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THE ORIGINAL STATUS OF WOLVES IN EASTERN NORTH AMERICA

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ABSTRACT – Assessment was made of all available cranial specimens of wild *Canis* dating since the Blancan and prior to AD 1918 in the region east of the Great Plains and south of the Prairie Peninsula, Lakes Erie and Ontario, and the St. Lawrence River. The small wolf *C. priscolatrans* (= *C. edwardii*) of the early Irvingtonian seems unrelated to the modern red wolf (*C. rufus*), but gave rise to a lineage including the larger *C. armbrusteri* and culminating in *C. dirus* of the late Rancholabrean. A small wolf, possibly a descendant of the Eurasian *C. mosbachensis*, did not reappear in the east until near the end of the Rancholabrean. At the same time, the coyote (*C. latrans*) disappeared from the east, not to return until the small wolf was extirpated in the 20th century. Fragmentary remains of the small wolf, dating from around 10,000 and 2,000-200 ybp, show continuity with 14 complete, mostly modern, eastern skulls. Multivariate analysis indicates those 14 represent a well-defined species, *C. rufus*, distinct from large series of the western gray wolf (*C. lupus*) and coyote. There is no evidence that the red wolf originated as a hybrid of the latter two species, though early specimens from central Texas suggest it began to interbreed with *C. latrans* by about 1900. Three long-recognized red wolf subspecies appear valid: *C. r. floridanus*, Maine to Florida; *C. r. gregoryi*, south-central United States; and *C. r. rufus*, central and coastal Texas, southern Louisiana, and probably now represented in the captive/reintroduced populations. The subspecies *C. lupus lycaon* of southeastern Ontario and southern Quebec is statistically intermediate to *C. rufus* and western *C. lupus*, and may have resulted from natural hybridization of those two species. Such could explain how the red and gray wolf differ so sharply where their ranges meet in the west but morphologically approach one another in the east.

INTRODUCTION

Two species of wild *Canis*, the gray wolf (*C. lupus* Linnaeus) and the coyote (*C. latrans* Say), occurred in most of northern and western North America in historical time (Fig. 1). The situation is less clear in this study's region of interest: east of the Great Plains and south of the Prairie Peninsula, Lakes Erie and Ontario, and the St. Lawrence River (Fig. 2). A third species, the red wolf (*C. rufus* Audubon and Bachman), reportedly inhabited much of that region (Hall 1981; Nowak 1979, 1995), but the full extent of its range and the nature of its relationship with the gray wolf, coyote, and fossil species have never been resolved. By the early 1900s, people had extirpated wolves from that part of the

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region of interest east of the Mississippi River. Wolves persisted in an ever-shrinking area between the Mississippi and Great Plains but were gone from the wild by about 1980. Their disappearance, together with human habitat modification, opened a niche for the coyote, which now occupies nearly the entire east. The coyote evidently hybridized with some remnant wolf populations, further confusing the situation. A few individuals were removed from the last population that appeared morphologically close to original *C. rufus*, in southeastern Texas and south-

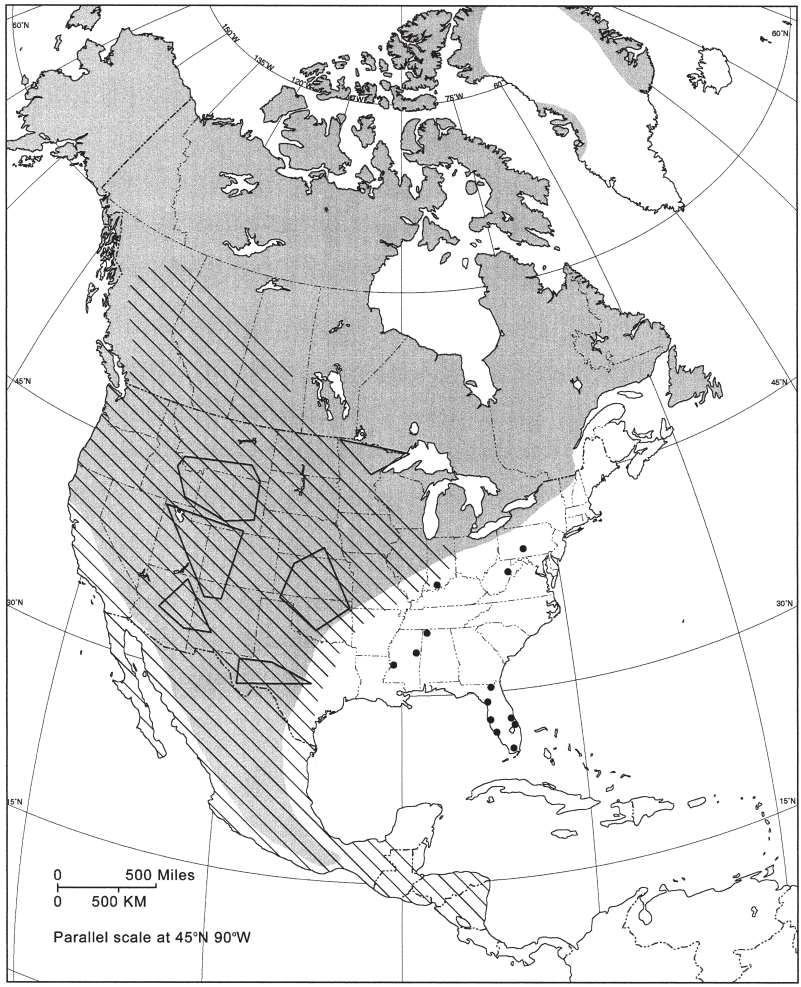

Figure 1. Distribution of North American *Canis*. Shading, *C. lupus* about AD 1500; diagonal hatching, *C. latrans* about AD 1500; dots, eastern records of *C. latrans* in late Rancholabrean; polygons, limits of six western series of *C. lupus* used in multivariate analyses.

ern Louisiana, and were used to found extant captive and reintroduced populations (Nowak 1979, 1999; Nowak et al. 1995). Whether those populations will be maintained and used in further conservation efforts is in question, in part because of controversy regarding their systematic background (Brownlow 1996).

Audubon and Bachman (1851) named *rufus* as a subspecies of *C. lupus* and assigned it a range centering in south-central Texas. They regarded another subspecies, then called *ater* and subsequently designated *floridanus* or, incorrectly, *niger*, to occur east to Florida and Kentucky. They treated *C. latrans* as a separate species, restricted to the west. That basic view held for another century, with *rufus* and *floridanus* being considered subspecies or full species but, in either case, no more or less valid than the other named kinds of North American wolves. Goldman (1937, 1944) was the first to combine *rufus* with other southeastern wolves to form a single species distinct from *C. lupus*; the latter was thought to comprise all other North American wolves. That position was supported by most later assessments of mod-

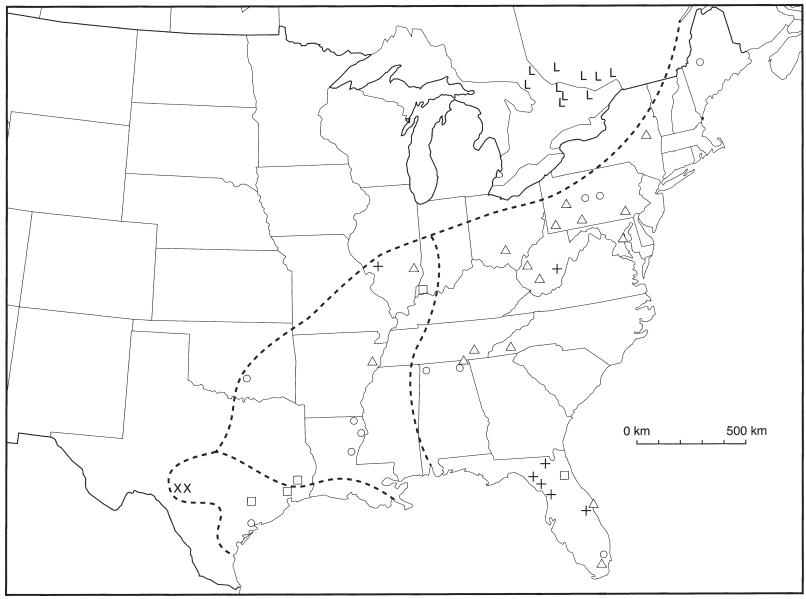

Figure 2. Distribution of eastern *Canis*. Open circles, pre-1918 complete skulls of male *C. rufus* used in multivariate analyses (precise localities of Pennsylvania specimens are unknown); squares, pre-1918 complete skulls of female *C. rufus*; triangles, archeological fragments (2,000-200 ybp) referable to *C. rufus*; crosses, paleontological fragments (c. 10,000 ybp) referable to *C. rufus*; X's, apparent hybrids of *C. rufus* x *C. latrans*, 1899-1906; L's, *C. lupus lycaon*, 1905-1933; dashed lines, subspecific ranges: *C. rufus floridanus* (east), *C. rufus gregoryi* (central), *C. rufus rufus* (southwest).

ern and fossil material (Atkins and Dillon 1971, Elder and Hayden 1977, Freeman 1976, Gipson et al. 1974, Hall 1981, Kurten and Anderson 1980, Nowak 1979, Paradiso 1968, Paradiso and Nowak 1972). However, based on a multivariate analysis of skulls, Lawrence and Bossert (1967, 1975) concluded that the original wolf populations of the southeast were not more than subspecifically distinct from *C. lupus*.

Some analyses of mitochondrial and nuclear DNA have suggested that *C. rufus* is not a valid species or subspecies but is the product of hybridization, most likely within historical time, between *C. lupus* and *C. latrans* (Reich et al. 1999; Roy et al. 1994a, 1994b, 1996; Wayne 1992; Wayne and Gittleman 1995; Wayne and Jenks 1991; Wayne et al. 1995, 1998). That there indeed has been hybridization between southeastern wolf populations and the coyote long has been recognized (Elder and Hayden 1977, Freeman 1976, Gipson et al. 1974, Goldman 1944, Jackson 1951, Lawrence and Bossert 1967, McCarley 1962, Nowak 1979, Paradiso 1968). However, such hybridization generally was considered a modern phenomenon that contributed to the demise, not the origin, of the red wolf. In any case, hybrid derivation of *rufus* has not been supported by morphometric analysis (Nowak 1979, 1992, 1995; Nowak and Federoff 1996, 1998), by observation of living animals (Nowak et al. 1995, Phillips and Henry 1992), or by some geneticists who have reviewed the issue (Cronin 1993; Dowling et al. 1992a, 1992b).

Recently, Wilson et al. (2000), also using DNA analysis, suggested that *rufus* and the subspecies *C. lupus lycaon* Schreber constitute a single species, independent of all other *C. lupus* and *C. latrans*. Goldman (1944) had assigned *lycaon* a large range in eastern North America, but more recent studies argue that it was restricted to extreme southeastern Ontario, extreme southern Quebec, and possibly some adjacent parts of the northeastern United States (Kolenosky and Standfield 1975, Mech and Frenzel 1971, Nowak 1995, Nowak and Federoff 1996, Skeel and Carbyn 1977, Van Ballenberghe 1977). Like *rufus*, *lycaon* evidently has been affected through hybridization with *C. latrans* (Kolenosky and Standfield 1975, Lehman et al. 1991, Nowak 1979, Sears 1999).

