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A Multivariate Analysis of Systematic Relationships among Populations of the Short-Tailed Shrew (Genus *Blarina*) in Nebraska

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A MULTIVARIATE ANALYSIS OF SYSTEMATIC RELATIONSHIPS AMONG POPULATIONS OF THE SHORT-TAILED SHREW (GENUS *BLARINA*) IN NEBRASKA

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Abstract

Genoways, H. H., and J. R. Choate (Museum of Natural History, The Univ. Kansas, Lawrence, Kansas 66044. Present addresses: The Museum, Texas Tech University, Lubbock, Texas 79409 and Division of Biological Sciences and Agriculture, Fort Hays Kansas State College, Hays, Kansas 67601). 1972. A multivariate analysis of systematic relationships among populations of the short-tailed shrew (genus Blarina*) in Nebraska. Syst. Zool., 21:106–116.*— The genus *Blarina* (Mammalia: Soricidae) is represented in Nebraska by two well-differentiated, geographically exclusive phena that generally have been regarded as subspecies. Field studies conducted along their zone of contact resulted in the collection of representatives of both phena at each of five localities. Cluster analysis of distance matrix readily separated reference samples of the phena as well as test samples from near the zone of contact. A three-dimensional projection of the specimens onto their first three principal components, together with a discriminant function analysis, served further to elucidate the degree of differentiation among the phena and to confirm that their characteristic differences are maintained even where they occur sympatrically. The latter technique also indicated that one specimen not singled out by other analyses might be a natural hybrid, but none of the analyses provided even the slightest evidence for panmictic intergradation. The possibility that the phena represent the ends of a circularly intergrading species is considered, as is the possibility that the phena are distinct, biological species. Two means of speciation, one "classical" and the other involving formation of "stasipatric species," are discussed. [Multivariate analysis; Systematics; *Blarina*; Populations; Hybridization.]

Shrews of the Nearctic genus *Blarina* (Mammalia: Soricidae) historically have been classified as representatives of two species—one, *B. brevicauda* (Say), wide-ranging and geographically variable, and the other, *B. telmalestes* Merriam, restricted to the Dismal Swamp region of coastal Virginia and North Carolina and of uncertain taxonomic status (see Hall and Kelson, 1959:53, 55). This arrangement stems primarily from Merriam's (1895) revision of *Blarina* and Bole and Moulthrop's (1942) later synopsis of the genus. As presently understood, the ranges of four nominal subspecies—*B. b. brevicauda, B. b. kirtlandi* Bole and Moulthrop, *B. b. churchi* Bole and Moulthrop, and *B. b. talpoides* (Gapper)—all characterized by large external and cranial dimensions, geographically abut the range of *B. b. carolinensis* (Bachman), which is characterized by much smaller size. This zone of contact extends from Nebraska to Maryland and effectively divides the range of the species into two parts—a northern segment occupied by comparatively large shrews and a southern segment occupied by smaller shrews (Hall and Kelson, 1959: 53).

Jones and Findley (1954), and subsequently Jones and Glass (1960), studied the geographic relationships of taxa of *Blarina* west of the Mississippi River. They demonstrated the presence of a clinal increase in size from the Gulf coastal region to northern Nebraska. The cline exhibited a significant "step" in southern Nebraska, which was considered to constitute the line of demarcation between *B. b. brevicauda* and *B. b. carolinensis*. The magnitude of the "step" is such that Nebraskan specimens of *B. brevicauda* invariably can be assigned to subspecies without regard for location of capture; external and cranial dimensions in *B. b. brevicauda* are substantially greater than (and seldom over-

lap) those in *B. b. carolinensis* (Jones, 1964:67, 69, 72). Jones (1964:67) found no specimens from Nebraska that could be described as exactly intermediate between *brevicauda* and *carolinensis*, and (1964:28) regarded the two phena as "markedly different subspecies . . . that now meet along a fairly well-defined line in Nebraska with little intergradation between them."

The geographic relationship of large northern taxa to small southern taxa of *Blarina* apparently has remained unchanged, except for latitudinal shifts in position, for a long period of time. Parmalee (1967:135–136) reported two distinctive phena of *Blarina* in a Recent bone deposit in Illinois; Oesch (1967:171) found the two phena in a Pleistocene (late Wisconsin) deposit in Missouri; and Guilday et al. (1964:147–151) described large and small phena of *Blarina* from Pleistocene (Wisconsin) deposits in Pennsylvania and Virginia. These findings generally have been interpreted to demonstrate that climatic fluctuations have effected sequential geographic replacement of one subspecies by another although, as Parmalee (1967:136) admitted, "it is problematical as to whether these races were contemporaneous or occupied the . . . [areas] during different periods." Hibbard (1970:423) treated the two phena as distinct species in earlier (Illinoian) Pleistocene deposits, and preliminary cytogenetic studies (Elmer C. Birney, personal communication; Meylan, 1967; Lee and Zimmerman, 1969:337; Hoffman and Jones, 1970:389) have indicated that, indeed, more than one species might be involved (*brevicauda* has 48–50 chromosomes and *carolinensis* 46).

