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TAXONOMY OF SHORT-TAILED SHREWS (GENUS *BLARINA*) IN FLORIDA

RUSSELL A. BENEDICT, HUGH H. GENOWAYS, AND JERRY R. CHOATE

ABSTRACT

Three nominal taxa of short-tailed shrews historically were recognized in Florida: *Blarina carolinensis carolinensis* in the north, *Blarina carolinensis peninsulae* on the southern peninsula, and *Blarina carolinensis shermani* in the vicinity of Fort Myers. The taxonomy of these shrews is complex, and researchers have suggested they may represent one, two, or even three species. To assess relationships among these taxa, we measured eight cranial characters on 363 specimens from Florida and used discriminant function analysis to characterize the mensural features of reference samples and to assign unknown specimens to a particular taxon. The reference sample of *shermani* averaged 7.8% larger than *peninsulae* and 9.5% larger than *carolinensis*; these differences are similar to those that exist between other species in the genus. Discriminant scores for *shermani* did not overlap with those of *carolinensis* or *peninsulae*, and only two possible hybrids were identified between *shermani* and *peninsulae*. Given the extent of differentiation of *shermani* and the paucity of possible hybrids, we recognize *Blarina shermani* as a distinct species. However, *peninsulae* and *carolinensis* are less well differentiated and show evidence of intergradation. Therefore, we regard *peninsulae* as a subspecies of *B. carolinensis*.

Keywords: *Blarina carolinensis carolinensis*; *Blarina carolinensis peninsulae*; *Blarina shermani*; Florida; taxonomy; short-tailed shrews

INTRODUCTION

Short-tailed shrews of the genus *Blarina*, common inhabitants of the eastern United States and adjacent southern Canada, have aroused considerable systematic interest since the early 1970s. Historically, the genus

was divided into two species—*B. brevicauda* ranging throughout the eastern United States and southern Canada, and *Blarina telmalestes* occurring only in the Dismal Swamp of Virginia and North Carolina (Bole

and Moulthrop 1942; Hall and Kelson 1959). That arrangement was challenged by Genoways and Choate (1972), who presented evidence that two nominal subspecies (*B. brevicauda brevicauda* and *B. b. carolinensis*) were behaving as distinct biological species where their ranges abutted in Nebraska. Subsequent studies by Bowles (1975) in Iowa, Ellis et al. (1978) in Illinois, and Tate et al. (1980) in Virginia revealed a similar situation in those states. In each instance, the geographic range of a larger short-tailed shrew to the north abutted with that of a smaller shrew to the south with little or no hybridization in the zone of overlap. In some instances, the zone of overlap was <3 km wide (Benedict 1999b).

These studies prompted several investigators to reevaluate taxonomic relationships within the genus. Based on morphometric (Benedict 1999a; Braun and Kennedy 1983; Ellis et al. 1978; French 1981; George et al. 1981; Handley and Varn 1994; Moncrief et al. 1982; Tate et al. 1980), karyotypic (Beck et al. 1991; Elrod 1992; Elrod et al. 1996; Genoways et al. 1977; George et al. 1982; Lee and Zimmerman 1969; Meylan 1967; Qumsiyeh et al. 1997), mitochondrial DNA (Benedict 1999a), and fossil data (Jones et al. 1984), three species eventually were recognized in the genus *Blarina*. The northern short-tailed shrew (*B. brevicauda*) occurs in the northern United States and southern Canada as far west as Nebraska and Manitoba, and on the Appalachian Mountains as far south as Georgia (Laerm et al. 1981). It includes the former species *B. telmalestes* and a recently recognized subspecies (*B. brevicauda knoxjonesi*) along the coast of North Carolina (Webster 1996). The southern short-tailed shrew (*B. carolinensis*) occurs in the southeastern United States as far north as coastal Virginia, west into East Texas, and along the Mississippi River lowlands as far north as Illinois (Genoways and Choate 1998). Elliot's short-tailed shrew (*B. hylophaga*) occupies the southwestern portion of the geographic range of the genus from northwestern Louisiana and northeastern Texas to southern Nebraska and eastern Colorado (George et al. 1981; Stangl and Carr 1997).

In addition to differences in size, the three species are characterized by their karyotypes. *B. brevicauda* has a diploid number (2N) of 48, 49, or 50, and a fundamental number (FN) of 48 (Genoways et al. 1977; George et al. 1982; Lee and Zimmerman 1969; Meylan 1967). *B. carolinensis* is characterized by 2N = 46 and FN = 44 or 45 throughout most of its geographic range, but a karyotypically variable population (2N = 34, 35, 36, 37, 38, 39, 40, or 41; FN = 41, 42, 43, 44, or 45) was described in Shelby County, Tennessee (Beck et al. 1991; Elrod 1992; Elrod et al. 1996; George et al. 1982; Qumsiyeh et al. 1997). *B. hylophaga* is characterized by 2N = 52 and FN = 60, 61, or 62 (George et al. 1982).

Although the specific status of short-tailed shrews and their geographic ranges now are relatively well understood, the details of these relationships require additional study in several regions. Two of the more troubling regions are the Ozarks and surrounding areas, where all three species may occur, and peninsular Florida.

