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THE CRANIAL EVIDENCE FOR HYBRIDIZATION IN NEW ENGLAND CANIS

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ABSTRACT. Using the technique of linear discrimination to compare known dog-coyote hybrids, it is shown that skulls of these animals have a mean discriminant function value almost exactly between those of the two parent stocks.

Applying this same technique to the canids which are presently invading the empty predator niche in New England, it is shown that this population differs from the known hybrids. They are predominantly coyote and evidence is given showing that they probably have some dog and wolf genes as well. The New England animals are an extreme expression of a trend already apparent in *Canis latrans thomasi* from Minnesota. The high degree of variability demonstrated is evidence that the shift away from coyoteness is the result of hybridization rather than of a rapid evolution to fit a new niche.

INTRODUCTION

Having shown (Lawrence and Bossert, 1967) that the three species of the genus *Canis*: *lupus*, *latrans*, and *familiaris*, can be clearly and significantly distinguished by the technique of linear discrimination, the question arises as to whether or not this same technique can be used to identify hybrids of these species. Part One of the present paper discusses a linear discrimination study of known *latrans* × *familiaris* hybrids; Part Two discusses the application of both this study and our earlier work to the unraveling of the ancestry of the canids that have recently been moving into the empty predator niche in New England. As in our earlier paper (1967), the measurements used for this analysis were the fifteen found to be most

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diagnostic and the technique of using the linear discriminant function to reduce the multiple measurements to a single value for each specimen was applied.

PART I KNOWN HYBRIDS

Specimens examined. Ten F_1 hybrids were measured. Five of these were from the collections of H. F. Gier at Kansas State University: two of a Labrador retriever and one of a collie crossed with two different female coyotes, two of a coyote crossed with a basenji bitch. Five more were from the collections of the University of Kansas and were offspring of a small, mongrel terrier bitch crossed with a coyote. A few additional specimens, unusable because they were either broken or not adult, seemed by eye to fall within the range of the above.

Twelve other specimens from the Gier collection, the results of variously breeding the original hybrids amongst themselves or back to a springer spaniel, are treated separately.

Comparisons. The discriminant function values of known F_1 *latrans* $\times$ *familiaris* hybrids were calculated, on the basis of the pairwise discrimination of the two species described by Lawrence and Bossert (1967). The resulting values are intermediate between those for each species. Their range of variation is rather wider than it is for each of the parent species, but there is no overlap with either. One specimen at each end of the range is within three standard deviations of each parent form; otherwise, the F_1 hybrids cluster around a point midway between the two species. Apparently then, if the question is one of hybridization between two known species, this technique, in the majority of cases, will properly show the intermediate position of individual specimens. To what extent it would also suggest a relationship to other species was next considered.

The difference between dogs and wolves, as was shown earlier (Lawrence and Bossert, 1967), is considerably less than between any other pairs of species. For this reason, to determine how wolf-like these dog-coyote hybrids are, discriminations were also tried using first the *latrans-lupus* discriminant functions and then the *familiaris-lupus*. In both instances, where only one of the paired species was actually involved in the ancestry of the hybrids, the distribution of values overlapped the values for both species used in the discrimination. While the *latrans* $\times$ *familiaris* tended to be coyotelike rather than wolflike in the first discrimination, in the

second they were more evenly distributed between dog and wolf, with the majority of the specimens actually intermediate. These relationships are shown in Figure 1.