The initial purpose of this study, therefore, was to search the zone of contact between the nominal subspecies *B. b. brevicauda* and *B. b. carolinensis* in Nebraska (see Jones, 1964:66) for evidence of intergradation or hybridization, and thereby to shed light on the systematic relationships of these taxa.

METHODS AND MATERIALS

Intermittent field studies were conducted in the period 1965 to 1969 in three areas of Nebraska where the ranges of *B. b. brevicauda* and *B. b. carolinensis* were thought to be contiguous (see also Choate and Genoways, 1967; Genoways and Choate, 1970). One area in northeastern Adams and northern Clay counties was selected because a specimen identified as *carolinensis* had been obtained previously by Genoways at a place 1½ mi. N and 6 mi. E Hastings, Adams County, and Jones (1964:68) had reported one specimen of *brevicauda* from just 18 miles to the east at Saronville, Clay County. Additional collecting indicated that the zone of contact was between Harvard and Saronville in northern Clay County, and specimens tentatively identified as *brevicauda* were caught together with specimens of *carolinensis* at each of three localities (1 mi. N and 3 mi. W Saronville; 1 mi. N and 2 mi. W Saronville; 1 mi. N and 1 mi. W Saronville). At the first two localities representatives of both taxa were taken together in the same traplines on 20 December 1965, whereas at the last locality a specimen identified in the field as *brevicauda* was caught on 20 November 1965 and a specimen identified as *carolinensis* was taken on 2 April 1966.

In eastern Saline County the two taxa also were known from only 18 miles apart (*brevicauda* from 4 mi. NE Crete and *carolinensis* from 1½ mi. W De Witt). We were unable to define the exact area of contact in Saline County, but the known distance between the taxa was reduced to seven miles with the capture of a specimen tentatively identified as *carolinensis* at a place 5 mi. S and 3 mi. E Crete.

The third area in which field studies were conducted was in Cass County, which was selected because a specimen definitely identified as *brevicauda* was known from just north of the county line at a place 1 mi. W Meadow, Sarpy County, and two undoubted specimens of *carolinensis* had been reported previously (Jones, 1964:70)