Two nominal taxa of short-tailed shrews are recognized (Hall 1981) in peninsular Florida—*Blarina carolinensis peninsulae* (described by Merriam in 1895 from the Miami River, Dade Co.) and *B. carolinensis shermani* (described as *B. brevicauda shermani* by Hamilton [1955] from 2 mi N Fort Myers, Lee Co.). A third taxon, *B. carolinensis carolinensis*, occurs throughout the Southeast and is known from northern Florida (Hall 1981). These taxa have been regarded as comprising one species (Hall and Kelson 1981), two species (George et al. 1982), or even three species (as suggested by Genoways and Choate 1998). The purpose of our study was to assess taxonomic relationships between *B. c. shermani* and *B. c. peninsulae* in peninsular Florida and between these taxa and *B. c. carolinensis* in the panhandle of Florida and adjacent areas.

MATERIALS AND METHODS

We studied specimens of *Blarina* from the following collections: American Museum of Natural

History (AMNH); Carnegie Museum of Natural History (CM); Cornell University, Vertebrate Collections

(CUVC); Florida State University Museum (FSUM); Fort Hays State University, Sternberg Museum of Natural History (MHP); National Museum of Natural History (NMNH); University of Central Florida (UCF); University of Florida, Florida Museum of Natural History (UF); University of Georgia, Museum of Natural History (UGAMNH); University of Kansas, Natural History Museum (KU); and University of Michigan, Museum of Zoology (UMMZ). We recorded eight cranial measurements, selected from those used by Choate (1972), Genoways and Choate (1972), Tate et al. (1980), George et al. (1981), Moncrief et al. (1982), and Braun and Kennedy (1983), from each specimen with digital calipers (level of accuracy, 0.01 mm): occipital-premaxillary length, length of molariform tooththrow, cranial breadth, breadth of zygomatic plate, maxillary breadth, interorbital breadth, height of mandible, and articular breadth. We pooled age groups and sexes for analysis because shrews of the genus *Blarina* exhibit little variation attributable to age or gender in the trap-pable population (Benedict 1999a; Choate 1972; Ellis et al. 1978; French 1981; Graham and Semken 1976; Moncrief et al. 1982). Only individuals with complete sets of measurements were used in our analyses.

We selected three reference samples for use in analyses: 16 specimens from the type locality of *Blarina carolinensis shermani* (2 mi N Fort Myers, Lee Co., Florida); 44 specimens from Dade County, Florida, where the type specimen of *B. c. peninsulae* was captured; and 20 specimens from well within the geographic range of *B. c. carolinensis* (Aiken County, South Carolina). The last of these locations is approximately 300 km N of the northern border of Florida and 160 km NW of the restricted type locality of *B. c. carolinensis* (Charleston County, South Carolina; Handley and Varn 1994). Two hundred eighty-three specimens from Florida were treated as unknowns.

We compared measurements from the three reference samples with t-tests using SPSS Student Ware (Norusis 1991). We then used discriminant function analysis (PROC DISCRIM; SAS Institute Inc. 1991) to identify specimens from areas other than the three reference localities. Discriminant function multipliers were calculated for each pair-wise comparison of taxa. The relative contribution of each measurement to discriminant scores was determined by multiplying its discriminant function multiplier by the mean of that measurement for all reference animals combined. This was repeated for each pair-wise comparison. When comparing *shermani* to *peninsulae* and *carolinensis*, we entered all three reference samples as a priori groups and all other specimens as unknowns. When comparing *peninsulae* and *carolinensis*, we entered reference samples from these taxa as a priori groups, excluded all individuals previously identified as *shermani*, and entered all remaining specimens as unknowns. When identifying unknowns, we assigned a specimen to a taxon if its probability of correct identification was 75.0% unless noted otherwise. This criterion was used for convenience only, and it has nothing to do with the long-discredited “75% Rule” (e.g., Mayr 1969).

To further examine geographic patterns of morphometric variation, we compared frequency distributions of discriminant scores of reference samples to samples from three regions across the state. The sample from the northern peninsula consisted of specimens from Alachua, Putnam, Marion, and Citrus counties ($n = 58$); the sample from the central peninsula consisted of specimens from Orange, Indian River, Osceola, Polk, Hillsborough, and Pinellas counties ($n = 51$); and the sample from the southern peninsula was from Highlands County ($n = 147$).

RESULTS

Reference samples of the three taxa differed in size (Table 1). The nominal taxon *shermani* averaged 7.8% larger than *peninsulae* for all 8 measurements, and all differences were significant ($P=0.001$). Likewise, *shermani* averaged 9.5% larger than *carolinensis*, and all differences were significant ($P=0.001$). The

nominal taxon *peninsulae* averaged 1.7% larger than *carolinensis* for all 8 measurements combined but was smaller for length of molariform tooththrow and breadth of zygomatic plate. The differences in size between *peninsulae* and *carolinensis* were significant at $P=0.001$ for occipital-premaxillary length, cranial

Table 1.—Comparison of means (X), standard deviations (SD), and ranges of morphological measurements (mm) among 3 reference samples of *Blarina*. *OCPM* = Occipital-premaxillary length, *MOLAR* = Length of molariform tooththrow, *CRBTH* = Cranial breadth, *ZYGPL* = Breadth of zygomatic plate, *MXBTH* = Maxillary breadth, *IOBTH* = Interorbital breadth, *HTMAN* = Height of mandible, *ARBTH* = Articular breadth.