There never has been a detailed study centering on the oldest available series of eastern *Canis*, and their relationships to one another and to known series of *C. lupus* and *C. latrans*. Both morphological and molecular analyses have been limited by the scarcity of specimens representing original wolf populations in the region of interest, especially those present before the modern invasion of, and hybridization with, the coyote. The following assessment covers all available material from the region dating from before that invasion – modern, archeological, and paleontological. Specimens of *lycaon*, from the restricted version of its range, as delineated above, also have been considered.

MATERIALS AND METHODS

This study relies entirely on cranial and dental morphology. Most remains of eastern *Canis* dating prior to 1800 – those from paleontological or archeological sites – are fragmentary. Many consist only of one or a few teeth and/or small sections of bone. Such material is of limited value, as the various species of *Canis* show considerable overlap in size and other characters (Lawrence and Bossert 1967, Nowak 1979). However, univariate and bivariate analysis, or evaluation of dental cusps and cingula, sometimes helps determine whether fragments are within the range of variation shown by a population defined by more substantive material. If a series of complete skulls indicates presence of a given species, a series of chronologically or geographically proximal fragments, showing no significant difference in those characters that can be evaluated, may offer reasonable evidence of the presence of the same species. Means and standard deviations were calculated for substantive series used in the univariate analyses. In one of those analyses (see Table 1), the raw measurements were tested for homogeneity of variances, using Bartlett's test, and analysis of variance (ANOVA) was used to test for significant differences among groups; group means then were analyzed by the Tukey-Kramer Multiple Comparison Test and Tukey's Studentized Range (HSD) Test. Most paleontological and archeological specimens assessed in this study are listed in Appendix I.

Most complete skulls of eastern *Canis* date from after 1800. Those specimens usually can be evaluated by multivariate procedures that simultaneously utilize a number of measurements to compare series. Species of *Canis* tend to be highly mobile and adaptable to a wide range of habitats. Therefore, significant morphometric difference between populations that are geographically proximal and not isolated would most likely result from true phylogenetic distinction. In this study, 10 measurements were taken on each skull: greatest length, zygomatic width, alveolar length from P1 to M2, maximum width across outer sides of P4, palatal width between alveoli of P1, width of frontal shield, height from alveolus of M1 to most ventral point of orbit, depth of jugal, crown length of P4, and greatest crown width of M2. The measurements were subjected to canonical discriminant analysis using the Statistical Analysis System (SAS Institute 1987). In that procedure, the various measurements, 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 canonical variable, and so on. Commonly, a single graphical position for each specimen of a group is plotted based on the first two canonical variables arranged as perpendicular axes. Individual specimens can be assigned

positions in relation to established groups. Illustration and further description of the measurements, and more detailed explanation of statistical procedures, were provided in previous publications (Nowak 1979, 1995). Most complete skulls used in multivariate analysis in this study are listed in Appendix II (more detailed information is provided for specimens from the region of interest).

All skulls used in multivariate analyses were considered to have reached full size, which occurs at about one year of age in small species of *Canis* and by about two years of age in large species. For that part of the region of interest east of the Mississippi River there are only nine known complete skulls of all wild *Canis* (none of them *C. latrans*) dating from the end of the Pleistocene to AD 1917. One of them, USNM 1804 from the Adirondacks of New York, may not be fully developed; it is discussed further below. An additional specimen, ANSP 2259 collected prior to 1859 at an unknown locality in Ohio, is from an immature individual and lacks most of the components that must be measured for multivariate analysis.

As in several previous studies (Nowak 1992, 1995; Nowak and Federoff 1996), only the skulls of males were used in multivariate 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 and that males average significantly ($p < 0.05$) larger than females in all of the dimensions indicated above. Of the eight fully developed skulls from that part of the region of interest east of the Mississippi, two are females: USNM 38488, Horse Landing, St. John's River, Putnam County, Florida, collected 1890, and AMNH 112, New Harmony, Posey County, Indiana, collected 1832. The latter specimen was incorrectly reported to be from Wabash County in northeastern Indiana by Goldman (1944) but actually is from the extreme southwestern tip of the state, well south of the Prairie Peninsula (Mumford and Whitaker 1982).

For specimens lacking data, assignment to sex was based primarily on size in relation to individuals of known sex in the same series. Both of the known females are smaller than are the remaining six skulls from east of the Mississippi (Appendix II). Of those six, the smallest, from Fern Cave, Alabama, is known to be a male because of the presence of a baculum with the skeleton. It thus would not be unreasonable to treat the remaining five as males, even though sex (male) was recorded only for the specimen from near Cherokee, Alabama. The specimen from Miami, Florida, is the largest of the group and is larger than any known female wolf from the region of interest. Some postcranial elements are with the skull from Moosehead Lake, Maine; the pelvis was examined by A. J. Bezuidenhout (Department of Biomedical Sciences, College of Veterinary Medicine, Cornell University), whose opinion (pers. comm., 30

July 1999), based mainly on evidence of penile crura attachment to the ischium, is that the specimen is a male. Goldman's (1944) table of measurements listed one of the skulls from Pennsylvania as a male, the other as a female, and those designations were cited by Williams et al. (1985). However, T. Daeschler (Academy of Natural Sciences, Philadelphia, pers. comm., 7 October 1999) reported that sex had not been recorded for either specimen and that no postcranial elements are known. Moreover, review of Goldman's table indicates that many of his assignments to sex were based on judgment, not recorded data.

Of the seven specimens taken 1898-1905 in northeastern Louisiana and used in multivariate analysis (Appendix II), two lack recorded sex, but both are much larger than two known females from the same area and period (USNM 136105, 136106). Those two females closely resemble one another, as well as the two females from east of the Mississippi, in size and other characters. Of the five skulls taken in 1900 in Calhoun County, Texas, and used in multivariate analysis, four lack sex data, but the one known male is smaller than all the others, and the one known female from the same area is smaller still. Three additional early females from southeastern Texas were collected in 1906 at Kountze, Hardin County (USNM 147701), in 1906 near Dayton, Liberty County (USNM 136563), and in 1904 at Frelsburg, Colorado County (USNM 135445). Most of the females were assessed in previous study (Nowak 1979) and all appear to exhibit the same relationships, as that of their male counterparts, to *C. lupus* and *C. latrans*. A few skulls of immature wolves were collected in northeastern Louisiana and coastal Texas during the same period but do not appear to have any characters differing from the pattern evident in the adult material.

The sex recorded for two specimens assessed by this study is considered erroneous. A reported female, USNM 289995 from upper Michigan, is among the three largest skulls known from that area and is here included as a male. A reported male, CNM 5575 from southern Quebec, is smaller than all males and nearly all females collected in that region in 1905-1933 and is here regarded as a female. In addition, the specimen collected near Avery Island, Louisiana in 1919, and questionably listed as a female by Nowak (1979), has been reassessed and treated as a male in this study.

Some chronological flexibility was used in selecting the series thought to represent the original wolf populations of the region of interest, such depending in part on the period in which *C. latrans* moved into different parts of the east, replacing or hybridizing with the native wolves. The skull collected in 1917 in Alabama seems acceptable, as the coyote is not known to have crossed the Mississippi River, south of the Prairie Peninsula, until the 1960s (Nowak 1979). Of the other five skulls from east of the Mississippi and used in multivariate

analysis, four are known to date from before 1870 and one, from Fern Cave, Alabama, probably does (Paradiso and Nowak 1973). The seven skulls taken 1898-1905 from northeastern Louisiana date from about 50 years before the coyote is known to have entered Louisiana (Nowak 1979). The small series (Appendix II) collected in 1900 from Calhoun County, coastal Texas, is much closer geographically to the range of *C. latrans*, but coyotes and other wild *Canis* are not known from that area and time. The larger series (Appendix II) taken 1919-1943 from coastal Texas, the Big Thicket area, and southern Louisiana and Mississippi was used not so much to define the original population as to ascertain evidence of intergradation between the Calhoun County and northeast Louisiana populations.

A skull (USNM 8098), collected prior to 1869 from Cherokee Town, Garvin County, south-central Oklahoma, has been grouped with the other old eastern specimens in some multivariate analyses. Although taken from well within the range of *C. latrans* and immediately adjacent to the known range of *C. lupus*, previous study (Nowak 1979) and recent reassessment show it statistically and morphologically well removed from both those species. It once had been placed within the USNM collection of *C. lupus nubilus* Say. Goldman (1944) did not include it in any of his lists of specimens examined, but he did write *"C. rufus"* on the specimen tag. The original USNM catalog entry designates the specimen *"Lupus occidentalis niger,"* apparently following Bartram's (1791) description of *"Lupus niger"* from Florida. Unfortunately, the skin (USNM 9302) has been lost, but "black wolf" is written directly on the skull. There thus is evidence of continuity of the black color phase, known to have occurred in eastern wolves, from Florida to Louisiana (Gregory 1935) and Oklahoma.

Goldman (1944) assigned a skull (AMNH 4609), reportedly collected in 1893 from Warsaw, Hancock County, west-central Illinois, to *C. rufus*. Paradiso and Nowak (1972) suggested that the specimen had been brought to that area by a local animal dealer. Hoffmeister (1989) made an exhaustive study of the matter and concluded that the specimen was taken from the wild in that area, but that it probably was a domestic dog (*C. familiaris* Linnaeus) x coyote hybrid.

The specimens from the region of interest were compared with six series of male *C. lupus* from the western conterminous United States (Fig. 1). Those samples represent six nominal subspecies (Appendix II), though all were placed in the synonymy of *C. lupus nubilus* by Nowak (1995). Three of the samples are the available series of *C. lupus* that are geographically most proximal to the western edge of the region of interest, and just west of those series are the other three samples. The six series therefore may help determine whether *C. lupus* tends to grade morphometrically towards the eastern wolf as the two approach geo-

graphically. Also used for comparison was a series (Appendix II) of 10 male *lycaon* collected 1905-1933 from southeastern Ontario and Quebec, long before *C. latrans* became established in that region, and a series (Appendix II) of 16 male *C. lupus* taken before 1966 from the upper peninsula of Michigan, when the original population was still present (that population was extirpated shortly thereafter, though *C. lupus* recently was reestablished in upper Michigan through migration from Minnesota). Each of those wolf samples comprises every available fully developed male from the involved area and period; no other selectivity was used. The comparative series (Appendix II) of coyotes contains 96 male *C. latrans lestes* from Colorado and Idaho; that subspecies is considered a relatively large coyote (Jackson 1951).

A survey was made to locate additional specimens from the original wolf populations of the region of interest. All of the depositories reported in the FAUNMAP electronic data base (Illinois State Museum) to hold any kind of wild *Canis* from that region were contacted, as were many other natural history, archeological, paleontological, historical, and general museums, and individual authorities. Approximately 400 potential sources of specimens or information were surveyed, but the project was largely unsuccessful. Many parties did not respond. Many others indicated that the specimens had been lost, were curatorially inaccessible, or consisted of material (postcranial and/or highly fragmentary) not directly usable for this study. The existence of a few old mounted "wolves" was ascertained but responsible parties were understandably reluctant to authorize an effort to uncover any underlying skull.