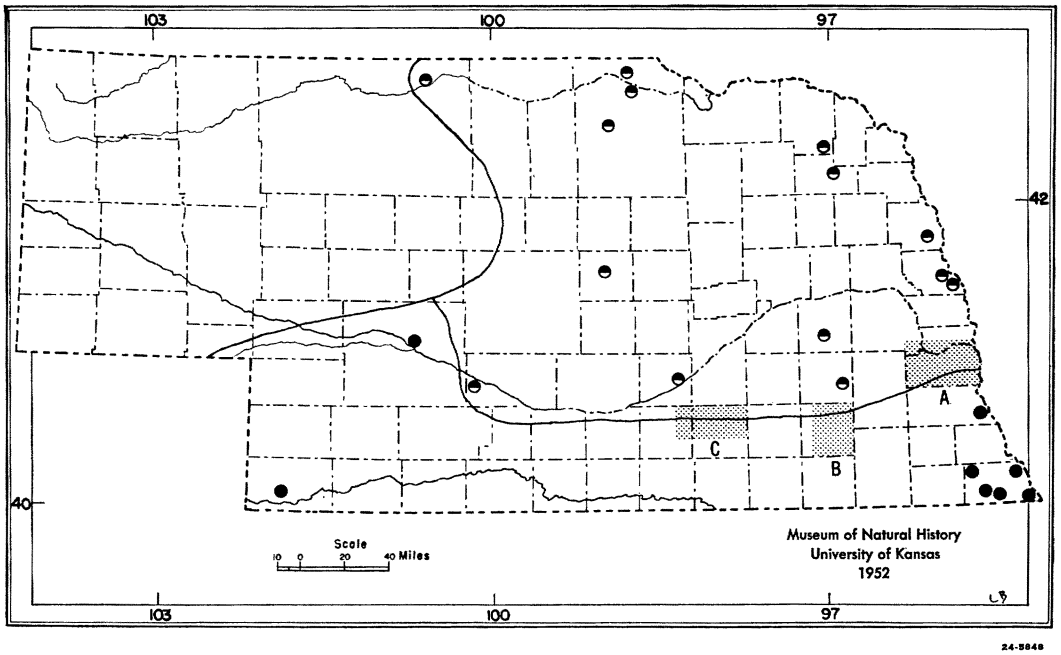


FIG. 1.—Map of Nebraska showing distribution of the *brevicauda* (half solid circles) and *carolinensis* (solid circles) phena of *Blarina* (modified from Jones, 1964:66). Localities plotted are those from which specimens were drawn for reference samples (see text). The shaded areas are enlarged in Fig. 2.

from the county to the south (1 mi. SE Nebraska City, Otoe County); furthermore, Jones (1964:67) assigned five specimens from Louisville (in extreme northern Cass County) to *B. b. brevicauda,* but remarked that they "are smaller externally and average slightly smaller cranially than topotypes of that subspecies. . . ." By trapping along a transect extending southward from Louisville to a place just south of Weeping Water, we were able to locate the zone of contact between the two taxa. On 24 November 1968, three specimens (one tentatively identified as *brevicauda* and two as *carolinensis*) were caught together in the same trapline at a place 1 mi. S and 1½ mi. W Weeping Water. In addition, two specimens identified in the field as *brevicauda* were caught on the same morning at a place 2 mi. N and 2 mi. W Weeping Water, and four specimens of *brevicauda* and 27 of *carolinensis* were caught at other localities in the same area.

Specimens thus collected (together with a few reported from near the zone of contact by Jones, 1964) were tested against reference samples from Nebraska of *brevicauda* and *carolinensis*. Localities of reference samples in the following lists are arranged from north to south and correspond to localities plotted in Figure 1; localities or counties at about the same latitude are listed from west to east. Numbers in parentheses indicate how many specimens from each locality were included in analyses. Numbers (bold face) of test samples refer to localities numbered in Figure 2.

brevicauda reference sample

CHERRY CO.: 3 mi. SSE Valentine (1). KEYA PAHA CO.: 12 mi. NNW Springview (1). BOYD CO.: 5 mi. WNW Spencer (1). HOLT CO.: 1 mi. S Atkinson (1); 6 mi. N Midway (1). KNOX CO.: 3 mi.