Trait	<i>carolinensis</i> (n=20)			<i>shermani</i> (n=16)			<i>peninsulae</i> (n=44)		
	X	SD	range	X	SD	range	X	SD	range
OCPM	18.87	0.35	18.31-19.60	20.63	0.35	19.20-21.30	19.61	0.43	18.56-20.53
MOLAR	5.25	0.10	5.08- 5.48	5.57	0.12	5.34- 5.77	5.19	0.14	4.80- 5.48
CRBTH	9.99	0.33	9.01-10.50	10.60	0.26	10.13-11.02	10.28	0.28	9.69-10.97
ZYGPL	2.31	0.12	2.13- 2.54	2.51	0.12	2.30- 2.71	2.17	0.16	1.80- 2.52
MXBTH	6.43	0.21	6.17- 6.92	7.23	0.17	6.94- 7.56	6.64	0.21	6.24- 7.33
IOBTH	4.95	0.13	4.74- 5.23	5.41	0.12	5.18- 5.61	5.17	0.18	4.82- 5.71
HTMAN	5.31	0.20	4.95- 5.80	6.12	0.18	5.76- 6.37	5.59	0.16	5.15- 5.93
ARBTH	1.97	0.08	1.86- 2.14	2.16	0.07	2.08- 2.31	1.99	0.10	1.81- 2.29

breadth, maxillary breadth, interorbital breadth, and height of mandible, and were significant at $P=0.01$ for breadth of zygomatic plate. Length of molariform tooththrow and articular breadth did not differ between the two taxa ($P>0.05$).

Comparison of shermani to other taxa.—Discriminant scores of the reference sample of *shermani* and reference samples of *carolinensis* and *peninsulae* did not overlap (Fig. 1). Comparing *shermani* to *peninsulae*, the average discriminant score was -194.50 for *shermani* (range -187.42 to -199.92) and -172.79 for *peninsulae* (range -163.83 to -182.82). Length of molariform tooththrow, cranial breadth, maxillary breadth, and height of mandible were weighted most heavily in calculating discriminant scores (Table 2). Comparing *shermani* to *carolinensis*, the average discriminant score was -271.74 for *shermani* (range -260.92 to -279.05) and -237.46 for *carolinensis* (range -226.39 to -253.09). Occipital-premaxillary length, cranial breadth, maxillary breadth, and height of mandible were weighted most heavily (Table 2). All reference specimens of *shermani* were identified as *shermani* with probability values $>97.5\%$ (mean, 99.8%). Nineteen of 20 reference specimens of *carolinensis* were identified as *carolinensis* with probability values $>75.0\%$. The remaining specimen had probability values of 54.6% *carolinensis*, 33.4% *peninsulae*, and 12.0% *shermani* and thus could not be assigned with certainty. Likewise, of 44 specimens comprising the *peninsulae* reference sample, 38 were identified as *peninsulae* with probability values $>75.0\%$. The

remaining six individuals could not be assigned with certainty, but none of these were misidentified as *shermani* (probability values of being *shermani* were 0.0 [$n = 4$], 0.1 , and 22.4%).

When 283 specimens of unknown identity were compared with reference samples of *shermani*, *peninsulae*, and *carolinensis*, 246 were identified as *peninsulae* or *carolinensis* with probability values $>75.0\%$. Two specimens were identified as *shermani*, and 35 individuals could not be identified to taxa with a probability value $>75.0\%$. The two specimens identified as *shermani* (NMNH 300004 and 300005) were collected at the type locality of that taxon at the same time as the type series. Those specimens were not included in the reference sample for *shermani* because our original data sheets incorrectly described their locality of capture. The probability values that those specimens represented *shermani* were 99.9 and 100% , respectively.

Of the 35 animals that could not be identified and the 246 that were identified as *peninsulae* or *carolinensis*, four had probability values indicating they resembled *shermani*. The first of those specimens (KU 147074) was obtained in Collier County about 75 km south of the type locality of *shermani*. That animal had probability values of 67.6% *shermani* and 32.3% *peninsulae*. Importantly, another shrew obtained at the same locality the following day (KU 147075) was identified as *peninsulae* with a probability of 99.2% (0.8% *carolinensis*). The second specimen resembling *shermani* (UF 20911), captured in Lee County about