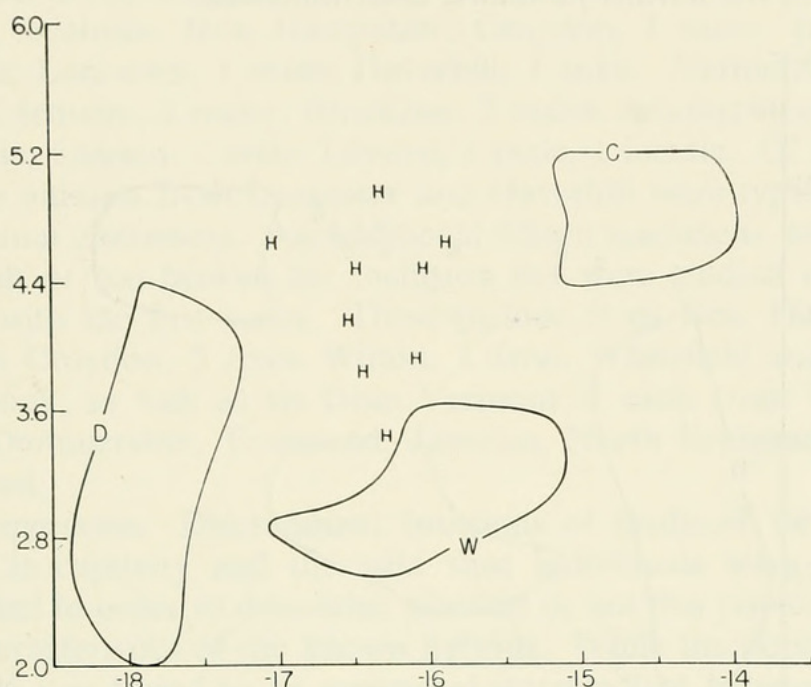


Fig. 1. Linear discriminant values of known dog-coyote hybrids (H). The *latrans-familiaris* discriminant function is used as the abscissa and the *latrans-lupus* discriminant function is used as ordinate (from Lawrence and Bossert, 1967). The contours are extreme ranges of individuals of *C. latrans* (C), *C. lupus* (W), and *C. familiaris* (D) used in computing the discriminant functions.

F₂ skulls were also studied. These were the result of subsequent crossing in various combinations, using the collie and labrador hybrids as well as a male springer. Discriminant functions were evaluated for these as for the F₁ hybrids. All fourteen proved to be intermediate between *latrans* and *familiaris* but showed a larger proportion falling within three standard deviations of one or the other. Interestingly, in the *latrans-lupus* discrimination they differ from the F₁ series in being uniformly *latrans*-like, though in the *familiaris-lupus* discrimination they coincide exactly with the F₁ series. The F₂ relationships are shown in Figure 2.

The evidence then is that, while the discriminant functions of both groups of hybrids are intermediate between those of the two parent stocks, further discrimination to see whether the trend towards dogness in particular individuals is expressed as wolfness

in a *latrans-lupus* discrimination is negative. The most doglike specimens fall within the range for *latrans* in this latter discrimination and the few specimens which are wolflike are exactly intermediate in the *latrans-familiaris* discrimination.

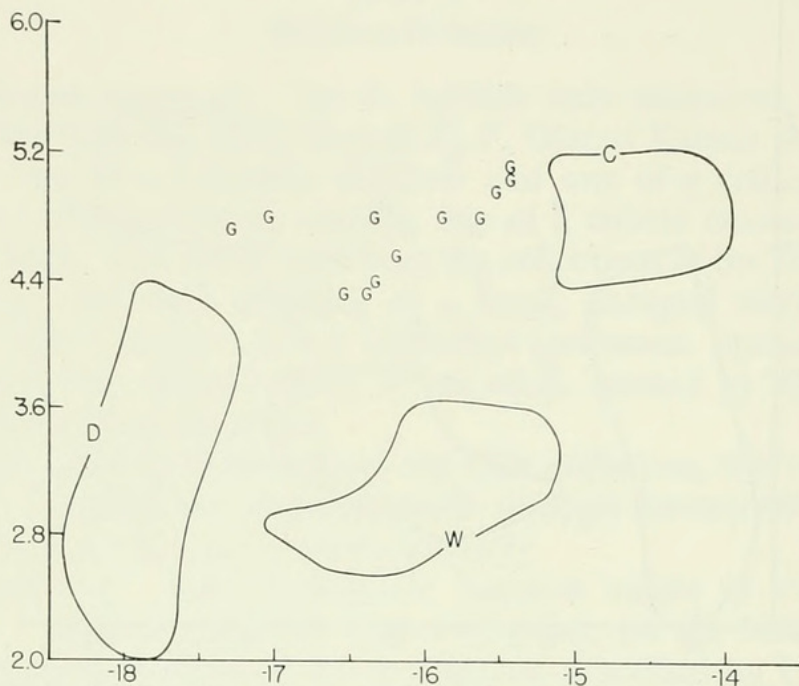


Fig. 2. Linear discriminant values of variously bred F_2 dog-coyote hybrids (G). The coordinate axes and contours are identical to those of Figure 1.