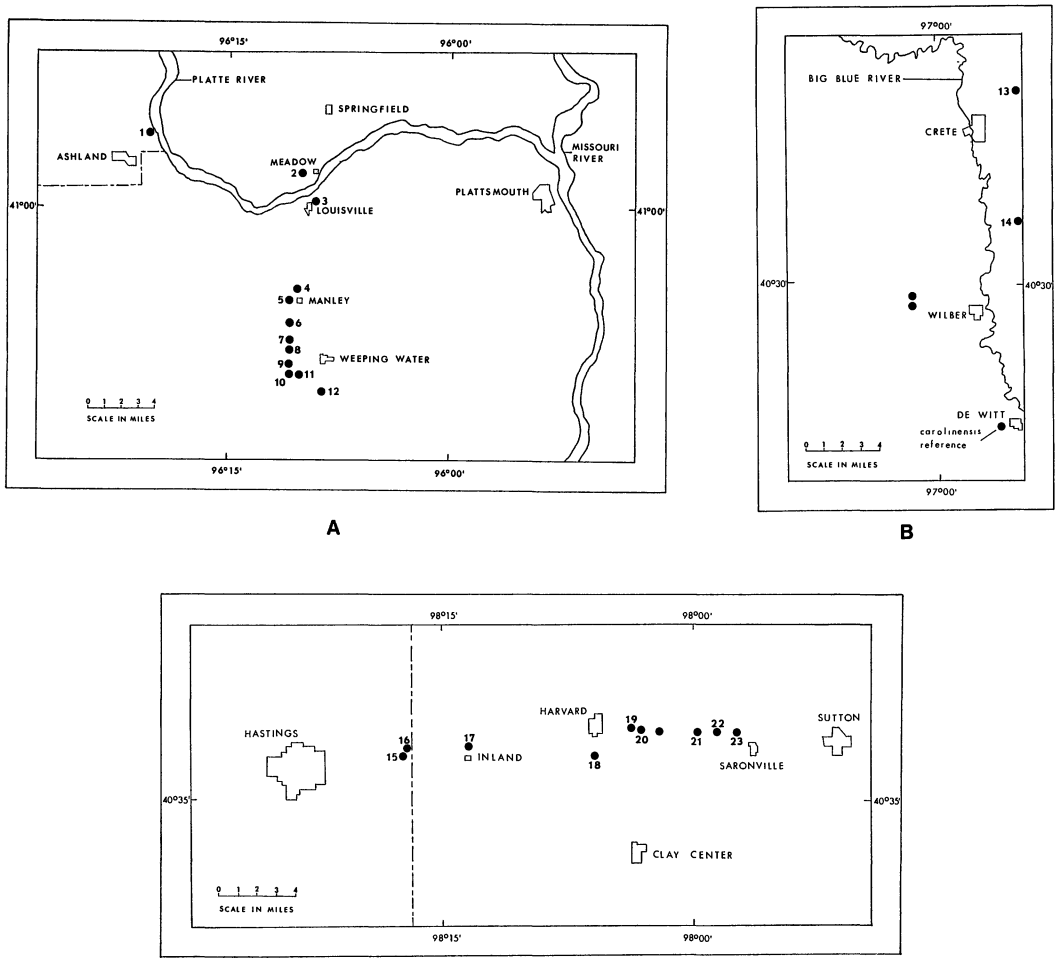


FIG. 2.—Areas in eastern Nebraska where two phena of *Blarina* were found to be contiguous or sympatric. A, Cass County and adjacent parts of southern Saunders and Sarpy counties; B, eastern Saline County; C, northeastern Adams County and northern Clay County. Numbered localities refer to test samples identified in text. Unnumbered localities indicate places where specimens of *Blarina* have been taken that could not be used in statistical analyses because we were unable to obtain some measurements from them.

W Niobrara (1). CEDAR CO.: 4 mi. SE Laurel (6). WAYNE CO.: ½ mi. W Wayne (2); Wayne (7). BURT CO.: 1 mi. E Tekamah (2). VALLEY CO.: 2½ mi. N Ord (2). WASHINGTON CO.: 6 mi. SE Blair (4). BUTLER CO.: 4 mi. E Rising City (1); 5 mi. E Rising City (2). DAWSON CO.: 5 mi. S Gothenburg (1). HALL CO.: 6 mi. S Grand Island (1). SEWARD CO.: 1 mi. N Pleasant Dale (3).

carolinensis reference sample

LINCOLN CO.: 2 mi. N North Platte (3). OTOE CO.: 3 mi. S, 2 mi. E Nebraska City (6). SALINE CO.: ½ mi. W De Witt (1). DUNDY CO.: 5 mi. N, 2 mi. W Parks (18). RICHARDSON CO.: 4 mi. E Barada (4); 5 mi. N, 2 mi. W Humboldt (2); 3½ mi. S, 1 mi. W Dawson (3); 8 mi. S, 1 mi. E Dawson (1); 6 mi. W Fall City (1); ½ mi. S, 1½ mi. W Rulo (2).