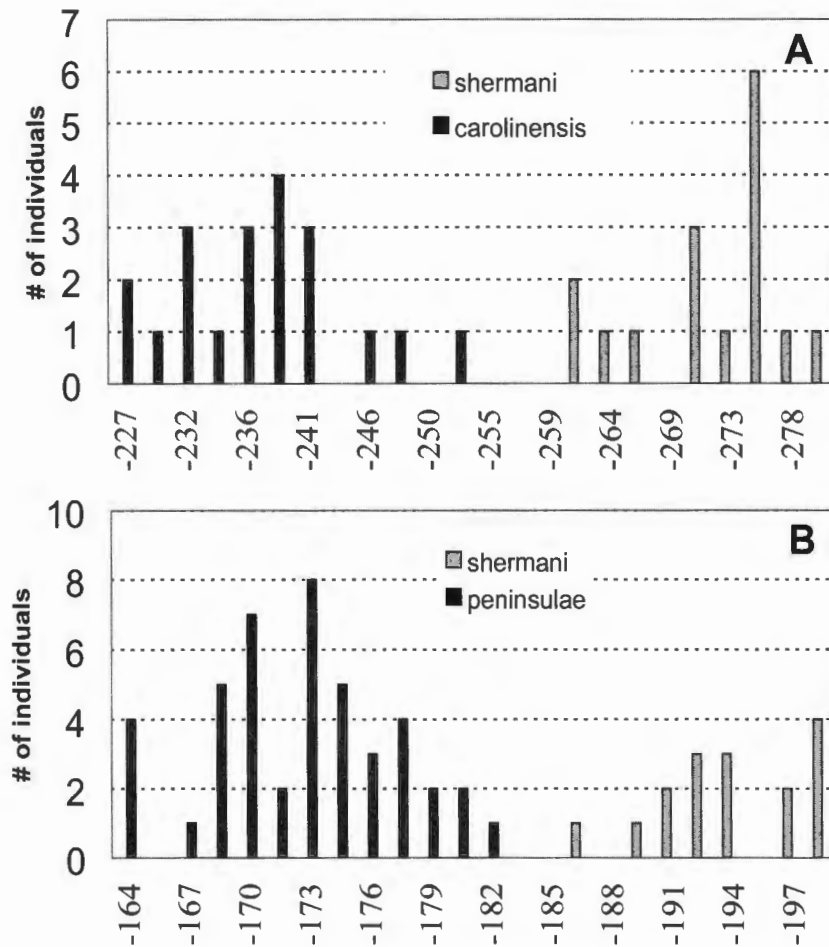


Figure 1. A, Frequency distribution of discriminant scores of reference samples of *shermani* (n = 16) and *carolinensis* (n = 20). B, Frequency distribution of discriminant scores of reference samples of *shermani* and *peninsulae* (n = 44).

Table 2.—Discriminant function multipliers and contributions (cont.) of individual measurements to discriminant scores for comparing taxa of *Blarina*.

Measurement	<i>carolinensis</i> / <i>peninsulae</i> multiplier ^a (cont. ^b)	<i>shermani</i> / <i>carolinensis</i> multiplier (cont.)	<i>shermani</i> / <i>peninsulae</i> multiplier (cont.)
Occipital-premaxillary length	-7.450 (-144.5)	-7.578 (-148.9)	-0.809 (-16.1)
Length of molariform toothrow	21.330 (111.1)	7.076 (38.1)	-12.686 (-67.1)
Cranial breadth	0.497 (5.1)	7.120 (73.0)	7.741 (80.3)
Breadth of zygomatic plate	6.292 (14.0)	-9.294 (-22.3)	-15.562 (-35.2)
Maxillary breadth	-0.734 (-4.8)	-14.100 (-95.6)	-12.890 (-87.7)
Interorbital breadth	-9.033 (-46.1)	-3.899 (-20.1)	3.658 (19.2)
Height of mandible	-8.285 (-45.6)	-19.801 (-112.3)	-13.591 (-77.9)
Articular breadth	17.458 (34.6)	17.232 (35.3)	2.928 (5.9)

^a Multiplier is number that an individual's measurement is multiplied by to compute discriminant score.

^b Contribution is relative contribution of a given measurement to discriminant scores. Contribution was calculated by multiplying discriminant multiplier for a particular measurement by the mean of that measurement for all reference animals combined, for the two taxa being compared.

4.5 km E of the type locality of *shermani*, had probability values of 43.6% *peninsulæ*, 43.3% *carolinensis*, and 13.0% *shermani*. The third specimen (AMNH 243164), collected in Highlands County about 75 km NE of the type locality of *shermani*, had probability values of 72.1% *peninsulæ*, 16.2% *shermani*, and 11.8% *carolinensis*. The final specimen (UF 26060), obtained in Pinellas County more than 150 km N of the type locality of *shermani*, had probability values of 89.1% *peninsulæ* and 10.9% *shermani*.

Comparison of carolinensis and peninsulæ.—Discriminant scores of the reference samples of *carolinensis* and *peninsulæ* did not overlap (Figure 2). The average discriminant score was -68.11 for *carolinensis* (range -64.17 to -73.19) and -79.71 for *peninsulæ* (range -73.39 to -89.39). Occipital-premaxillary length, length of molariform toothrow, interorbital breadth, and height of mandible were weighted most

heavily in the discriminant function formula (Table 2). All but one of the 20 reference specimens of *carolinensis* were identified as *carolinensis* with probability values $>75.0\%$ (17 had probability values $>90.0\%$). The remaining specimen (UGAMNH 5164) was not assignable, having a probability value of being *carolinensis* of 67.2%. The average probability value for *carolinensis* reference specimens was 95.7%. Of 44 reference specimens of *peninsulæ*, 38 were identified as *peninsulæ* with probability values $>75.0\%$ (36 had probability values $>90.0\%$). The remaining specimens could not be assigned with certainty (their probability values of being *peninsulæ* were 74.8, 64.6, 55.6, 45.1, 42.4, and 37.3%). The average probability value of *peninsulæ* reference specimens was 92.4%.