In summary, it can be said that the technique of linear discrimination can be useful for identifying hybrids between two known ancestors on the basis of multiple characters. Specimens in this category may be expected to fall between the two parent stocks. Referring specifically to *Canis*, the population of known F_1 hybrids studied is characterized by having a mean *latrans-familiaris* discriminant function value (-16.3) almost exactly between that for *latrans* (-14.6) and that for *familiaris* (-17.8). The F_2 generation is also intermediate, but the discriminant value (-16.6) tends toward that of *familiaris*.

PART II

NEW ENGLAND CANIS

Specimens examined. Twenty-two animals, offspring of siblings, dug from a den near Croydon, New Hampshire, were studied; of these, sixteen were included in the multiple character analysis. A sibling of the parents was also included, although the parents

themselves were not, as they have been kept alive for breeding. This entire series is referred to as the Boscawen series.

Of the animals collected in the wild, fifteen were suitable for inclusion in the multiple character analysis and came from the following localities: New Hampshire, Croydon, 1 male; Temple, 2 females; Lancaster, 1 male; Haverhill, 1 male. Vermont, Wardsboro, 2 females, 2 males; Brookline, 2 males. Massachusetts, Otis, 1 female; Colrain, 1 male; Leyden, 1 male, 1 female. Of these, all but the animals from Lancaster and Haverhill were typically wild in external characters. An additional fifteen specimens were either subadult or too broken for inclusion but were studied and compared with the first series. These include from New Hampshire: 2 from Croydon, 3 from Wilton, 1 from Whitefield and 3 from Colebrook, as well as six from Vermont: 1 each from Newfane, West Dummerston, Townsend, Jamaica, North Bridgewater, and Hereford.

Comparisons. Discriminant functions of skulls of the animals raised in captivity and the wild shot individuals were similarly evaluated in order to determine whether or not this population had the characteristics of the known hybrids. While the population as a whole was found to be somewhat intermediate between *latrans* and *familiaris* on the one hand, there was considerable overlap with *latrans* on the other. Even the most doglike is widely separated from *familiaris*. The mean discriminant function (-15.2) falls rather close to the range for *latrans*, and the Mahalanobis D^2 distance statistic between *latrans* and the New England animals is less than two-thirds of that between the latter and *familiaris*. On the *latrans-lupus* discrimination, the population is more completely intermediate. While the overlap with *latrans* is less, a number of specimens approach *lupus* rather closely (see Fig. 3). The average specimen is close to halfway between the two and the D^2 distances are about the same. On the *lupus-familiaris* discrimination the unknowns are again more *lupus*-like than the known hybrids. All, except one intermediate specimen, have values which fall within the range for *lupus*, whereas the known hybrids are predominantly intermediate and overlap about equally with both *familiaris* and *lupus*. These pairwise comparisons are shown in Figure 5.

The conclusions that can be drawn from these comparisons are that the unknowns differ from all three species and that they resemble coyotes more closely than the known hybrids do. They also are more wolflike. Since dogness in known coyote-dog hybrids seldom shows up as wolfness in a *latrans-lupus* discrimination, it