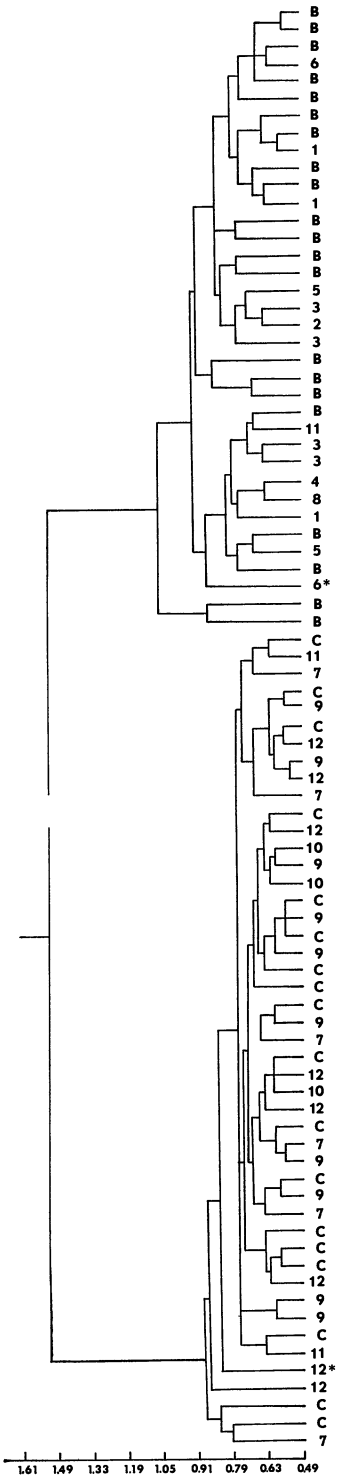
Test samples

1—2 mi. NE Ashland, Saunders Co. (3). **2**—1 mi. W Meadow, Sarpy Co. (1). **3**—Louisville, Cass Co. (4). **4**—½ mi. N Manley, Cass Co. (1). **5**—½ mi. W Manley, Cass Co. (2). **6**—2 mi. N, 2 mi. W Weeping Water, Cass Co. (2). **7**—1 mi. N, 2 mi. W Weeping Water, Cass Co. (6). **8**—4/10 mi. N, 2 mi. W Weeping Water, Cass Co. (1). **9**—3/10 mi. S, 2 mi. W Weeping Water, Cass Co. (10). **10**—1 mi. S, 2 mi. W Weeping Water, Cass Co. (3). **11**—1 mi. S, 1½ mi. W Weeping Water, Cass Co. (3). **12**—2 mi. S Weeping Water, Cass Co. (8). **13**—2 mi. NE Crete, Saline Co. (3). **14**—5 mi. S, 3 mi. E Crete, Saline Co. (1). **15**—1½ mi. N, 6 mi. E Hastings, Adams Co. (2). **16**—1 7/10 mi. N, 5 7/10 mi. E Hastings, Adams Co. (2). **17**—½ mi. N Inland, Clay Co. (1). **18**—1 mi. S Harvard, Clay Co. (3). **19**—1½ mi. E Harvard, Clay Co. (3). **20**—1 mi. N, 6 mi. W Saronville, Clay Co. (1). **21**—1 mi. N, 3 mi. W Saronville, Clay Co. (3). **22**—1 mi. N, 2 mi. W Saronville, Clay Co. (2). **23**—1 mi. N, 1 mi. W Saronville, Clay Co. (2).

Specimens listed above are housed in The University of Kansas Museum of Natural History. The age of each individual selected for analysis was estimated (Choate, 1968:253; 1970:214), and no specimen judged to be less than adult size was included in reference or test samples. Nine cranial measurements (Choate, 1972) were taken from each specimen by Choate (by means of dial calipers) as follows: occipitopremaxillary length; length of P4-M3; cranial breadth; breadth of zygomatic plate; maxillary breadth; interorbital breadth; length of mandible; height of mandible; articular breadth.

Computations were performed using a system of multivariate statistical computer programs (NT-SYS) developed by F. J. Rohlf, R. Bartcher, and J. Kishpaugh for the GE 635 computer at The University of Kansas (see Schnell, 1970:42). Matrices of Pearson's product-moment correlations were computed, and taxonomic distance coefficients were derived from standardized character values. Cluster analyses were conducted using UPGMA (unweighted pair group method using arithmetic averages) on the correlation and distance matrices, and a phenogram was generated for each. Phenograms were compared with their respective matrices, and a coefficient of cophenetic correlation was computed for each comparison. A matrix of correlation among characters then was computed, and the first three principal components extracted. A three-dimensional projection of the OTUs onto the first three principal components was made; this projection then was drawn using a Benson-Lehner incremental plotter. Rising (1968, 1970) used principal component analysis to assess interbreeding between species of chickadees (genus *Parus*) and orioles (genus *Icterus*), respectively.

Discriminant function analysis was performed using the MULDIS subroutine of the NT-SYS system. This program uses variance-covariance mathematics to differentially weight characters relative to their within- and between-groups variation. For the discriminant analysis in this paper, two reference samples from areas geographically removed from zones of suspected hybridization were used. A discriminant multiplier was calculated for each character, and this was multiplied by the value of its respective character; all such values were summed for each individual to yield its discriminant score. The discriminant scores were plotted on a frequency histogram to compare individuals of the two reference samples and to compare the test sample from the intermediate geographical areas where hybridization was suspected. A good discussion of discriminant functions is given by Jolicoeur (1959); Lawrence and Bossert (1969) used this test to identify hybrids in their study of members of the genus *Canis* as did Birney (1970) in a study of woodrats of the genus *Neotoma*.