Discriminant function analysis identified 217 of 281 unknowns as *peninsulæ* and 35 as *carolinensis*. The remaining 29 could not be assigned to a taxon with

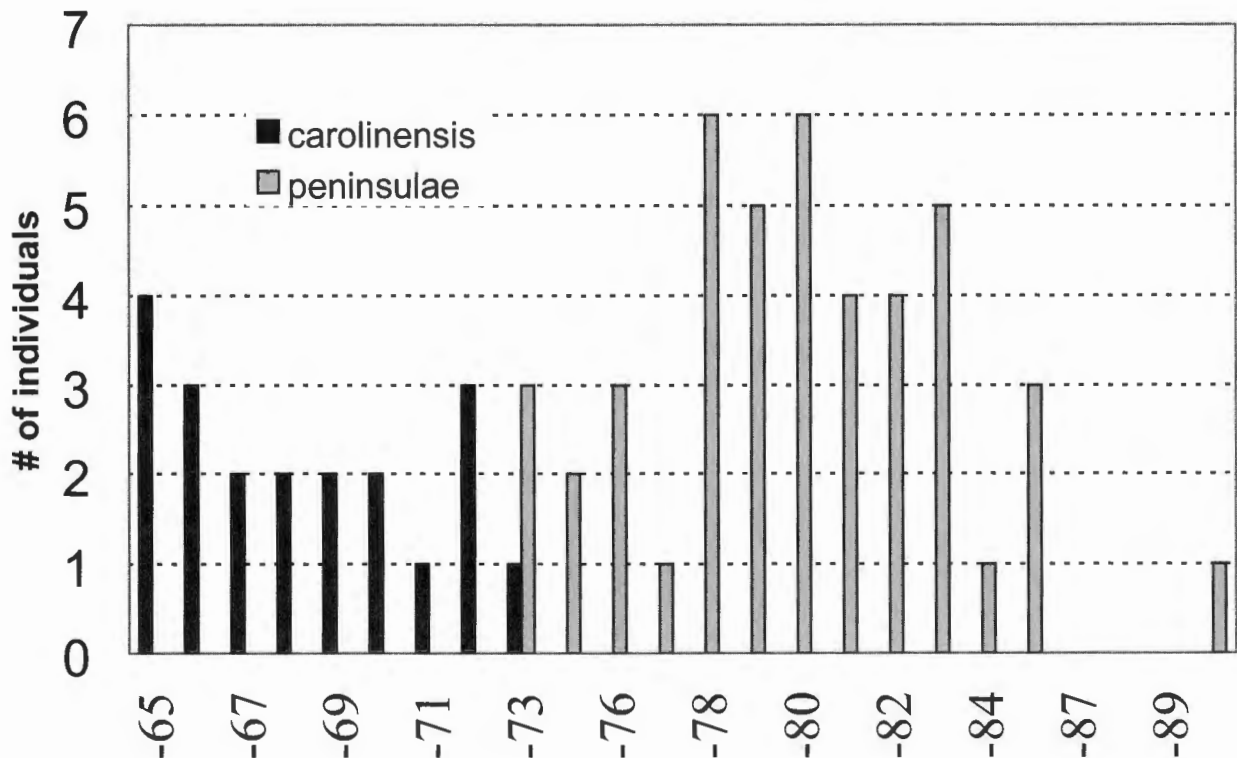


Figure 2. Frequency distribution of discriminant scores of reference samples of *carolinensis* (n = 20) and *peninsulæ* (n = 44).

a probability >75.0%. Specimens with morphometric attributes of *peninsulae* were from throughout the state, including five specimens collected from the northernmost tier of counties in Florida. Of nine counties with samples of five or more specimens (Dade, Highlands, Indian River, Hillsborough, Citrus, Marion, Putnam, Alachua, and Leon), all but Marion County were dominated by specimens assignable to *peninsulae*. Specimens with morphometric attributes of *carolinensis* likewise were found throughout the state, including 14 specimens from Highlands and Indian River counties. Likewise, specimens that could not be assigned with certainty were collected from localities scattered across the state. These misassigned or unassignable specimens further illustrate the degree of overlap in measurements of these taxa.

Frequency distributions of discriminant scores of unknowns from the southern peninsula were similar to

those of the *peninsulae* reference sample but included several individuals with scores higher than the reference sample, indicating an overall smaller body size (Fig. 3A). The sample from the central peninsula also was similar to the *peninsulae* reference sample, but the peak of the distribution was slightly higher and several individuals had scores noticeably higher than the reference sample (Fig. 3B). The distribution of discriminant scores in the sample from the northern peninsula included individuals with scores intermediate between the reference samples of *peninsulae* and *carolinensis* and some with very high and very low discriminant scores (Fig. 3C). None of the samples had a bimodal distribution, as would be expected if *peninsulae* and *carolinensis* were discrete species within an area of geographic overlap. Overall, the distribution of discriminant scores appeared to follow a gradual cline of decreasing size (resulting in increasing discriminant scores) from south to north.