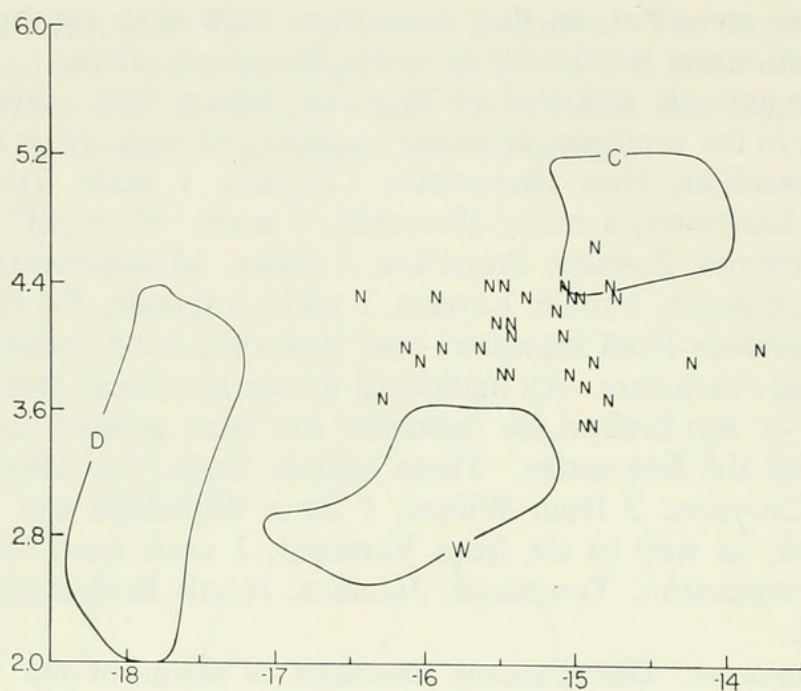


Fig. 3. Linear discriminant values of New England *Canis* (N). The coordinate axes and contours are identical to those of Figure 1.

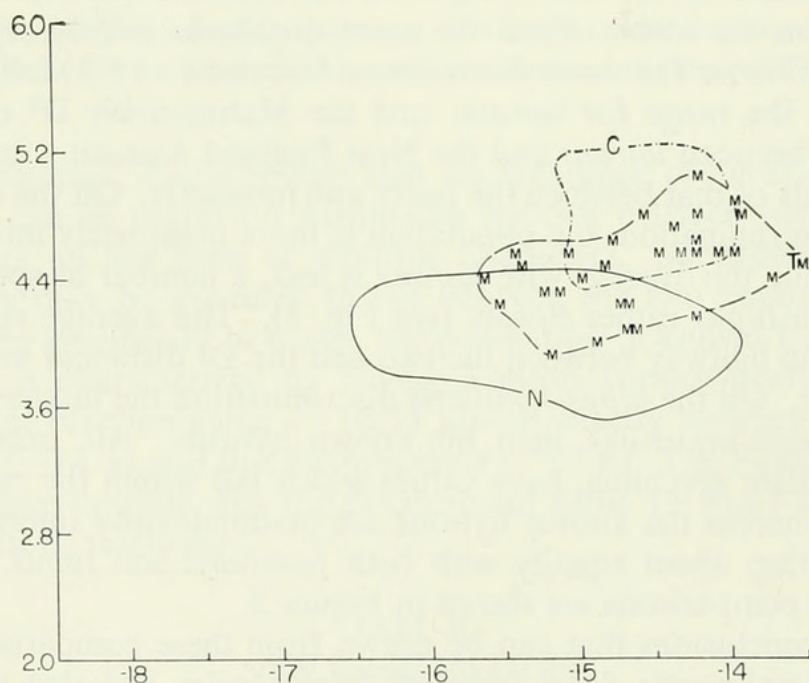


Fig. 4. Range of the linear discriminant values for *latrans* (dotted), *latrans thamnoides* (dashed), and New England *Canis* (line). The coordinate axes are identical to those of Figure 1. Individual values for *latrans thamnoides* specimens are shown (M).

is unlikely that the trend of the unknowns towards *lupus* can be attributed entirely to an increase of dog genes in this series.

In an effort to determine what might be responsible for the differences between the known hybrids and the unknown animals, a population of coyotes from the eastern fringe of the range of *latrans* was analyzed. Using the three pairwise discriminations described above, the discriminant functions of this series of thirty-two *C. latrans thamnus* from Minnesota were calculated and compared, not only with the original three series but also with the known hybrids and the New England population. While the Minnesota population overlaps strongly with *latrans* and has a D^2 distance