RESULTS

A distance phenogram (Fig. 3) was prepared using 21 reference specimens of *B. b. brevicauda* and 18 of *B. b. carolinensis,* together with 44 test specimens from localities at or near the zone of contact of those taxa in Saunders, Sarpy, and Cass counties (Fig. 2A). The phenogram is divided into two major clusters separated by an appreciable phenetic distance (1.82). The upper cluster contains all the reference specimens of *brevicauda,* whereas the lower cluster contains all the reference specimens of *carolinensis*; specimens from test samples appear in both clusters. All specimens from as far south in Cass County as sample 6 are in the upper part with the *brevicauda* reference sample. Specimens denoted by an asterisk (6* and 12*) are discussed below. The six specimens from sample 7 and the 10 from sample 9 fall in the lower cluster with the reference specimens of *carolinensis*; however, a specimen from a geographically intermediate locality (sample 8) fell with the *brevicauda* specimens. Of the three specimens from sample 11, two are in the lower part with *carolinensis,* whereas the third is in the upper part with *brevicauda.* All eight specimens from sample 12 and the three from sample 10 are grouped with *carolinensis.* The two reference specimens of *brevicauda* at the lower end of the upper cluster of the phenogram, and at a substantial "distance" from other specimens in that group, are young adults with relatively small dimensions.

A three-dimensional projection of the specimens onto the first three principal

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FIG. 3.—Phenogram computed from distance matrix based on standardized characters and clustered by the unweighted pair-group method using arithmetic averages (UPGMA). Numbers refer to individuals from test samples identified in text and in Fig. 2. Specimens labelled "B" are from reference samples of *brevicauda,* whereas specimens labelled "C" are from reference samples of *carolinensis.* An asterisk indicates that special reference is made to the specimen in text.

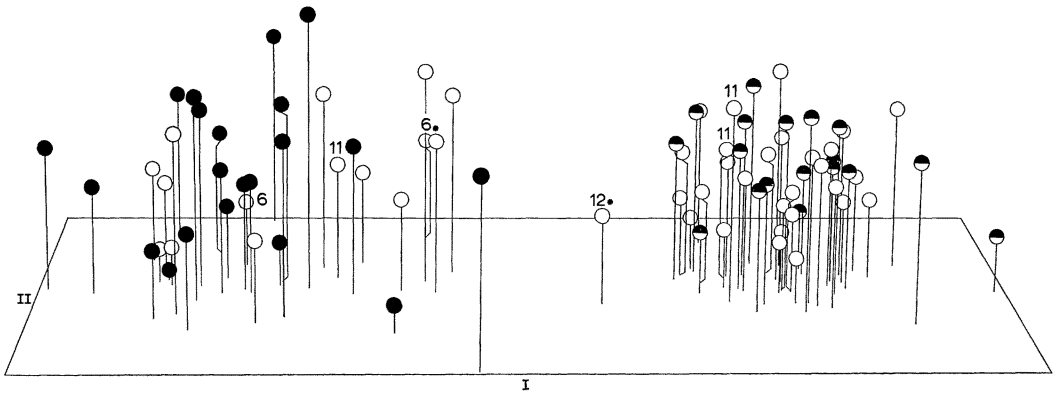

FIG. 4.—Three-dimensional projection of 83 specimens onto the first three principal components based on a matrix of correlations among 12 external and cranial measurements. I and II are indicated in the figure and III is represented by height. The first three components include approximately 92 per cent of the total variance, with component I accounting for 83.92, II for 4.88, and III for 3.15 per cent, respectively. Numbers refer to individuals from test samples identified in text and in Fig. 2. An asterisk indicates that special reference is made to the specimen in text.

components (Fig. 4) likewise shows two groups, one (on the right in the figure) containing all the reference specimens of *carolinensis* and the other (on the left) all the reference specimens of *brevicauda*. One specimen from sample 12 (designated 12*) is situated between the groups, as would be expected of a hybrid or intergrade, although it was grouped with the *carolinensis* reference specimens in the distance phenogram. However, a note made by us when that specimen was measured suggests that it may have abnormal proportions ("skull unusually long, rostrum barrel-shaped, cranium narrow relative to length"). The remainder of the specimens are clustered as would be expected on the basis of the distance phenogram. Note that the three specimens from locality 11 still are divided with two in the *carolinensis* cluster and one in the *brevicauda* cluster. Also, note the position of specimen denoted as 6* toward the lower limit of the *brevicauda* group; this specimen is discussed below.

Discriminant function analysis (Fig. 5) was conducted using reference specimens totaling 37 for *brevicauda* and 40 for *carolinensis*. From the table of discriminant multipliers (Table 1), it can be seen that all the cranial measurements excepting length of the mandible were weighted heavily, whereas the three external measurements were weighted comparatively lightly. The discriminant scores for the *brevicauda* reference sample ranged from 38.158 to 43.330 and those for the *carolinensis* reference sample ranged from 31.199 to 34.827, thus yielding a separation between the taxa of 3.331. The specimen (12*) that fell in the intermediate area of the three-dimensional plot (Fig. 4) has a

TABLE 1. DISCRIMINANT MULTIPLIERS RESULTING FROM A DISCRIMINANT FUNCTION ANALYSIS COMPARING *Blarina brevicauda brevicauda* WITH *B. b. carolinensis* IN NEBRASKA.