DISCUSSION

Short-tailed shrews in Florida present two distinct taxonomic problems—the relationship of the taxon *shermani* to the taxa *carolinensis*, *peninsulae*, and other nominal taxa, and the relationship of *carolinensis* to *peninsulae*. Layne (1992) treated *shermani* and *peninsulae* as subspecies of *Blarina carolinensis*. Later, Genoways and Choate (1998) excluded both *peninsulae* and *shermani* from *B. carolinensis* based primarily on the unique karyotype (2N = 50, 51, or 52; FN = 52) in *peninsulae* from Dade and Highlands counties (George et al. 1982). The results of morphometric analyses presented herein indicated that neither of these arrangements is completely correct and that *shermani* and *peninsulae* require a revised taxonomic treatment.

Status of shermani.—Members of the *shermani* reference sample were significantly larger than reference samples of *peninsulae* and *carolinensis* in all measurements analyzed. The amount of difference—7.8 and 9.5%, respectively—is of the magnitude seen between species elsewhere in this genus (*Blarina brevicauda* versus *B. hylophaga* in Nebraska and Iowa, and *B. brevicauda* versus *B. carolinensis* in Illinois and Virginia). When compared in a discriminant function analysis, the reference sample of *shermani* differed substantially from the reference samples of *peninsulae*

and *carolinensis*. The discriminant score of the smallest *shermani* was 2.5% less than that of the largest *peninsulae* and 3.1% less than that of the largest *carolinensis*. The extent of morphometric separation of *B. brevicauda* and *B. hylophaga* in Nebraska was greater, with the smallest reference individual of *B. brevicauda* having a discriminant score 11.1% smaller than that of the largest *B. hylophaga* (Benedict 1999a).

Admittedly, our samples were small. However, we found no evidence of intergradation between *shermani* and *peninsulae* to the east or north of the type locality of *shermani*. Three specimens from 9 mi E Fort Myers were considered by Layne (1992) as possible intergrades between *shermani* and *peninsulae*, but only one of these specimens (UF 20911) had complete data and could be used in our analyses. That specimen had probability values of 43.7% *peninsulae*, 43.3% *carolinensis*, and 13.0% *shermani*. Given its similarity to the smaller *carolinensis*, UF 20911 likely represents an atypical *peninsulae* rather than an intergrade between *peninsulae* and *shermani*. Our analyses also revealed that two specimens (NMNH 300004 and 300005) collected as part of the original type series but not included in our reference sample had probabilities values of 99.9 and 100% of being *shermani*, respectively. We therefore assigned those specimens to *shermani*. The three