RESULTS

There have been suggestions that *C. rufus* is closely related to, if not identical with, *C. edwardii* Gazin, a small wolf known from early Irvingtonian (2-1 million ybp) sites in Arizona, California, Colorado, Kansas, Oregon, Texas, and Mexico (Albright 2000, Anderson 1996, Kurten and Anderson 1980, Nowak 1979). *C. edwardii* was placed in the synonymy of *C. priscolatrans* Cope from the Irvingtonian Port Kennedy Deposit in Montgomery County, Pennsylvania, by Kurten (1974) and Kurten and Anderson (1980); the latter designation is used henceforth. A cranial fragment from the early Irvingtonian Inglis 1A site in Citrus County, Florida, had been assigned to *C. rufus* (Nowak 1979, Webb 1974), but Berta (1995) and Morgan and Hulbert (1995) referred that and most other early Florida specimens of *Canis* to *C. priscolatrans*. Examination of extensive material from Florida now indicates that *C. priscolatrans* is a distinct species and that it, not *C. rufus*, was present in the Irvingtonian. The largest collection of early Florida *Canis* is from the Leisey Shell Pits in Hillsborough County. Berta (1995) identified

both *C. priscolatrans* and *C. armbrusteri* Gidley from that site, as well as from Haile 21A, Alachua County. The latter species attains a much larger size and has been found in abundance at several other eastern sites from the middle Irvingtonian (1 million-600,000 ybp) to the early Rancholabrean (300,000-130,000 ybp). Martin (1974) considered it synonymous with *C. lupus*, but most authorities (Berta 1988, 1995; Gidley and Gazin 1938; Kurten and Anderson 1980; Morgan and Hulbert 1995; Nowak 1979) have treated it as distinct.

Most Irvingtonian material from Florida consists of teeth and small cranial fragments (Appendix I). Upper molars are well represented and show modest over-all size, a relatively large talon (medial section), pronounced sculpturing, and trenchant cusps. The occlusal surface of M1 is characterized by a relatively wide and deep basin between the high outer ridge, formed by the metacone and paracone, and the lower but prominent medial cusps, the protocone and metaconule, and by another deep basin between the latter cusps and the hypocone at the inner edge of the tooth. M1 also has a well-defined buccal cingulum and usually a pronounced anterior cingulum. Although comparable characters often are present in modern specimens referred to *C. rufus*, they are not sufficiently pronounced to justify treating *C. priscolatrans* as conspecific. Moreover, there now are morphometric indications that the latter species was the progenitor, not of *C. rufus*, but of an entirely separate line of wolves.

Figure 3 depicts a bivariate analysis of the size of M1 in Irvingtonian and Rancholabrean specimens of wolves from the region of interest (Appendix I). The early Irvingtonian material from Florida is clinal, with no clear demarcation between specimens designated (Berta 1995) *C. priscolatrans* (= *C. edwardii*) and *C. armbrusteri*. The later Irvingtonian and early Rancholabrean specimens, here considered to represent *C. armbrusteri*, are all larger. The material from the late Rancholabrean (130,000-10,000 ybp), all designated *C. dirus* Leidy (Kurten 1984, Morgan and Hulbert 1995, Nowak 1979), is mostly even larger. The progressive increase in size of M1 (Fig. 3) accompanied an enlargement of the outer cusps, decrease in relative size of the talon (medial section), and lessening of sculpturing and buccal and anterior cingula. The reduction of the talon in *C. dirus*, even though the overall size of M1 is generally greater, contributes to the overlap seen between that species and *C. armbrusteri*. The trend expressed by M1 suggests evolution from a small, generalized canid, with some dependence on dietary vegetation, to a large wolf, highly specialized for carnivory. The development of M1 was associated with overall growth and broadening of the skull and attainment of relatively larger teeth. This progression seems to represent a single evolutionary sequence; there is no evidence of another lineage, a smaller wolf, continuing into the late Irvingtonian and early Rancholabrean.

Further perspective on such a progression may be seen in the development of m1 (lower carnassial), which is perhaps the most commonly preserved of the larger, diagnostic teeth found at paleontological and archeological sites (Fig. 4). Inclusion of m1 allows assessment of a few additional specimens (Appendix I) extending back to the late Blancan (2.5-2 million ybp). A small coyote-like species of that age, *C. lepophagus* Johnston, seems to be near the stem line from which arose the later coyotes and wolves; it is known mainly from the western United States but also has been recorded from Florida (Martin and Hulbert 1995, Nowak 1979). Whether all Blancan *Canis* from North America is referable to *C. lepophagus* is not certain, but available specimens do indicate presence only of coyote-sized individuals.

The size of m1 in all available eastern *Canis* from the Blancan to late Rancholabrean (Appendix I) is plotted in Figure 4. The Blancan specimens are small and presumably represent *C. lepophagus*. Early Irvingtonian material, all from Leisey and other Florida sites, is decidedly larger. Although some of it could represent *C. armbrusteri* (Berta 1995), here it all is referred tentatively to *C. priscolatrans*. In contrast, nearly all of the later Irvingtonian and early Rancholabrean specimens are much larger, show no overlap with *C. priscolatrans*, and can be assigned to *C. armbrusteri*. A single available specimen from

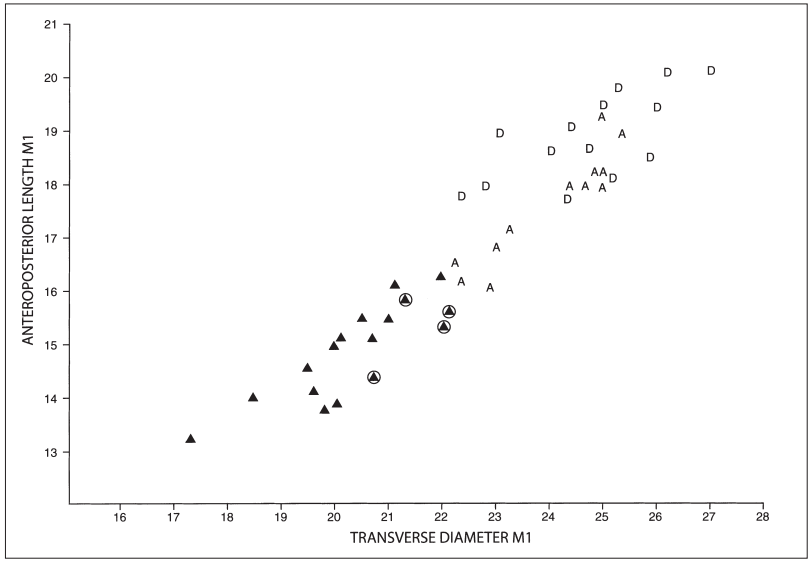

Figure 3. Bivariate analysis comparing measurements (in millimeters) of transverse diameter and anteroposterior length of M1 in individual specimens of fossil eastern *Canis*. Solid triangles, *C. priscolatrans*; circled triangles, specimens identified as *C. armbrusteri* by Berta (1995) but considered here to represent *C. priscolatrans*; A's, *C. armbrusteri*; D's, *C. dirus*.

Cumberland Cave, Maryland, is much smaller and indistinguishable from *C. latrans*. The late Rancholabrean specimens, likewise, show almost no overlap with *C. armbrusteri*, but apparently represent three other species. One, substantially larger, is *C. dirus*. Another, far smaller, apparently is an eastern form of *C. latrans*. A third, intermediate-sized, represents a small wolf, most likely the emergence of a modern species, herein considered to be *C. rufus*.

The data plotted in Figure 4 extend the evolutionary sequence shown in Figure 3. *C. lepophagus*, or some related small Blancan species, may have given rise to *C. priscolatrans* of the early Irvingtonian, which in turn evolved into the larger *C. armbrusteri* of the late Irvingtonian and early Rancholabrean. That line apparently culminated in the large *C. dirus* of the later Rancholabrean. The progressive increase in size of that line seems to have allowed reopening of the niche for a smaller kind of *Canis*, initially just *C. latrans* by the late Irvingtonian, but also another wolf at the end of the Pleistocene.

There is no evidence of the presence of a small wolf in the later Irvingtonian or early Rancholabrean (Figs. 3, 4). Small wolves seem to disappear from eastern North America following the extinction of *C. priscolatrans* and do not reappear until the terminal Pleistocene, around 15,000-10,000 ybp, a gap of nearly 1 million years. There have been a few reports of a small wolf in the east during that interval but they are not valid. Martin (1974, Fig. 3.13) indicated nine specimens of *C. lupus*

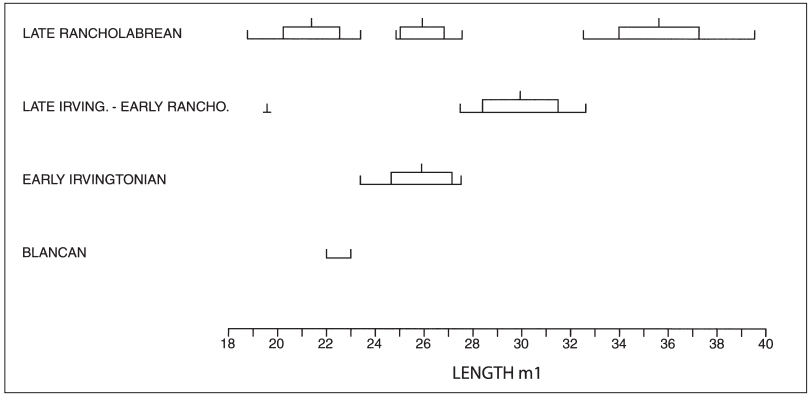

Figure 4. Length (in millimeters) of m1in eastern fossil *Canis*. The slender horizontal line with vertical lines at each end represents the range in size, the bar indicates one standard deviation on either side of the mean, and the vertical line above the bar shows the mean. Ages and apparent species identifications (with number of specimens) are: Blancan, *C. lepophagus* (3); early Irvingtonian, *C. priscolatrans* (15); late Irvingtonian to early Rancholabrean, *C. latrans* (single individual to left, represented by a vertical line above a short horizontal line), *C. armbrusteri* (right, 19); late Rancholabrean, *C. latrans* (left, 15), *C. rufus* (center, 7), *C. dirus* (right, 20).

or *C. rufus* at the early Rancholabrean Haile 7A site, Alachua County, Florida. However, these specimens actually represent modern *C. rufus* from other areas that were used for comparison (Robert A. Martin, pers. comm., 7 April 1999). One specimen, UF 11845, is from Haile 7A, but recent reexamination shows it to be *C. armbrusteri* (Figs. 3, 4). Nowak (1979) reported still another specimen of *C. rufus* from Haile 7A, but that was a double error. The specimen, unnumbered by Nowak, is actually UF 11516 and is not from Haile 7A but Haile 12B. Moreover, whereas Haile 12B sometimes has been considered early Rancholabrean, it actually is late Blancan (S. David Webb, pers. comm., 6 March 2000). UF 11516, listed by Nowak (1979) as a small example of *C. rufus*, most likely represents a different species. Haile 12B also contains the mandible of another specimen of *Canis*, which Nowak (1979) referred to *C. latrans*. Taken together, the two specimens from Haile 12B may represent the transition from *C. lepophagus* to *C. priscolatrans* and thus part of the overall evolutionary sequence shown in Figures 3 and 4. Nowak (1979) also listed UF 17074 from the Crystal River Power Plant, Citrus County, Florida, as *C. rufus*, and indicated the site to be late Rancholabrean, but Morgan and Hulbert (1995) reported it to be early Irvingtonian and assigned the specimen to *C. priscolatrans*.