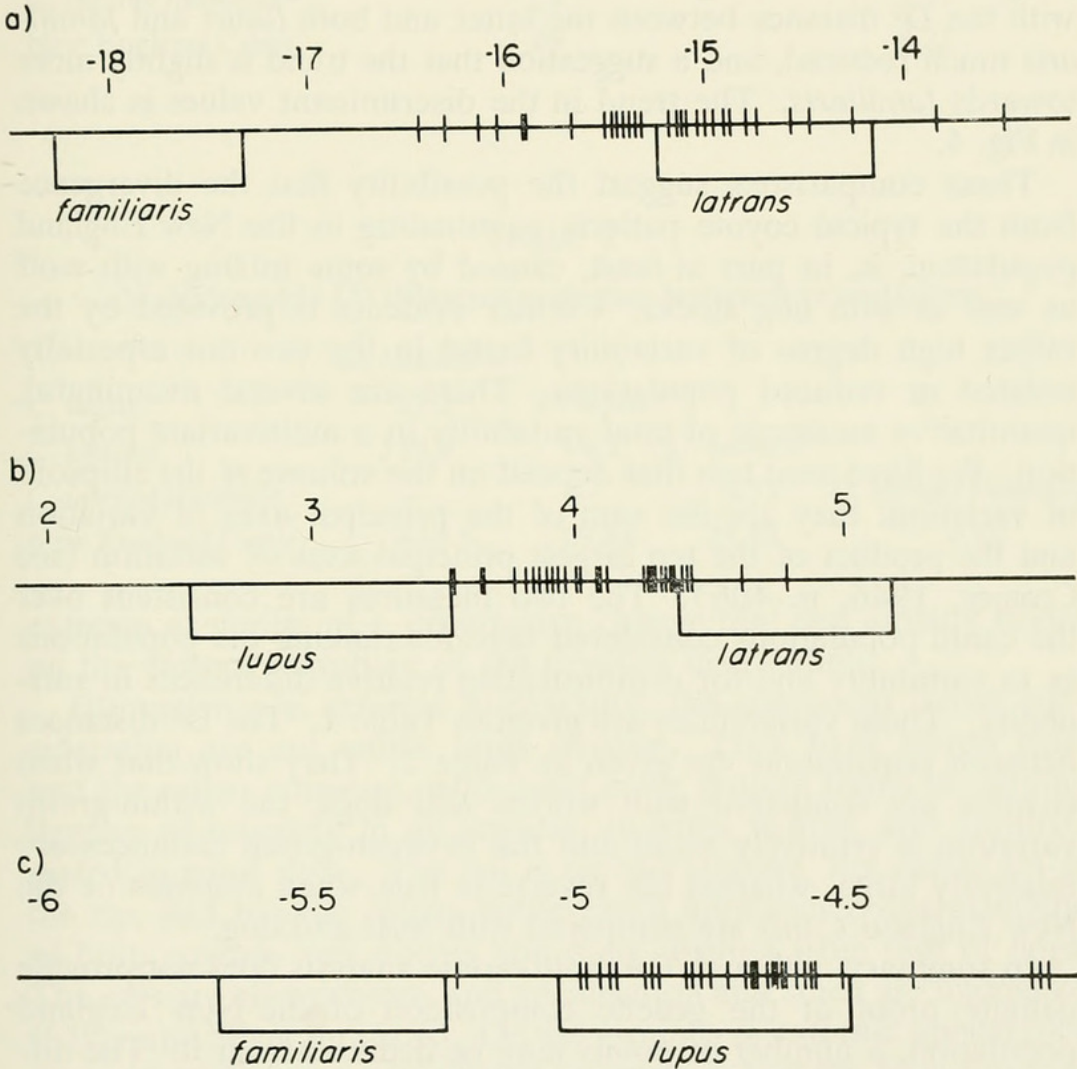


Fig. 5. One dimensional linear discriminant values of New England *Canis*: (a) on *latrans*-*familiaris* axis, (b) on *latrans*-*lupus* axis, (c) on *lupus*-*familiaris* axis. The range of the populations used to compute the discriminant functions are indicated by brackets.

from it that is not significant, six individuals fall well outside the range of variation as determined (Lawrence and Bossert, 1967) for the latter. Five of these are intermediate towards *lupus* in the *lupus-latrans* discrimination and only one towards *familiaris* in the *latrans-familiaris* discrimination.

Further, *thamnos* is intermediate between *latrans* and the New England population and, while it overlaps strongly with the former, it overlaps almost equally strongly with the latter, the D^2 differences between *thamnos* and each of the others being about the same. The trend away from typical coyote and towards both *lupus* and *familiaris*, already apparent in the Minnesota *thamnos*, has progressed considerably farther in the New England population, with the D^2 distance between the latter and both *lupus* and *familiaris* much reduced, and a suggestion that the trend is slightly more towards *familiaris*. The trend in the discriminant values is shown in Fig. 4.