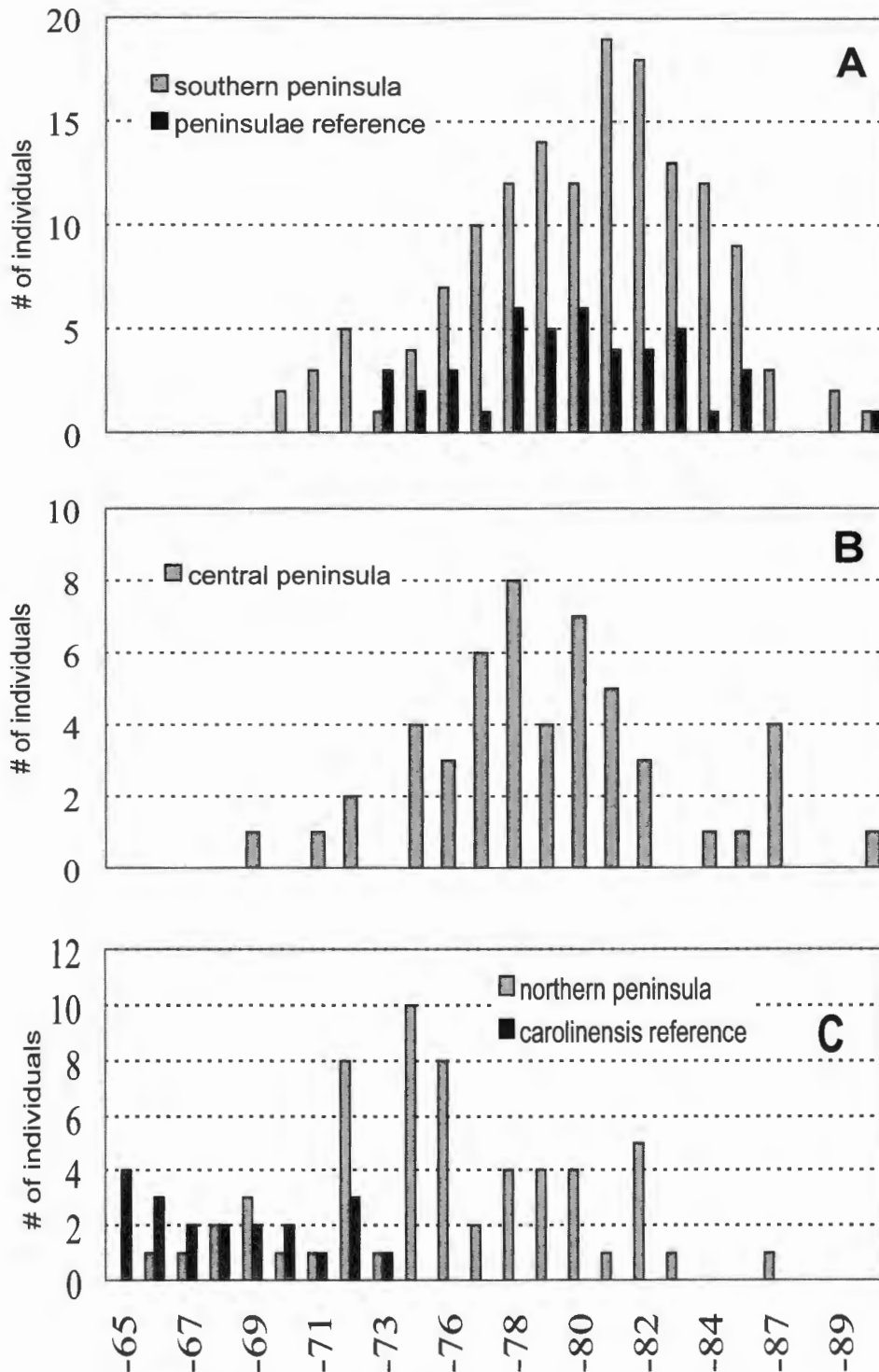


Figure 3. A, Frequency distribution of discriminant scores of the reference sample of *peninsulae* (black, n = 44) and unknown individuals from the southern peninsula of Florida (gray, n = 147). B, Frequency distribution of discriminant scores of unknown individuals from the central peninsula of Florida (n = 51). C, Frequency distribution of discriminant scores of the reference sample of *carolinensis* (black, n = 20) and unknown individuals from the northern peninsula of Florida (gray, n = 58).

specimens in our analyses from Collier County were informative. A specimen from Deep Lake (AMNH 231463) had probability values of 99.2% *peninsulae* and 0.8% *carolinensis*. Clearly, this specimen is assignable to *peninsulae*. Two specimens from 4.5 mi E Royal Palm (KU 147074 and 147075) had probability values of 67.6% *shermani*, 32.3% *peninsulae* and 99.2% *peninsulae*, 0.8% *carolinensis*, respectively. These results indicate that KU 147075 should be assigned to *peninsulae* but that KU 147074 is a possible hybrid between *shermani* and *peninsulae* that should be assigned to *shermani*. We regard this specimen as a possible hybrid rather than an intergrade because one of the parental types also is present at the locality. If this were a zone of intergradation, then all individuals present presumably would show intermediate tendencies (as discussed by Benedict 1999a and 1999b, and Genoways and Choate 1972).

Two additional specimens had probability values indicating partial resemblance to *shermani*. AMNH 243164, obtained at Archbold Biological Station, 8 mi S Lake Placid, Highlands Co., had probability values of 72.1% *peninsulae*, 16.1% *shermani*, and 11.8% *carolinensis*. This specimen is slightly larger than others collected at Archbold Biological Station, but we assigned it to *peninsulae*. The second specimen (UF 26060) was taken at an unspecified location in Pinellas County, about 150 km north of the type locality of *shermani*. This individual's probability values were 89.1% *peninsulae* and 10.9% *shermani*. We likewise assigned this specimen to *peninsulae*.

The degree of morphometric differentiation between *shermani* and adjacent populations of *peninsulae* is similar to that seen between other species in *Blarina*, and the number of intermediate-sized individuals is low. We therefore recognize *Blarina shermani* as a distinct species.

Another issue to resolve is the relationship of *B. shermani* to *B. brevicauda*. Since its description, *shermani* has been recognized as being larger in all measurements than other southeastern populations of *Blarina* except *B. brevicauda* in Georgia (French 1981; Hamilton 1955). Genoways and Choate (1998) suggested that *shermani* might be a relictual population of *B. brevicauda*, citing as circumstantial evidence 1) the presence of a population of *B. brevicauda* in southern

Georgia and Alabama that appears to be isolated to the south of the main population of that species (French 1981), and 2) the presence of an isolated population of *Microtus pennsylvanicus* (a species that is sympatric with *B. brevicauda* over much of eastern North America) on the central Gulf Coast of Florida (Woods 1992; Woods et al. 1982).

The hypothesis that *shermani* is a relictual isolate of *B. brevicauda* probably is incorrect. For one thing, the distribution of *shermani* is about 600 km S of the main population of *B. brevicauda* in central Georgia. In contrast, the apparently isolated population of *brevicauda* in southern Georgia described by French (1981) is separated by a distance of just 40 km from the contiguous population that inhabits the southern Appalachian Mountains. Moreover, the isolated population of *Microtus pennsylvanicus* described by Woods (1992) is located approximately 250 km N of the type locality of *shermani*, and there is no indication in the extensive fossil record in Florida that the meadow vole ever occurred south of this relictual population (Webb 1974). Unfortunately, the fossil record of *Blarina* in Florida is uninformative with respect to this issue. Neither *B. brevicauda* nor *B. shermani* have been found in fossil sites in Florida, and the fossil deposit nearest the type of locality of *shermani* (the Bradenton 51st Street site) contained specimens that were referred to *peninsulae* (Jones et al. 1984).