There are only two more reports of an eastern wolf, other than *C. armbrusteri* or *C. dirus*, from the period between the disappearance of *C. priscolatrans* and the appearance of modern wolves at the end of the Pleistocene. Brown (1908) listed *C. lupus* at the early Rancholabrean Conrad Fissure, Newton County, Arkansas. However, the specimens (AMNH 11761, 11762) are fragments that include no diagnostic teeth; they could be referable to *C. armbrusteri*. Ray (1967) reported *C. lupus* from a late Rancholabrean (10,000-35,000 ybp) site at Ladds, Georgia, based on a single M1 (USNM 23698). The specimen is heavily worn and its length, 18.0 mm, and diameter, 22.7 mm, are within the lower range of *C. dirus* (Kurten 1984).

If there is no definitive evidence of a small wolf in the east for nearly a million years prior to the latest Rancholabrean, where was the progenitor of the modern wolf population of the region? It has been suggested (Nowak 1979) that *C. priscolatrans*, or a close relative, extended its range to Eurasia via the Bering Land Bridge, and there evolved into extant *C. lupus*, which subsequently reinvaded North America. *C. etruscus* Major, a small wolf of the European early Pleistocene (Kurten 1968, Kurten and Anderson 1980), may be an Old World counterpart of *C. priscolatrans* and the ancestor of *C. lupus*. There was, however, an intermediate stage in the transition from *priscolatrans/etruscus* to *lupus*. That stage is represented by *C. mosbachensis* Soergel, a modest-sized wolf of the Eurasian Pleistocene. Five mandibles and two maxillary fragments of that species, on loan to Richard Tedford (American Mu-

seum of Natural History, pers. comm., 24 March 1999), were examined. They were collected in the Lake Baikal region of south-central Siberia and date from about 700,000 ybp, which would be a period corresponding to the mid- to late Irvingtonian of North America. Mean length of m1 is 25.4 mm (range 23.0-27.5) in the five *C. mosbachensis*, 25.8 mm (24.8-27.5) in the seven late Rancholabrean eastern wolves (Fig. 4), 26.7 mm (25.0-28.6) in the eight complete and mostly modern skulls from east of the Mississippi, 28.4 mm (25.9-31.6) in a series of 123 male and female *C. lupus nubilus* from the western United States, and 29.8 mm (26.4-33.0) in 217 male and female *C. lupus occidentalis* Richardson from Alaska and western Canada. Two mandibles and one maxillary fragment (AMNH 67173, 67181, 67186) from the Cripple Creek Sump of Alaska were examined. They date from about the same period and appear to represent the same population as the Siberian material; the two m1 have lengths of 26.6 and 27.2 mm. Since the Alaskan and Siberian specimens are close to the size of the later material from eastern North America, and smaller than western *C. lupus*, and since wolf evolution generally involves progression from smaller to larger size, *C. mosbachensis* seems a logical candidate for the ancestor of modern North American (as well as Eurasian) wolves.

Although the late Irvingtonian population in Alaska and Siberia may represent the progenitor of modern wolves, there is little evidence that it moved to the south of the glaciated region before the late Rancholabrean. Western North America appears to have much the same evolutionary sequence of *Canis* that occurred in the east. *C. lepophagus* and *C. priscolatrans* were widespread, respectively, in the Blancan and early Irvingtonian, and *C. dirus* was abundant in the late Rancholabrean (Kurten 1974, 1984; Kurten and Anderson 1980; Nowak 1979). Unlike eastern North America, the west has yielded no substantial collections of middle Irvingtonian to early Rancholabrean *Canis*. Three fragments from Hay Springs and Mullen, Nebraska, which do date from that period, were assigned to *C. lupus* by Nowak (1979), and one from Rushville, Nebraska, was referred to *C. armbrusteri*. In retrospect, it is questionable whether a population identical to modern *C. lupus* was then present to the south of the glaciers. Each of the Nebraska specimens is considerably larger than *C. mosbachensis*; the Hay Springs and Mullen fragments include two m1's, with lengths of 29.9 and 29.8 mm. It is unlikely that *C. lupus* could then have been so far removed, morphologically and geographically, from its progenitor species. Perhaps the Nebraska material represents a population of *C. armbrusteri* that was beginning to develop in the direction of *C. dirus*; both the latter species and *C. lupus* have some parallel differences from *C. armbrusteri*. In any case, *C. lupus* is not otherwise known from North

America before the late Rancholabrean, when for a time it evidently was sympatric with *C. dirus* (Graham and Lundelius 1994, Nowak 1979).

By the terminal Pleistocene, the east had been reoccupied by a wolf differing from *C. dirus*, *C. armbrusteri*, and *C. latrans* (Fig. 4). Assessment of later specimens (Appendices I, II) indicates continuity of this small eastern wolf. There is no significant difference in size of m1 of paleontological fragments dating about 10,000 ybp, archeological fragments dating 2,000-200 ybp, and complete, mostly modern skulls (Fig. 5). However, there is a significant difference in m1 between each of those samples and western *C. lupus* and *C. latrans* (Table 1). That the latter two species overlap at all with the other samples may be attributable in part to inclusion of both sexes in Figure 5.

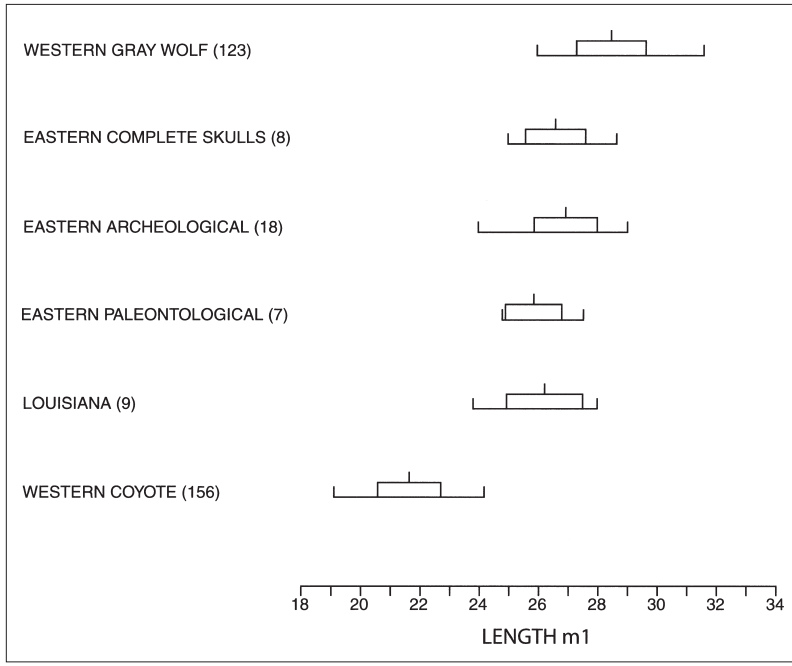

Figure 5. Length (in millimeters) of m1 in six samples (number of specimens in parentheses) of both sexes of *Canis*. The slender horizontal line with vertical lines at each end represents the range in size, the bar indicates one standard deviation on either side of the mean, and the vertical line above the bar shows the mean. The western gray wolf (*C. lupus*) and coyote (*C. latrans*) series are from the mountainous region of the western conterminous United States. The eastern complete skulls are the same six used in multivariate analysis (Fig. 6), plus two females, all dating prior to 1918. The Louisiana specimens are the same seven used in multivariate analysis (Fig.7), plus two females, all dating 1898-1905. The eastern archeological specimens date 2,000-200 ybp. The eastern paleontological specimens date c. 10,000 ybp.

The number of early mandibular fragments that has been recovered east of the Mississippi is considerably greater than that of maxillary fragments (Appendix I). Of the latter, eight contain both P4 and M1 and seven of those date 2,000-200 ybp. They are from Ohio, Pennsylvania, New York, Maryland, and North Carolina (Appendix I) and seem closely related. Range is 23.1-24.8 mm for length of P4 and 20.0-22.0 mm for diameter of M1. In the eight complete, mostly modern skulls from east of the Mississippi, including two females, range is 21.8-25.2 mm for P4 and 20.5-22.0 mm for M1. The ninth eastern maxillary fragment (CM G-756), from Frontenac Island, Cayuga County, western New York, dates from at least 5,000 ybp. At 27.5 mm in P4 length and 24.4 in M1 diameter, it is the size of a large *C. lupus* (Nowak 1979, 1995) and may represent an early movement of that species into the northeast.

The Frontenac Island specimen is the only indication that, at least for a time, two different wolf species (*C. lupus* and *C. rufus*) occurred in parts of the east subsequent to the Pleistocene, as was suggested by earlier studies (Goldman 1944, Nowak 1979). However, measurements of the other eastern material show no more variation than do those of other wolf populations. Moreover, the diagnostic teeth of the fragmentary specimens are approximately the same size as those in the series of complete eastern skulls.

The complete skulls (Appendix II) can be assessed through multivariate procedures to determine whether they represent a single species

Table 1. Results of the Tukey-Kramer Multiple Comparison Test of length of m1 in the six groups of *Canis* shown in Figure 5. The q value is a measure of statistical distance. Degree of affinity is given in descending order, with groups closest to one another at the top of the table and those farthest apart at the bottom. Statistically significant differences (ANOVA) are indicated by *** ($P < 0.001$). The groups so indicated also are all statistically different ($P < 0.05$) using Tukey's Studentized Range (HSD) Test.

Group comparisons			q Value
Eastern Archeological	vs.	Eastern Complete	0.569
Eastern Complete	vs.	Louisiana	1.149
Eastern Paleontological	vs.	Louisiana	1.160
Eastern Archeological	vs.	Louisiana	1.960
Eastern Paleontological	vs.	Eastern Complete	2.208
Eastern Archeological	vs.	Eastern Paleontological	3.108
Western Gray Wolf	vs.	Eastern Complete	6.054 ***
Western Gray Wolf	vs.	Eastern Archeological	7.796 ***
Western Gray Wolf	vs.	Louisiana	8.014 ***
Western Gray Wolf	vs.	Eastern Paleontological	8.626 ***
Western Coyote	vs.	Eastern Paleontological	13.354 ***
Western Coyote	vs.	Louisiana	16.755 ***
Western Coyote	vs.	Eastern Complete	17.385 ***
Western Coyote	vs.	Eastern Archeological	26.289 ***
Western Coyote	vs.	Western Gray Wolf	70.585 ***

that differs from other well-defined species. One such analysis, the graphical results of which are shown in Figure 6, deals with the six available skulls of fully developed males dating prior to 1918 and collected in the region of interest (Fig. 2). Those six specimens are compared as a group with the six groups of *C. lupus* from western North America, including the three samples geographically most proximal to the eastern group (Fig. 1). The series of *C. lupus* all overlap one another and are not similar morphologically to the eastern material, even as they approach the latter geographically. The eastern specimens group together separate from all the western specimens and, although they were taken from a much larger region than were any of the western samples, they show less statistical variation than do most of the latter.