Character	Discriminant Multiplier
Total Length	0.045
Length of Tail Vertebrae	–0.239
Length of Hind Foot	0.274
Occipito-premaxillary Length	–0.482
Length of P4-M3	3.814
Cranial Breadth	1.023
Breadth of Zygomatic Plate	–0.358
Maxillary Breadth	–2.709
Interorbital Breadth	0.529
Length of Mandible	0.068
Height of Mandible	2.302
Articular Breadth	3.941

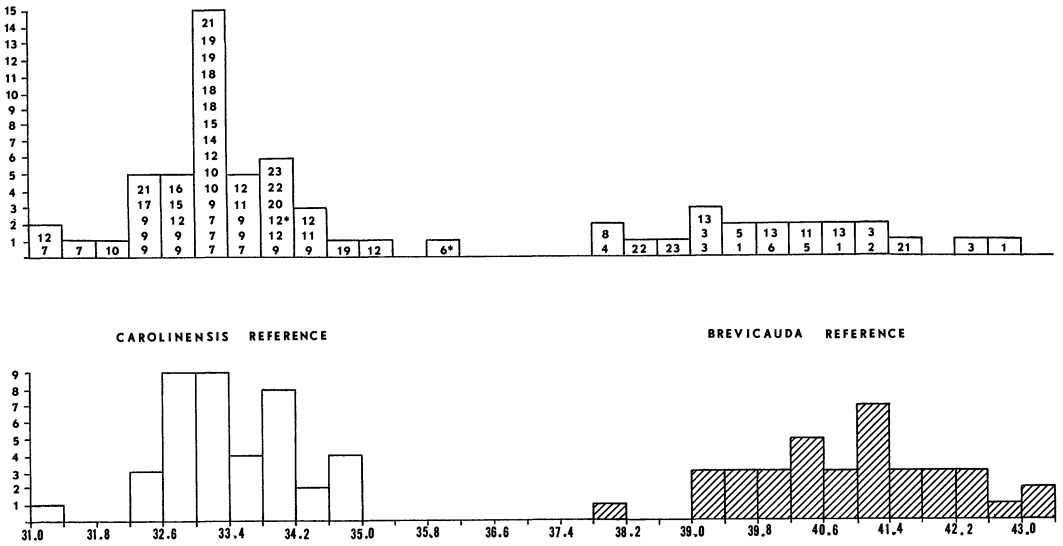

FIG. 5.—Histogram of linear discriminant scores for short-tailed shrews from Nebraska. Discriminant scores are indicated along the bottom of the histogram and frequency of individuals is indicated on the left-hand side. Individuals arranged below are from reference samples of *brevicauda*, at right, and *carolinensis*, at left. Individuals arranged above are numbered according to test samples, which are identified in text and in Fig. 2. The specimens denoted by an asterisk are discussed in text.

value of 34.027 and clearly pertains to *carolinensis*. However, two test specimens from Cass County have values between those of the reference samples, as would be expected of hybrids or intergrades (see especially Lawrence and Bossert, 1969, and Birney, 1970). One of those specimens (from sample 12) has a value of 35.034 and probably is best considered a representative of *carolinensis*. The other specimen (6*), with a discriminant score of 36.070, might actually be a hybrid between the taxa. It is of special interest to note that the discriminant score of this specimen was nearer the upper limit for *carolinensis* than the lower limit for *brevicauda*, although in both the distance phenogram and three-dimensional plot (Figs. 3 and 4) the specimen was grouped with *brevicauda*. Other specimens from Saunders, Sarpy, and Cass counties were arranged within the same phena as they were in the distance phenogram and three-dimensional plot; this includes those from sample 11, where two specimens fell with the *carolinensis* reference sample and one fell with *brevicauda*. From Saline County (Fig. 2B), the one specimen comprising sample 14 had a discriminant score that fell within the range of the *carolinensis* reference sample, whereas the three specimens from sample 13 all fell within the range for *brevicauda*. Among Clay County (Fig. 2C) specimens, three samples (21, 22, and 23) include representatives of both taxa, thus confirming tentative field identifications. However, at none of those localities or any other locality from which we have examined specimens is there any indication of intergradation between the taxa.