These comparisons suggest the possibility that the divergence from the typical coyote pattern, culminating in the New England population, is, in part at least, caused by some mixing with wolf as well as with dog stocks. Further evidence is provided by the rather high degree of variability found in the two not especially isolated or reduced populations. There are several meaningful, quantitative measures of total variability in a multivariate population. We have used two that depend on the volume of the ellipsoid of variation; they are the sum of the principal axes of variation and the product of the ten largest principal axes of variation (see Cramér, 1946, p. 406). The two measures are consistent over the canid populations considered here for ranking the populations as to variability and for demonstrating relative differences in variability. These variabilities are given in Table 1. The D^2 distances between populations are given in Table 2. They show that when coyotes are compared with wolves and dogs, the within-group variation is relatively small and the between-group distances are relatively large, whereas the reverse is true when *thamnos* or the New England *Canis* are compared with wolf and dog.

In summary: although the multivariate analysis does not provide definite proof of the genetic composition of the New England population, a number of points may be deduced from it. The differences between the New England population and the known dog-coyote hybrids are sufficient to show that the former are not "coydogs." It establishes that they are, in fact, predominantly coyote, and that they are not a purely local phenomenon but are

TABLE 1

Multiple character variability within populations: Two measures of the scatter of the cranial proportions in multivariate space.

Population	Sum of principal axes of variation ($\times 10^3$)	Product of ten largest axes of variation ($\times 10^{42}$)
<i>C. familiaris</i>	3.40	13.5
<i>C. lupus</i>	1.00	0.14
<i>C. latrans</i>	0.66	0.02
<i>C. latrans thamnus</i>	1.28	1.42
New England <i>Canis</i>	1.69	8.22

TABLE 2

Mahalanobis D^2 distance statistics between populations.

	<i>C. familiaris</i>			
<i>C. lupus</i>	27.2	<i>C. lupus</i>		
<i>C. latrans</i>	119.9	64.1	<i>C. latrans</i>	
<i>C. latrans thamnus</i>	—	—	6.71	<i>C. latrans thamnus</i>
New England <i>Canis</i>	44.55	29.84	26.83	9.12

extreme examples of a progressive change that had already begun on the eastern periphery of the coyote's distribution.

Discussion. In external appearance, the specimens under consideration are not unlike large coyotes. They have agouti hair, and the rather common, wild-canid color pattern found in varying degrees of intensity in all coyotes, in some wolves, and approximated in some dogs. The tail is carried straight, not curled up at the tip, and has the rather bottle-brush appearance characteristic of both coyotes and wolves and quite distinct from that of dogs. The ears are always erect, and vocalization and smell are undoglike (Silver and Silver, in press). On the grounds of external appearance alone, it might seem a justifiable assumption that the New England animals are examples of a rapid evolution of a race of coyotes characterized by large size and more powerful teeth suited to preying on large mammals.

The multiple character analysis, which shows a definite trend away from coyote towards both dog and wolf, slight in the Minnesota animals and more extreme in the New England population, could also be interpreted this way. Such a composite picture of the characters, however, masks the extent to which usually diagnostic features of different species may be developed in the same individual. These combinations of non-homogeneous characters strongly suggest multiple ancestry.

In considering cranial variations, it is important to keep in mind that the animals raised in captivity in Boscawen, offspring of a single pair of adults, have a common genetic background while the wild shot individuals come from a scattered, spottily distributed population which may be anything but homogeneous.

Individual skulls of the Boscawen series (F_1 litters) vary from coyotelike (cf. MCZ 51726, 27) to ones which are coyotelike in narrowness of rostrum, shape of brain case and interorbital region, but are uncoyotelike (cf. MCZ 51865, 66) in their widely spreading zygomatic arches, reduced bullae, shortened rostrum, and somewhat elevated forehead with a well-developed frontal concavity between the broadly spreading frontal processes. Most agree in having length of jaw incompatible with size of teeth and, in many, the premolars actually overlap. All have $M2/$ well developed as in coyotes and, in general, the cusps of the molars are rather blunt and rounded as in dog/wolf. Otherwise, variation in $P/4$ and $M/1$ and in $P4/$ and $C/$ spans the range between coyote and dog/wolf.

The wild shot specimens examined, setting aside those that on the basis of external characters were at least part dog, are similarly heterogeneous. Some have a broad brain case and zygomatic arches, combined with a narrow rostrum. A number have the premolars crowded and overlapping but none have the rostrum as shortened, relative to the size of the teeth, as do some of the Boscawen series. In addition, a given tooth row often combines, interestingly, coyote with wolf/dog characters. The most coyotelike of the characters are the rather uniformly large inner portion of $M1/$ and the large size of $M2/$. These are combined with short, broad canines, a reduction of the metaconid of $M/1$, upper carnassials that tend towards wolf/dog not only in plumpness but also in the slight development of the deutercone, and an overall massiveness of the teeth in relation to size of skull.