A second analysis (Fig. 7) compares the same six specimens, as a group, with the six samples of western *C. lupus*, combined as one group, and the series of 96 western male *C. latrans* (Appendix II). In addition, the seven skulls of males, taken just west of the Mississippi in northeastern Louisiana in 1898-1905, and the one specimen from Garvin County, Oklahoma (Fig. 2), were tested as individuals against the three defined series. Again, the six eastern skulls form a statistical group distinct from *C. lupus* and also far separated from *C. latrans*. The Louisiana and

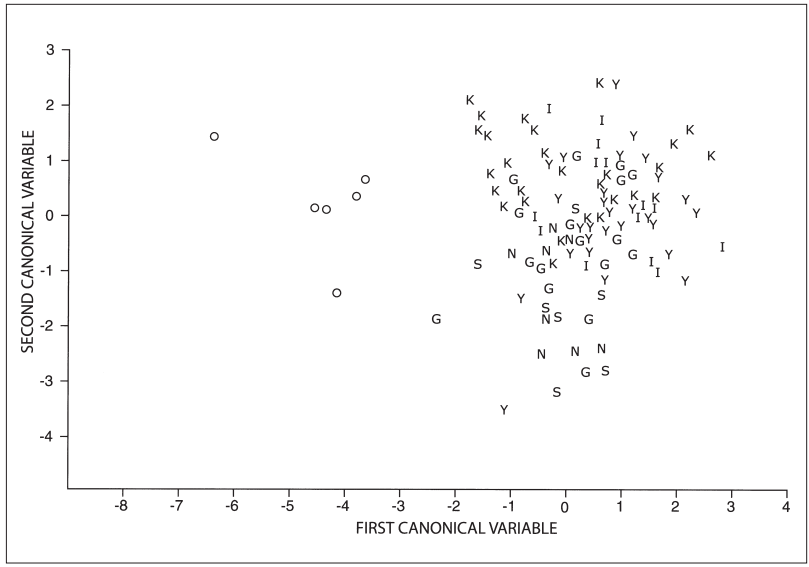

Figure 6. Statistical distribution of seven groups of North American male *Canis*, plotted on the first and second canonical variables. G's, *C. lupus* from southern Rocky Mountains; I's, *C. lupus* from northern Rocky Mountains; K's, *C. lupus* from Minnesota; N's, *C. lupus* from Nebraska, Kansas, and Oklahoma; S's, *C. lupus* from central and western Texas; Y's, *C. lupus* from central Rocky Mountains); open circles, pre-1918 *C. rufus* from east of Mississippi River.

Oklahoma specimens fall within or near the range of variation of the six skulls from farther east.

The 14 pre-1918 skulls of eastern male wolves evidently represent a statistically well-defined species. They were combined in a single group and compared to western *C. lupus*, likewise in a single group (Fig. 8). Another series tested in that analysis comprised the 10 oldest available specimens of male *C. lupus lycaon* from southeastern Ontario and extreme southern Quebec (Appendix II). Those 10 skulls were taken 1905-1933 and are unlikely to represent hybridization with *C. latrans*, which apparently subsequently affected *lycaon* in southeastern Canada (Kolenosky and Standfield 1975, Lehman et al. 1991, Sears 1999). The coyote was first reported in southeastern Ontario in 1919, but that record was only 100 km northeast of Detroit, Michigan, and the species did not become established farther east until the 1940s (Nowak 1979). Also used in the analysis was the series of *C. lupus* collected from 1905 to 1965 in the upper peninsula of Michigan.

The analysis (Fig. 8) once again shows complete and wide statistical separation between the series of southeastern wolves and western *C. lupus*. *Lycaon* is intermediate to those populations, just about filling the statistical gap between them. While *lycaon* does not overlap with the southeastern wolves and only slightly with western *C. lupus*, it does show more affinity to the sample from upper Michigan. That sample is from an area geographically between the range of *lycaon* and that of the Minnesota/Isle Royale sample of western *C. lupus*. A single specimen (USNM 1804), collected prior to 1855 in the Adirondacks of northern

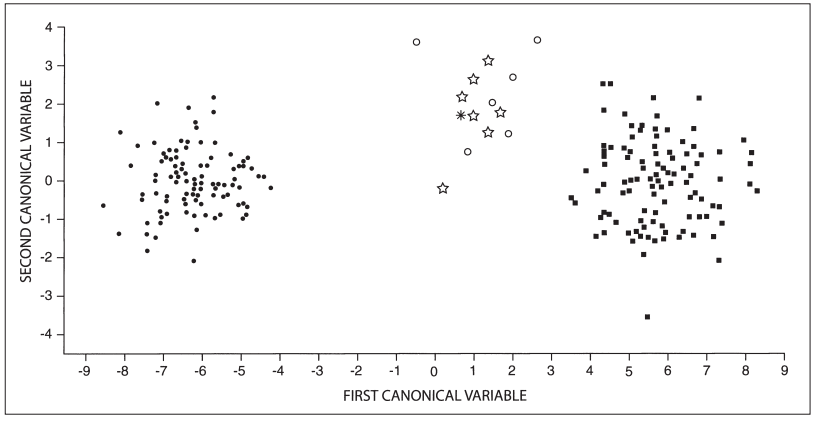

Figure 7. Statistical distribution of three groups and certain individuals of North American male *Canis*, plotted on the first and second canonical variables. Dots, western *C. latrans*; solid squares, western *C. lupus*; open circles, pre-1918 *C. rufus* from east of Mississippi River; open stars, individual northeastern Louisiana *C. rufus* dating 1898-1905; asterisk, individual Oklahoma specimen dating prior to 1869.

New York, was tested as an individual against the four series used in the analysis. Its statistical position falls among those of *lycaon* from just to the northwest and it may be part of the same population. It was not included in any of the series, as it may not be fully developed, but it probably would not have grown much larger. Its general size is about that of males from the southeastern series and smaller than that of any male *lycaon* or other *C. lupus* assessed in this study. In proportion and dental characters it more closely resembles *C. lupus* than it does the southeastern series. In those respects it contrasts sharply with an 1863 specimen from Maine (Appendix II), which has the slender proportions and well-sculptured molars typical of the southeastern wolves.

The morphological approach seen in the northeast is not evident as the wolf populations of the southeast geographically converge with western *C. lupus*. The original situation on the western edge of the range of the southeastern wolves, especially in central Texas, is partly obscured by hybridization with *C. latrans*, but prior studies have shown *C. lupus* to be statistically well removed from the affected population (Nowak 1979, Nowak and Federoff 1996, Nowak et al. 1995). There is

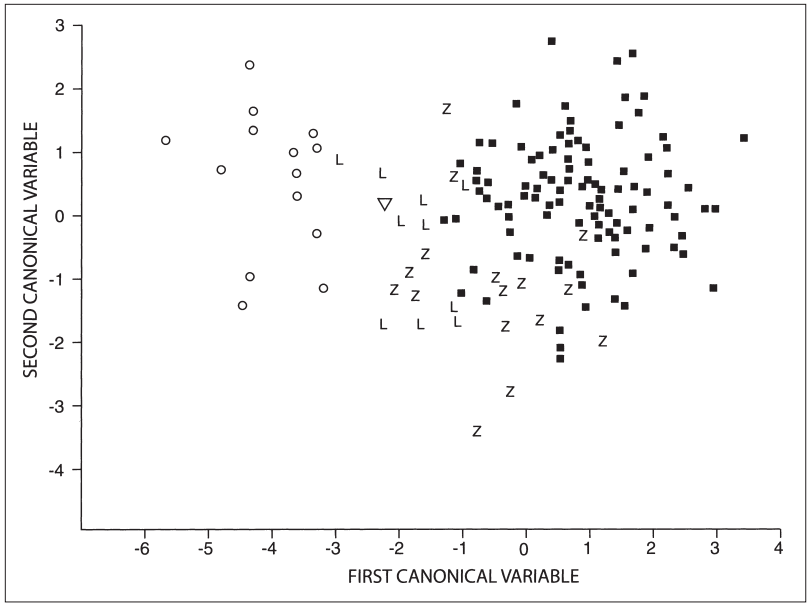

Figure 8. Statistical distribution of four groups and one individual of North American male *Canis*, plotted on the first and second canonical variables. Solid squares, western *C. lupus*; Z's, *C. lupus* from upper peninsula of Michigan; L's, *C. lupus lycaon* dating 1905 - 1933; inverted triangle, *C. lupus lycaon* (?) from Adirondacks of northern New York (pre-1855 specimen); open circles, pre-1918 *C. rufus* from east of Mississippi River, northeastern Louisiana, and Oklahoma (pre-1869 specimen).

one old series that may represent the unmodified southeastern wolf near the western extremity of its range: the five males collected in 1900 in Calhoun County on the south Texas Gulf coast (Appendix II). A single female (USNM 99720), morphologically compatible with those males, also was taken there, but no other specimens – identified as *C. rufus*, *C. latrans*, or any other wild *Canis* – are known from that area and period. The Calhoun County males were compared to three other groups of males (Fig. 9): the six specimens from east of the Mississippi and dating prior to 1918, the seven taken 1898-1905 in northeastern Louisiana, and western *C. latrans*. The Calhoun County group was found to occupy a statistical position separate from those of the more easterly series but not intermediate to those two and *C. latrans*. Visually, the Calhoun County specimens are smaller and narrower than the other two and have relatively smaller teeth.

Considered alone, the statistical distributions of Figure 9 may suggest that the Calhoun County skulls represent a separate species, intergrading neither with more easterly wolf populations nor *C. latrans*. Both the Calhoun County and northeastern Louisiana series date from about a century ago and, unfortunately, there are no contemporary samples of males from geographically intermediate areas, and hence no direct evidence for or against intergradation. A series of males was

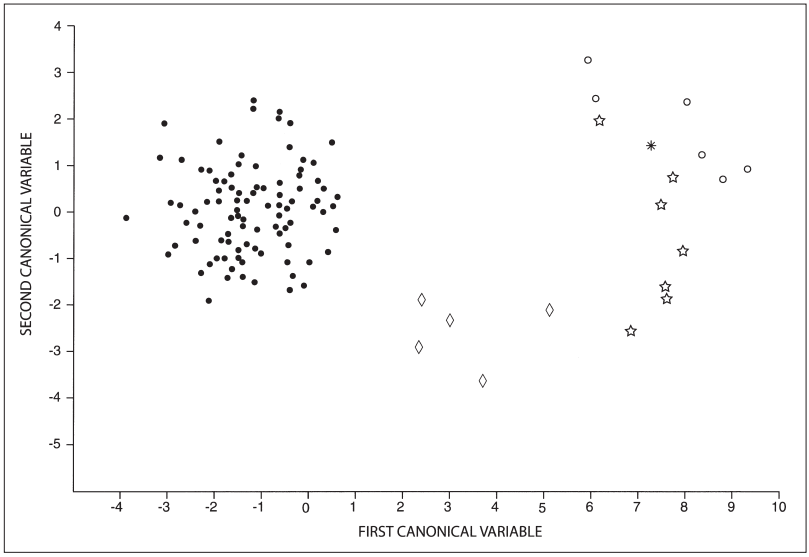

Figure 9. Statistical distribution of four groups and one individual of North American male *Canis*, plotted on the first and second canonical variables. Dots, western *C. latrans*; open circles, pre-1918 *C. rufus* from east of Mississippi River; open stars, northeastern Louisiana *C. rufus* dating 1898-1905; diamonds, *C. rufus* from Calhoun County, coastal Texas, dating 1900; asterisk, individual Oklahoma specimen dating prior to 1869.

collected from 1919 to 1943 farther north along the Texas coast, in the Big Thicket area of inland southeastern Texas, and in southern Louisiana and Mississippi (Appendix II).

