon* already has undergone extensive hybridization with *C. latrans* to the south of Algonquin Park, and probably elsewhere, and its continued integrity depends on proactive measures to maintain numbers and habitat. Moreover, if the still intact populations of *lycaon* undergo further introgression from *C. latrans*, and if *lycaon* is indeed spreading westward, physically or genetically, *C. lupus* would become exposed to intensified genetic introgression from *C. latrans*. Although the western gray wolf may not hybridize directly with the coyote, it apparently does interbreed or intergrade with *lycaon*. It may also have interbred with *rufus* in the south-central United States, but disappeared so early from that region that introgression from the coyote, through the red wolf, may never have developed.

The United States Department of the Interior did not discuss the hybridization threat, whether from *C. latrans* or from *C. lycaon*, in its recent rule removing the western Great Lakes population of *C. lupus* from the List of Endangered and Threatened Wildlife (Refsnider 2007). Presence on the List allowed *C. lupus* to rebuild numbers in Minnesota and recolonize Wisconsin and northern Michigan.

Under the new rules, states will for the most part continue to protect wolves on public forest lands and will mostly allow wolf populations to fluctuate with prey populations in these areas (A. P. Wydeven, personal communication). Special protections for den sites and management to maintain low road densities will continue on national forests and national parks, and many of the state and county forests will also provide such habitat protections. However, the states will oversee most management and maintenance of populations, and their ecological and genetic viability. In areas of agricultural land and mixed forest–farmland, wolf numbers will be more intensely controlled. Theberge and Theberge (2004) have indicated that hybridizations at least between *C. lycaon* and *C. latrans* are more likely in such fragmented habitats.

Introgressive hybridization in *Canis* was not known to science in the mid-twentieth century. The red wolf in the south-central United States then was subject to control and routinely reported to be common, while it vanished through interbreeding with the coyote (Nowak 1979). Hopefully, what has been learned since then, and follow-up studies by responsible agencies, will prevent repetition of that scenario for the gray wolf in the Great Lakes region.

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