The most conspicuous and possibly significant variation is in the size of these wild shot animals. The most wolflike one and one of the most coyotelike, as shown by the multiple character analysis, are also at opposite extremes in total size and, more particularly,

in size of teeth. Both specimens were shot in Leyden, Massachusetts, and apparently belonged to the same small pack.

In the series as a whole, the largest skulls are at the upper extreme of reported size for coyotes and in certain dimensions, notably zygomatic width and width across condyles, are actually larger than reported coyotes, (Young & Jackson, 1951). These specimens often resemble closely skulls of some of the southern, probably hybrid, animals sometimes called *Canis niger gregoryi*. They are almost equally close in size and general appearance to small specimens of the northern timber wolf, *Canis lupus lycaon*, on whose range they have begun to impinge. The same is true of certain tooth dimensions; extreme individuals have a massive upper carnassial with a breadth to length ratio that falls outside of the range for coyotes; even more conspicuous is the greater width of the often shortened canine. These largest teeth again approach certain of the specimens referred to above of so-called *niger gregoryi* and are close to those of some of the smallest wolves. Such big teeth are not, however, necessarily associated with the biggest skulls.

The similarities between both the wild shot and the Boscawen animals support the theory that the two are closely related. The multiple character analysis shows this total population to have certain characteristics in common and, further, to differ more from the known hybrids than it does from the Minnesota population. That this is not evidence of rapid evolution of pure coyote stock to suit the prey and habitat requirements of the Northeast is suggested by the extreme and uncoyotelike combinations of certain characters described above as well as by the high degree of variability discussed earlier. Further, it seems that some of the traits found, such as the slender rostrum and crowded teeth, would have no selective advantage for an animal preying on large game. Finally, some of the unmeasurable characters usually diagnostic for dog/wolf, such as reduction of the metaconid of M/1 and shape of the postorbital region, or for dog such as flattened bullae, suggest some heterogeneity. Probably what has occurred is that animals of mixed but predominantly coyote ancestry have survived and bred amongst themselves, adapting rather easily, as *Canis* does, to shifting environmental conditions as they have moved east. The differences between these animals and the known hybrids, their intermediate position when compared with *lupus*, and the rather large size, especially of teeth, all suggest further that wolf as well as domestic dog is involved in their ancestry.

Although studies have not been made in detail of animals from areas between New England and the erstwhile extreme eastern edge of the range of *latrans thamnus*, individual specimens from the Adirondacks and the St. Lawrence Valley, as well as reports of difficult-to-identify *Canis* from southern Ontario, all suggest that we are dealing with a rather widespread phenomenon, which very likely parallels that found in the southern states where, along the eastern edge of the coyotes' extending range, "red wolves" are reported. That these animals are not a distinct species and the possibility of hybridization were discussed in our earlier paper (1967: 230). While there is considerable resemblance between individual specimens from the different areas, the New England population on the whole seems less wolflike, though both populations agree in being highly variable.

SUMMARY

Cranial studies of the population of *Canis*, which is presently expanding into the empty predator niche in New England show that these animals are predominantly coyote and probably have some dog/wolf ancestry. A multiple character analysis shows that they differ from known dog-coyote hybrids, which are intermediate between the two parent stocks. The New England animals are closely related to *C. latrans thamnus*, a Minnesota population that has already begun to move away from typical *latrans* towards both *familiaris* and *lupus*. That these changes cannot be entirely accounted for as evidences of a rapid evolution of coyote stock is shown by the high degree of variability of the population, the non-homogeneous combinations of certain features, and the possession of some particular characters usually considered to be diagnostic for dog/wolf. The differences, as shown by the multivariate analysis, between this population and that of known dog-coyote hybrids further suggest that wolf as well as dog genes have been introduced. The conclusions arrived at in these cranial studies are in agreement with the behavioral trends noted by the Silvers (in press).

Because of our present imperfect knowledge of these animals, their probable hybrid ancestry, and undiagnostically wide variation of cranial characters, no trinomial is proposed for them; rather they should be called *Canis latrans* var. and may be referred to as the eastern coyote.

ACKNOWLEDGMENTS

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