The 1919-1943 specimens were tested as individuals against the four groups shown in figure 9. They fill most of the statistical gap between the Calhoun County and more easterly series (Fig. 10). The Big Thicket and south Mississippi skulls fall close to the northeast Louisiana sample, while the Texas coastal and south Louisiana skulls are nearer to the early Calhoun County series. The pre-1869 skull from south-central Oklahoma also was tested in this analysis and falls precisely between the northeast Louisiana and east-of-the-Mississippi series.

The 1919-1943 series shows no statistical tendency to approach or blend with *C. latrans*; such a tendency might have been expected if that series had experienced substantive introgression from the latter species. However, hybridization with *C. latrans* most certainly had begun at the western edge of the range of *C. rufus* earlier in the century. Five males,

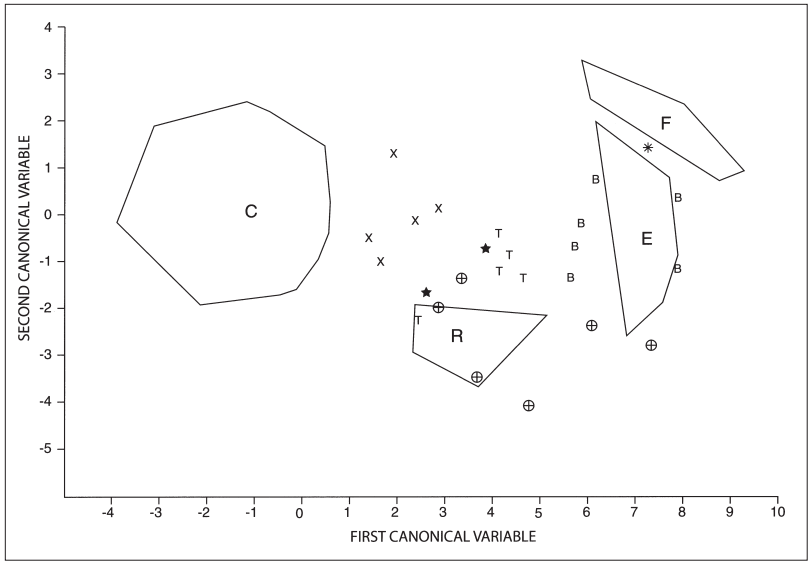

Figure 10. Statistical distribution of four groups (the same depicted in Fig. 9) and certain individuals of North American male *Canis*, plotted on the first and second canonical variables. Solid lines, limits of western *C. latrans* (letter C shows mean position), *C. rufus rufus* (letter R shows mean), *C. rufus gregoryi* (letter E shows mean), and *C. rufus floridanus* (letter F shows mean); B's, individuals from southern Mississippi and Big Thicket area of Texas; T's, individuals from coastal southeastern Texas; solid stars, individuals from southern Louisiana; circled crosses, individuals from reintroduced population in North Carolina; asterisk, individual Oklahoma specimen dating prior to 1869; X's, apparent hybrids of *C. rufus* x *C. latrans* from central Texas dating 1899-1906.

collected 1899-1906 in Edwards and Kerr counties, central Texas, are statistically intermediate to *C. latrans* and coastal wolves, and may represent initial hybridization between the two species (Fig. 10).

A much larger series from central Texas was collected 1915-1918 and shows a complete statistical blending of *C. latrans* and the southeastern wolf, though the entire involved population seemingly was extirpated by human agency shortly thereafter (Nowak 1979). Additional hybrid populations formed in the Ozark region and pushed to the south and east in ensuing decades. Nonetheless, a largely unmodified wolf population apparently persisted in extreme southeastern Texas and southern Louisiana until the 1970s. The close morphometric resemblance of that population, and of 14 individuals removed therefrom to begin the existing captive/reintroduced population, to the original southeastern wolf population has been documented (Nowak 1979, 1992). This study centers on the original, not current, status of eastern wolves. However, to briefly update the current situation, six recently collected individuals (seen at Alligator River National Wildlife Refuge, Dare County, North Carolina, 17 April 1999) were compared to the three series of old southeastern wolves and to *C. latrans* (Fig. 10). Those six are males that were born in the wild and raised to maturity in the population reintroduced in North Carolina (Nowak et al. 1995), and were the only available specimens meeting those criteria. The six skulls are statistically close to the century-old series from Calhoun County, though there is some approach to the old northeast Louisiana series.

DISCUSSION

The view (Nowak 1979) that the red wolf is a primitive species, closely related or identical to *C. priscolatrans* of the early Irvingtonian, is not supported by this study. It is conceivable that a small wolf, descended from *C. priscolatrans*, persisted in the eastern forests after that period and has not yet shown up in the fossil record, though that now seems unlikely. Available material suggests an archaic New World evolutionary sequence, from the Blancan *C. lepophagus* (or some related small species), through the early Irvingtonian *C. priscolatrans*, to the late Irvingtonian and early Rancholabrean *C. armbrusteri*, and finally culminating in the late Rancholabrean *C. dirus*. Certain specimens at several sites suggest transition, or at least are difficult to distinguish, between two sequential species: *C. lepophagus* and *C. priscolatrans* at Haile 12B, Florida (see above), *C. priscolatrans* and *C. armbrusteri* at Haile 21A and Leisey, Florida (Berta 1995), and Port Kennedy, Pennsylvania (Cope 1899), and *C. armbrusteri* and *C. dirus* at Cumberland Cave, Maryland (Martin 1974). In any case, the outline given here may be an oversimplification, as there probably were additional species

involved and some phases of the sequence that extended beyond eastern North America. In particular, one or two species of South America may represent part of the transition from *C. armbrusteri* to *C. dirus* (Berta 1988, Nowak 1979). With the extinction of the dire wolf, about 8,000 ybp, the entire New World wolf line terminated.

The New World evolutionary progression was primarily in the direction of increasing size, from a relatively small to a relatively large species of *Canis* (Figs. 3, 4). There was little or no overlap in the size of the species present during any one period. A coyote-like species of the Blancan (*C. lepophagus*) was replaced by the small wolf (*C. priscolatrans*) of the early Irvingtonian. A coyote-sized species reappeared in the east, in the form of modern *C. latrans*, only when the wolf line had grown much larger, becoming the species *C. armbrusteri* in the late Irvingtonian to early Rancholabrean. After *C. priscolatrans* disappeared, nearly a million years passed before a small wolf again was evident in the east. This wolf could have been a direct descendant of the Eurasian *C. mosbachensis*. The above data suggest that *C. mosbachensis* was considerably smaller than most modern wolves. Indeed, Kurten (1968) reported *C. mosbachensis* to be about the size of *C. lupus pallipes* Sykes, the living wolf of southwestern Asia, which Nowak (1995) indicated is smaller than *C. rufus*. Kurten (1968) noted that *C. mosbachensis* still was present in Europe during a period corresponding to the early Rancholabrean of North America and that transition to the larger *C. lupus* did not occur until the time of the late Rancholabrean. Such a background offers the possibility that *C. mosbachensis* gave rise to small wolves that entered North America, became isolated by glaciation, and developed into the modern eastern populations. Eurasian *mosbachensis* then may have evolved into *C. lupus* and subsequent invasions of North America may have led to the modern subspecific differentiation of the latter species (Nowak 1995). Ecological space for the modern small wolf, as well as the modern small coyote, became available in the east only when the archaic New World wolf line had grown to enormous size, becoming *C. dirus*, in the late Rancholabrean (Fig. 4). Both the small coyote and large wolf disappeared from the east at the end of the Pleistocene but the new small wolf persisted until the 20th century. Remarkably, when that wolf was itself extirpated in our own times, the coyote again occupied the east (Bekoff 1999, Hill et al. 1987, Nowak 1979).

Kurten (1974) regarded *C. priscolatrans* as part of the coyote line leading from *C. lepophagus* to modern *C. latrans*. This study suggests that while *C. lepophagus* may have given rise to both *C. priscolatrans* and *C. latrans*, the latter represents a separate line of descent. It may have remained primarily in the west, moving eastward only when the niche for a smaller *Canis* sufficiently widened. A large subspecies of *C.*

latrans was abundantly sympatric with *C. dirus* at Rancho La Brea and some other western Rancholabrean sites (Kurten 1974, 1984; Nowak 1979). Replacement of *C. dirus* by *C. lupus* may be a factor in the smaller size of modern *C. latrans* in the west. Eastern coyotes are not well represented in the fossil record (Fig. 1). It even has been suggested that the late Rancholabrean (about 10,000 ybp) records of *C. latrans* in Florida are referable to *C. familiaris* (Martin and Webb 1974). Reexamination of that material in the course of this study supports identification as *C. latrans*. The specimens are exceedingly small, perhaps as a consequence of sympatry with a small wolf as well as *C. dirus*, but are within the overall size range of modern *C. latrans* (Jackson 1951) and show other characters of that species, not *C. familiaris*. The earlier occurrence (c. 33,500 ybp) at Megenity Cave in southern Indiana is of a somewhat larger coyote; the only sympatric wolf there is *C. dirus* (R. L. Richards, Indiana State Museum, pers. comm., 3 January 2000). Frankstown Cave, a late Rancholabrean (c. 14,000 ybp) site in Pennsylvania, also has a large coyote, as well as a relatively small dire wolf, but no other *Canis* (Nowak 1979). Additional late Rancholabrean records of eastern *C. latrans* are from West Virginia (Graham and Lundelius 1994), Mississippi (Kurten 1974, Kurten and Kaye 1982), and Alabama (Morey 1994). The influx of a small wolf, apparently late in the Rancholabrean, may have been a factor in the ultimate disappearance of the coyote from most of the east.

From the end of the Pleistocene until the mid-20th century, the coyote was absent from the region of interest, except for a zone of perhaps 100 - 200 km extending eastward and southward from the prairies (Fig. 1). Archeological records indicate that *C. latrans*, at least at times, occurred as far as southern Indiana, southern Missouri, and northwestern Arkansas (Graham and Lundelius 1994). In 1919-1925, a series of *C. latrans* was collected in and around the St. Francois Mountains of southeastern Missouri, together with a large series apparently representing an isolated wolf population. Previous study showed no morphometric overlap between the two series, hence demonstrating that each represented a separate species and that hybridization had not yet developed in that area (Nowak 1979). All Recent specimens from that period and earlier, and from farther south and east within the zone of interest, are wolves.

It again is emphasized that there are only six known complete and fully developed skulls of male wild *Canis* dating prior to 1918 and collected in the region of interest: east of the Mississippi and south of the Prairie Peninsula, Lakes Erie and Ontario, and the St. Lawrence River. Using multivariate analysis (Fig. 6), those six skulls group together and have a statistical distribution completely separate from the extensively overlapping distributions of six samples of western *C. lupus*, including the samples most proximal to the eastern series (Fig. 1).