DISCUSSION

Data presented herein yield no indication that the nominal subspecies *B. b. brevicauda* and *B. b. carolinensis* intergrade in Nebraska. Only one specimen (6*, Fig. 5) was found to be intermediate between the phena using discriminant function analysis; a second possibly intermediate specimen (12*) was identified using the principal components analysis. Probably only the specimen from sample

6 is a "hybrid" or "intergrade" among the 66 specimens tested from the zones of contact between the two taxa. In other words, *brevicauda* and *carolinensis* behave as good biological species where their ranges are contiguous in southern Nebraska. Unpublished data (John B. Bowles, personal communication) indicate that a similar relationship between large and small phena of *Blarina* probably exists across southern Iowa. Panmictic intergradation resulting in numerous viable hybrids between *brevicauda* and *carolinensis* almost certainly does not occur west of the Mississippi River at the present time, and we know of no conclusive published evidence for intergradation east of the Mississippi River. That an occasional viable hybrid might be produced in the zone of contact between the phena is entirely consistent with their behavior as "species."

We recognize two possible explanations for the evolutionary relationship between these phena: (1) that they are an example of circular overlap (as defined by Mayr, 1963:507–512, 664) within the same species —this has been reported for several species of mammals, including *Sorex vagrans* (Findley, 1955:14), *Thomomys talpoides* (Long, 1965:603), and *Peromyscus maniculatus* (Dice, 1931; Hooper, 1942; King, 1948; Harris, 1954)—or (2) that the phena represent distinct species as suggested by Hibbard (1970:423).

Jones (1964:28–31) provided an explanation for the circumstances that might have resulted in Nebraskan populations of *B. brevicauda* becoming the ends of a circularly intergrading species. He hypothesized that *B. brevicauda,* which is a common inhabitant of the eastern deciduous forest, became widespread on the plains during the warm, wet segment of the Hypsithermal Period during post-Wisconsin times. The species probably varied clinally in size, ranging from small in the south to large in the north in typical Bergmannian fashion. During the subsequent Xerothermic Period, a general drying occurred and the distribution of *B. brevicauda* was divided into two segments as far east as the eastern limit of the so-called "prairie peninsula." Jones postulated that during reinvasion of the plains those populations to the northeast and southeast reached Nebraska sooner than those directly to the east; as a result, the middle portion of the cline was obliterated and two distinctly divergent phena achieved secondary contact.

One notable characteristic of the examples given for circular overlap that is lacking in *Blarina* is a high degree of ecological separation between the overlapping subspecies (defined as "microallopatry" by Smith, 1965:57). No ecological separation of the taxa is evident in *Blarina* in that all specimens from the zone of contact were trapped in grassy roadside ditches in otherwise highly agricultural areas; disruption of the original habitat, however, may have altered some original ecological differences. Another problem with this interpretation has to do with the fossil record; if available paleontological evidence is correct, the secondary zone of contact between the phena has fluctuated with regard both to latitude and longitude at least since the middle Pleistocene, long before the period of time suggested by Jones (1964) for elimination of the central part of the cline. Considering the element of time and the durability of the geographic relationship, the two taxa seem to us to be behaving more nearly like closely related species than like subspecies.

If, indeed, the phena represent distinct species, speciation classically would be interpreted as having resulted from geographic isolation of the phena during or before the Kansas glaciation, with the resultant taxa having maintained a parapatric distribution (in the sense used for mammals by Vaughan, 1967, although possibly without ecological divergence) at least since Illinoian times. Accordingly, the two species might have displaced one another north and south (and probably also east and west) across the plains in response to fluctuations in environmental

factors during the Pleistocene, with one species competitively excluding the other depending on the direction of the climatic shift.

Another possible interpretation is that the large and small phena of *Blarina* represent "stasipatric species" (Key, 1968; White, 1968; White et al., 1967). With development of a "tension zone," possibly as the result of the chromosomal differences between the two emergent phena, speciation might have occurred gradually without actual geographic isolation of the main body of the parental stock, although small peripheral populations undoubtedly must have undergone isolation and differentiation in the classical sense. The tension zone could have shifted position geographically, as described by Key (1968), in response to changing environmental conditions in the Pleistocene. Hybridization would have occurred regularly across the tension zone, especially early in the evolution of this complex. However, divergence now might have progressed to the level (at least in Nebraska) at which the tension zone of intergradation has ceased to function; the presence of only one probable hybrid in our combined samples of 66 specimens from at or near the zone of contact between the two phena strongly suggests that isolating mechanisms are actively preventing, or at least restricting, hybridization, and that introgression is negligible.

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