Those six specimens also are completely removed from the statistical distribution of *C. latrans*. Seven additional complete skulls of males from northeastern Louisiana, taken 1898-1905, and one collected prior to 1869 in south-central Oklahoma, have about the same statistical distribution as the six more easterly specimens, when compared to *C. lupus* and *C. latrans* (Fig. 7). Such an arrangement argues for recognition of the eastern sample as a distinct species that is appropriately named *C. rufus*. Moreover, that species, as defined by the complete eastern skulls, has diagnostic measurements that are statistically identical to those of two series of fragmentary specimens, collected in the same region and dating from around 10,000 ybp and from 2,000-200 ybp (Table 1). Although not conclusive, this evidence supports the view that *C. rufus* has continuously occupied the east since the terminal Pleistocene and that it is the only species of wild *Canis* that was present in most of the region.

None of the archeological or modern specimens, either examined as part of this study or reported by others (Graham and Lundelius 1994) indicate the presence of *C. latrans*, or hybridization between *C. latrans* and another wild species in the southeast between 10,000 and 100 ybp. Subsequently, *C. latrans* did recolonize the southeast and begin to hybridize with the native wolf, *C. rufus*. The hybridization process signaled the end of that species, not its beginning. This study thus is not in agreement with some of the recent DNA analyses, particularly the suggestion that *C. rufus* originated from hybridization between *C. latrans* and *C. lupus*, probably within the last 250 years as a result of environmental disruption by European colonists (Reich et al. 1999, Roy et al. 1996, Wayne et al. 1998).

Surprisingly, this investigation provides evidence that another named kind of eastern wolf did have a hybrid origin. The oldest available series of *C. lupus lycaon* from the northeast is statistically intermediate to *C. rufus* and western *C. lupus* (Fig. 8). The morphological similarity of *rufus* and *lycaon* has long been recognized and has confused the systematic status of eastern *Canis*. Recognition of *lycaon* – specifically the population of extreme southeastern Ontario and southern Quebec, and possibly northern New York – as a hybrid provides a solution to the problem of why the red and gray wolf differ so much along most of the line where their ranges meet, but resemble one another so closely in the northeast.

That solution also is in keeping with mitochondrial DNA analyses indicating that *C. rufus* and *lycaon* contain genetic sequences similarly divergent from *C. latrans* and differing from those of *C. lupus*. Wilson et al. (2000) interpreted those analyses to mean that *rufus* and *lycaon* form a single species, independent of *C. lupus* and *C. latrans*, that would appropriately be known as *C. lycaon*. However, another plau-

sible interpretation is that the modern range of *lycaon* originally had been occupied by *C. lupus*, which had moved in from the west following the retreat of the glaciers at the end of the Pleistocene, as attested by the large specimen from Frontenac Island in western New York. *C. rufus* would also then have moved northward to the southern edge of that area. That newly available and perhaps unstable habitat may have been conducive to hybridization.

The predominant flow of introgression probably was from *rufus* to *lycaon*, with consequent modification of the latter, rather than the reverse. Although *lycaon* is statistically near *rufus*, available material shows no definite overlap, whereas *lycaon* shows greater statistical similarity with *C. lupus*, especially the original population of northern Michigan, which is geographically most proximal. *Lycaon* also does not substantively differ ecologically and behaviorally from other gray wolf subspecies (Forbes and Theberge 1995, Mech 1970, Pimlott et al. 1969). *Lycaon* may still be regarded as a subspecies of *C. lupus*, but one that perhaps developed as a result of natural hybridization with *C. rufus*. While *lycaon* thus would not represent an early wave of *C. lupus* that had invaded North America and become isolated by glaciation, it and the other gray wolf subspecies suggested by previous study (Nowak 1995) should for now be retained.

There does remain the question of subspeciation in the red wolf. Audubon and Bachman (1851) had restricted *rufus* to Texas and some adjacent areas. Goldman (1937, 1944) thought that two more subspecies could be identified farther to the east: *C. rufus gregoryi* Goldman in the lower Mississippi Valley and *C. r. floridanus* Miller from Alabama to the Atlantic. Lawrence and Bossert (1967) suggested that inclusion of the larger eastern forms with the smaller *C. r. rufus* of Texas might never have occurred if the systematic delineation of southeastern wolves had been based initially on eastern, rather than Texas, material.

That, essentially, is what was done in this study: the oldest available eastern specimens were assessed first, then specimens from just west of the Mississippi, and finally material from Texas. The results support Goldman's original arrangement, both with respect to the east-west distribution of *C. rufus* and its separation as a species from *C. lupus* and *C. latrans*. The red wolf does become smaller to the west, especially in Texas, but such character displacement might be expected as it approaches a zone of sympatry with the larger gray wolf.

The multivariate analyses (Figs. 9, 10) reinforce Goldman's (1944) designation of three subspecies of *C. rufus*. However, some rearrangement of subspecific lines is advisable, based on assessment of the oldest available material (Fig. 2). *C. r. floridanus* apparently occurred all along the Atlantic coast, from Maine to Florida, and inland to Ohio and northern Alabama. *C. r. gregoryi* was found throughout the lower Mis-

sissippi Valley, including some country along the Ohio and Red rivers, and in the Big Thicket area of eastern Texas. *C. r. rufus* occupied the Texas coast and probably central Texas, though it is known from the latter area only as a hybrid with *C. latrans*. There is no conclusive evidence that it originally occurred farther north. Although Goldman reported its range to reach Oklahoma, southwestern Missouri, and northwestern Arkansas, the pertinent specimens probably express the spread of hybridization with *C. latrans* and hence smaller size (Nowak 1979). The oldest known Oklahoma skull, the pre-1869 specimen from Garvin County, shows statistical affinity to *gregoryi/floridanus*.

The range of *C. r. rufus* may have extended farther east along the Gulf coast than was indicated by Goldman. Specimens from the coastal counties of extreme southeastern Texas and from southern Louisiana have statistical affinity to the old series of *C. r. rufus* from Calhoun County, Texas, to the west (Fig. 10). All of those skulls are characterized by small size and relatively small teeth, perhaps reflecting a scarcity or small size of prey in coastal habitat and the semiarid country of central Texas.

Several specimens from central Texas (Fig. 10) show that *C. rufus* had begun to hybridize with *C. latrans* by 1900. The same process was evident not long afterwards in eastern Oklahoma and western Arkansas. The further spread of hybridization and of coyote-like animals through the southeast is well documented (Hill et al. 1987, Kennedy et al. 1986, Nowak 1979). However, statistical evidence also shows that the population of wild *Canis* that persisted in southeastern Texas and southern Louisiana until the 1970s, as well as individuals removed from that area and used to found the existing captive/reintroduced population, were similar to the original red wolf (Nowak 1979, 1992). Available specimens (Fig. 10) indicate that the breeding population now established in the wild in North Carolina retains the morphometric characterization of *C. rufus rufus*.

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Appendix 1. Paleontological and Archeological Specimens Examined. This list provides details for series from the region of interest, thought to date prior to AD 1800. Specific identifications are as determined in this study. Information on a few additional individuals is given in the text. Abbreviations used are: ANSP, Academy of Natural Sciences, Philadelphia; AMNH, American Museum of Natural History; CM, Carnegie Museum; CNM, National Museum of Canada; FGS, Florida Geological Survey; ILSM, Illinois State Museum; INSM, Indiana State Museum; MCZ, Harvard University Museum of Comparative Zoology; MSU, Michigan State University Museum; MVZ, University of California Museum of Vertebrate Zoology; NCSU, North Carolina State University Department of Zoology; PU, Purdue University Department of Forestry and Conservation; ROM, Royal Ontario Museum; UAR, University of Arkansas Department of Zoology; UF, Florida Museum of Natural History; UMI, University of Michigan Museum of Zoology; UMN, University of Minnesota Museum of Natural History; USNM, United States National Museum.

Canis lepophagus. – FLORIDA. Alachua County: Haile 12B, late Blancan, mandibular fragment (UF unnumbered). Gilchrist County: Santa Fe River 1B, late Blancan, five mandibular fragments (UF 10423, 10424, 10836, 10837, 10858); mandible (collection of D. Damrow, Mosinee, Wisconsin).

Canis latrans. – FLORIDA. Brevard County: Melbourne, late Rancholabrean (c. 10,000 ybp), rostral fragment (MCZ 5909), mandibular fragment (USNM 12947). Dade County: Cutler site, near Perrine, late Rancholabrean, maxillary fragment (UF 143286), mandibular fragment (UF 143279). Indian River County: Vero (stratum 3), late Rancholabrean, maxilla (FGS 7036). Levy County: Devil's Den, late Rancholabrean (c. 10,000 ybp), three mandibular fragments (UF 11514, 11515, 11517). INDIANA. Crawford County: Megenity Peccary Cave, late Rancholabrean (c. 33,500 ybp), cranium and maxillae (INSM 71-3-62-5-1), two maxillary fragments (INSM 71-3-60-5-6, 71-3-63-5-24), mandible (INSM 71-3-60-5-1), four mandibular fragments (INSM 71-3-62-5-59, 71-3-62-5-84, 71-3-62-5-85, 71-3-62-5-96), four P4 (INSM 71-3-62-5-44, 71-3-62-5-66, 71-3-63-5-22, 71-3-63-5-43), three M1 (INSM 71-3-62-5-129, 71-3-62-5-142, 71-3-62-5-129), three m1 (INSM 71-3-62-5-25, 71-3-62-5-117, 71-3-62-5-140). MARYLAND. Allegany County: Cumberland Cave, early Rancholabrean, mandibular fragment (USNM unnumbered). PENNSYLVANIA. Blair County: Frankstown Cave, late Rancholabrean (c. 14,000 ybp), two mandibular fragments from same individual (CM 11027). VIRGINIA. Shenandoah County: stone quarry 1 km NW Edinburgh, early Rancholabrean, maxillary fragment (USNM). WEST VIRGINIA. Pendleton County: New Trout Cave, late Rancholabrean (10,000 - 40,000 ybp), p4 (USNM unnumbered).

Canis priscolatrans (= *Canis edwardii*). – FLORIDA. Alachua County: Haile 12A, late Blancan, cranial fragment (UF 11516); Haile 21A, early Irvingtonian, cast of rostral fragment (UF 62561), mandible (UF 63175), casts of three mandibles (UF 62562, 62563, 62564), four mandibular fragments (UF 62568, 63174, 63527, 62565), two P4 (UF 18049, 124537), M1 (UF 63623), two p4 (UF 63311, 124539), m1 (UF 62567). Charlotte County: Punta Gorda, early Irvingtonian, mandibular fragment (UF 36429). Citrus County: Inglis 1A, early Irvingtonian,

three maxillary fragments (UF 18046, 18047, 67846), two mandibular fragments (UF 19323, 19324), P2 (UF 18050), P4 (UF 18049), two M1 (UF 19405, 19406), two M2 (UF 18048), m1 (UF 19404); Crystal River Power Plant, early Irvingtonian, maxillary fragment (UF17074). Hillsborough County: Leisey Shell Pits, early Irvingtonian, cranial fragment (UF 67092), seven maxillary fragments (UF 81654, 81655, 81663, 81664, 81665, 81666, 124531), mandible (UF 63667), three mandibular fragments (UF 64399, 87283, 95647), four P4 (UF 80662, 81656, 81661, 81668), two M1 (UF 81657, 81669), p2 (UF 81675), p3 (UF 81674), two p4 (UF 81658, 81659), six m1 (UF 81660, 81662, 81672, 81673, 84752, 87285), two m2 (UF 81689, 87297). Polk County: Phosphoria Mine, early Irvingtonian, cast of maxillary fragment (UF 58332). Sarasota County: Rigby Shell Pit, early Irvingtonian, maxillary fragment (UF 40090), mandibular fragment (UF 40091). PENNSYLVANIA. Montgomery County: Port Kennedy deposit, early Irvingtonian, P4, M1, M2, and p4 (ANSP 57-58).

Canis armbrusteri. – ARKANSAS. Newton County: Conrad Fissure, early Rancholabrean, cranial fragment, isolated teeth (AMNH 11761), mandibular fragment (AMNH 11762). FLORIDA. Alachua County: Haile 7A, early Rancholabrean, maxillary fragment and pair of mandibles (UF 11845). Levy County: McLeod lime rock mine, middle Irvingtonian, cranial fragment (AMNH 67286), two maxillary fragments, probably from same individual (AMNH 67287-67288), two mandibular fragments, probably from same individual (AMNH 67289-67290), mandibular fragment (AMNH 67291). Sumter County: Coleman 2A Local Fauna, late Irvingtonian, near-complete skull without mandibles (UF 11519), cranial fragment, maxillary fragment, and three mandibular fragments (UF 11520), mandibular fragment and two m1 (UF 12121), mandibular fragment (UF 11518), two P4 (UF 12114). MARYLAND. Allegany County: Cumberland Cave, early Rancholabrean, two skulls with mandibular fragments (USNM 8144, 11881), six skulls (USNM 7994,11883, 11885, 11886, 11887, 12288), 13 mandibular fragments (USNM 7482, 7661, 8144, 8168, 8169, 8172, 11881, 11882, 11888, 12290, 12291, 12293, 12295).

Canis dirus (all late Rancholabrean). – FLORIDA. Alachua County: Hornsby Springs, maxillary fragment (UF 3988), mandibular fragment (UF 3987). Brevard County: Melbourne, mandible (USNM 12946), two isolated P4, two M1, and four m1 (USNM unnumbered). Columbia County: Ichetucknee River, maxillary fragment (UF 8006), three mandibular fragments (UF 8005, 12899, 17717). Dade County: Cutler site, near Perrine, mandibular fragment (UF 156956), p4 and m1 (UF 135887). Indian River County: Vero (stratum 2), skull without mandibles (FGS 7166). Levy County: Devil's Den, incomplete skull (UF 7996); Wekiva River, mandibular fragment (UF 14204). Manatee County: Bradenton, maxillary fragment (UF 3276), mandibular fragment (UF 2259). Marion County: Eichelberger Cave, two mandibular fragments, probably from same individual (UF 1622, 1623); Reddick 1A, crushed skull with mandibles (UF 2923), two crushed skulls without mandibles (UF 3081 and unnumbered), mandibular fragment (UF unnumbered), isolated P4, two M1, M2, and m1 (UF unnumbered). Pinellas County: Seminole Field, mandibular fragment (AMNH 23568), M1 (AMNH 23582), M2 (AMNH 23569), two m1 (AMNH 23565, 23567). GEORGIA. Bartow County: Ladds, M1 (USNM 23698). INDIANA.

Vanderburgh County: Ohio River, maxillary fragment (ANSP 11614). KENTUCKY. Woodford County: Welsh Cave, cast of skull without mandibles (CM 12625), cast of mandible from different individual (CM 12625a). PENNSYLVANIA. Blair County: Frankstown Cave, maxillary fragment (CM 11023), three mandibular fragments (CM 11022, 11024, 11026). WEST VIRGINIA. Greenbrier County: Rennick, mandible (CM 24327).

Canis rufus. – ALABAMA. Jackson County: Crow Island Indian midden, c. 1,000 ybp, mandible (UMI 91100). ARKANSAS. Crittenden County: Banks Site, c. 425 ybp, mandible (ILSM). Washington County: Eddy Bluff shelter, early Recent, maxillary fragment (UAR unnumbered). FLORIDA. Brevard County: Melbourne, late Rancholabrean (c. 10,000 ybp), mandibular fragment (MCZ 17789). Citrus County: Withlacoochee River, late Rancholabrean (c. 10,000 ybp), m1 (collection of D. Wells, Falls Church, Virginia). Columbia County: Ichetucknee River, late Rancholabrean, m1 (collection of D. Damrow, Mosinee, Wisconsin). Dade County: Nichol's Hammock, c. 200 ybp, mandible (UF 16711). Gilchrist County: Santa Fe River bottom, late Rancholabrean or early Recent, mandibular fragment (collection of D. Damrow, Mosinee, Wisconsin). Indian River County: Jungerman Site, c. 250 ybp, m1 and m2 (UF unnumbered). Levy County: Devils's Den, late Rancholabrean (c. 10,000 ybp), cranial fragment (UF 16397), mandible (UF 11513). ILLINOIS. Crawford County: Palestine site, c. 2,000 ybp, maxillary fragment (ILSM CW4F67), mandibular fragment (ILSM CW4F66). Montgomery County: Litchfield, late Rancholabrean, mandible (collection of D. Damrow, Mosinee, Wisconsin). MARYLAND. Anne Arundel County: Doepkin's Farm site, c. 300 ybp, maxillary fragment (seen at site, current location unknown). NEW YORK. Fulton County: Garoga site, c. 400 ybp, maxillary fragment and two mandibular fragments (CM G-837). NORTH CAROLINA. Macon County: Franklin site, c. 300 ybp, maxillary fragment (NCSU unnumbered). OHIO. Ross County: Blain site, c. 800 ybp, maxillary fragment (ILSM unnumbered). PENNSYLVANIA. Bedford County: New Paris Sinkhole No. 2, c. 1,900 ybp, incomplete skull and pair of mandibles (CM 6548a, 6548b). Greene County: Hartley site, c. 500 ybp, mandibular fragment (CM 4531). Indiana County: Johnston site, c. 350 ybp, maxillary fragment (CM 802). Lancaster County: Eschelman site, c. 350 ybp, cranial fragment, pair of mandibles, and three mandibular fragments (CM 36 La 12). TENNESSEE. Hamilton County: Citico Mound, c. 1,000 ybp, mandible (USNM 200145). WEST VIRGINIA. Fayette County: Mount Carbon site, c. 500 ybp, m1 (CM 46 Fa 7). Greenbrier County: Piercy's Cave, late Rancholabrean, m1 (USNM unnumbered). Putnam County: Buffalo Village site, c. 300 ybp, three mandibular fragments and isolated m1 (CM 46 Pu 31).

Appendix 2. Specimens Used in Multivariate Analyses. This list provides information on those series subjected to canonical discriminant analysis. Greater detail is given for specimens from the region of interest; specific and subspecific identifications in that region are as determined in this study. Details on a few additional individuals, also used in multivariate analysis, are provided in the text. For abbreviations used, see Appendix I.

Canis latrans lestes. – COLORADO (44 USNM), IDAHO (52 USNM).

Canis lupus (western series). *C. l. irremotus*. – IDAHO (3 USNM). MONTANA (4 USNM). WYOMING (7 USNM). *C. l. lycaon* (original identification). – MICHIGAN, Isle Royale (5 PU). MINNESOTA (15 USNM, 8 UMN). *C. l. mogollonensis*. – ARIZONA (4 USNM). NEW MEXICO (13 USNM). *C. l. monstrabilis*. – TEXAS (7 USNM). *C. l. nubilus*. – KANSAS (2 USNM). NEBRASKA (3 USNM). OKLAHOMA (1 AMNH, 1 USNM). *C. l. youngi*. – COLORADO (5 USNM). NEW MEXICO (12 USNM). UTAH (6 USNM). WYOMING (5 USNM).

Canis lupus. – MICHIGAN, upper peninsula (3 MSU, 4 UMI, 9 USNM).

Canis lupus lycaon. – ONTARIO. Brent, 1922 (ROM 24-11-19-1); Carling, 1932 (ROM 32-11-30-1); Dacre, 1930 (ROM 31-2-12-1); Nipissing, 1933 (ROM 33-3-24-1); Opeongo Lake, Algonquin Provincial Park, 1910 (ROM 32213); Whitney, 1931 (MVZ 77344). QUEBEC. Jim's Lake, Pontiac County, 1924 (CNM 5572); Lucerne, 1931 (MVZ 77343); 67 km NE Mattawa, Ontario (locality in Quebec), 1905 (USNM 140562); Montebello, 1931 (ROM 31-12-29-2).

Canis rufus floridanus. – ALABAMA. Colbert County: 18 km S Cherokee, 1917 (USNM 223936). Jackson County: Fern Cave, probably prehistoric (USNM 348063). FLORIDA. Dade County: vicinity of Miami, 1854 (MCZ 11179. MAINE. Piscataquis County: Moosehead Lake, 1863 (MCZ 326). PENNSYLVANIA. Indefinite localities, prior to 1859 (ANSP 2261, 2262).

Canis rufus gregoryi. – LOUISIANA. Concordia Parish: 32 km SW Vidalia, 1905 (USNM 137125). Madison Parish: 4 km NW Tallulah, 1904 (USNM 133687); 29 km SW Tallulah, 1905 (USNM 136731); 37 km SW Tallulah, 1905 (USNM 136834). Morehouse Parish: Mer Rouge, 1898 (MCZ 9114); Mer Rouge, 1904 (USNM 132229). West Carroll Parish: 16 km SW Floyd, 1904 (USNM 133688).

Canis rufus rufus. – TEXAS. Calhoun County: 11 km SW Port Lavaca, 1900 (USNM 99705, 99706); O'Connorsport, 1900 (USNM 99718, 99719, 99721).

Canis rufus (1919-1943 series). – LOUISIANA. Beauregard Parish: near Sabine River, 1928 (USNM 248332). Iberia Parish: 18 km N Avery Island, 1919 (USNM 234227). MISSISSIPPI. Harrison County: Biloxi, 1931 (AMNH 100225). TEXAS. Brazoria County: Angleton, 1936 (USNM 261753); 14 km NE Angleton, 1943 (USNM 273537). Chambers County: 5 km E Mont Belvieu, 1926 (USNM 246552). Hardin County: indefinite locality, 1937 (USNM 262473). Liberty County: Cleveland, 1932 (USNM 289990); 2 km N Rye, 1943 (USNM 274080). Montgomery County: Porter, 1933 (USNM 251084, 251085). Polk County: near Wakefield, 1933 (USNM 250757); southern part of county, 1933 (USNM 250679).

Canis rufus x C. latrans. – TEXAS (central). Edwards County: Nueces River, 1900 (USNM 108680). Kerr County: Kerrville, 1901 (USNM 108657); indefinite locality, 1899 (USNM 108655); indefinite localities, 1906 (USNM 146744, 146745).