We studied two specimens of *B. brevicauda* from Quitman County, Georgia (AMNH 514944 and 514945) that were collected from the isolated population described by French (1981). Measurements of these two specimens were substantially larger than those of *shermani* measured during this project (Table 1). Measurements (in mm) for AMNH 514944 and 514945, respectively, were: occipital-premaxillary length, 21.6 and 22.6; length of molariform toothrow, 6.1 and 6.2; cranial breadth, 11.8 and 12.3; breadth of zygomatic plate, 2.7 and 2.6; maxillary breadth, 7.8 and 7.8; interorbital breadth, 5.7 and 5.9; height of mandible, 6.7 and 7.1; and articular breadth, 2.5 and 2.5. Furthermore, discriminant scores of these two specimens (−208.96 and −210.32 for AMNH 514944 and 514945, respectively) were substantially less than scores of reference individuals of *shermani* used in this study (mean = −194.50, range −187.42 to −199.92). Therefore, *shermani* appears to be considerably smaller than *B.*

brevicauda. Final resolution of the relationship of *B. shermani* and *B. brevicauda* will necessitate obtaining a karyotype or DNA sequence of a known specimen of *shermani*.

Status of carolinensis and peninsulae.—George et al. (1982:641) asserted that the “karyotypes of the peninsular [Florida] *Blarina* are so distinct from those of adjacent *B. carolinensis* that Group C [individuals from Dade and Highland counties] may represent a distinct species.” This conclusion was based on the fact that the three other species in the genus all have distinctive karyotypes. From Nebraska to Virginia, populations of *B. hylophaga* and *B. carolinensis* abut with populations of the larger, more northerly *B. brevicauda* along a narrow zone in which hybridization occasionally occurs. In that zone, the species are characterized by size and karyotypic differences. Our initial hypothesis was that a similar situation would exist between populations of *carolinensis* and *peninsulae* in peninsular Florida. Morphometric analyses did not support that hypothesis. Although there was no overlap in discriminant scores of reference samples, the largest specimen in the *carolinensis* reference sample had a discriminant score only 0.3% greater than that of the smallest *peninsulae* reference specimen. Furthermore, some individuals in the reference samples could not be assigned to a taxon with a probability of $\geq 75.0\%$. Overall, individuals in the reference sample of *peninsulae* averaged 1.7% larger than the *carolinensis* sample, although specimens of *peninsulae* averaged smaller in one measurement and two (length of molariform toothrow and articular breadth) of the eight measurements were not significantly different between the reference samples. Although *Blarina* in southern Florida are slightly larger than those from nearer the type locality of *B. carolinensis*, these differences are not of the magnitude seen between *B. shermani* and other Florida populations or among other species of *Blarina*.

When “unknown” specimens from across the state were identified with discriminant function analysis, the largest specimens were found in the southern peninsula and the smallest were in extreme northern Florida. However, there was no obvious step in the cline from south to north. The results of morphometric

analyses thus appear as would be expected for populations of a single species, with much of the northern third of peninsular Florida being a zone of intergradation. This leads us to reject our initial hypothesis and propose a new hypothesis—that the taxon *peninsulae* represents a peninsular subspecies of the more widespread *Blarina carolinensis* that is characterized by larger size than in typical *carolinensis* and by a unique karyotype in at least some populations.

In accordance with this new hypothesis, we have attempted to determine the zone of contact between populations of *carolinensis* and *peninsulae*. At no point can this line be drawn without some ambiguity, as would be expected between interbreeding populations, but it can be drawn to place most specimens identified as *peninsulae* south of the line and most specimens identified as *carolinensis* north of the line. Until more detailed study of short-tailed shrews in this region of Florida can be conducted, we propose that this line separates the subspecies *B. c. peninsulae* and *B. c. carolinensis*.

The line of contact begins along the west coast of Florida in Citrus County (Fig. 4). Of two specimens from Crystal River State Preserve, just west of the town of Crystal River, one (UF 20965) was assigned to *carolinensis* (probability level 99.8%) and the other (UF 20966) to *peninsulae* (probability level 99.8%). South of this location in Citrus County, a sample of 11 specimens from Homasassa Springs and one specimen from 1 mi SW Homasassa Springs were available for analysis. Of these 12 specimens, six classified as *peninsulae* with probability values =95.0% (UF 20962, 23586; AMNH 163864, 163866, 163880-81). Of the remainder, two classified as *carolinensis* with >75.0% probability (UF 20968, AMNH 163878). The other four specimens resembled *peninsulae* but at much lower probability levels (AMNH 163876, 73.6%; UF 20964, 66.0%; UF 20963, 59.7%; AMNH 163865, 52.1%). We assigned all specimens from Citrus County to *B. c. peninsulae* except the one from Crystal River State Preserve, and we drew the line of contact between *carolinensis* and *peninsulae* through Crystal River Preserve and Crystal River and then turning northeastward into Marion County.

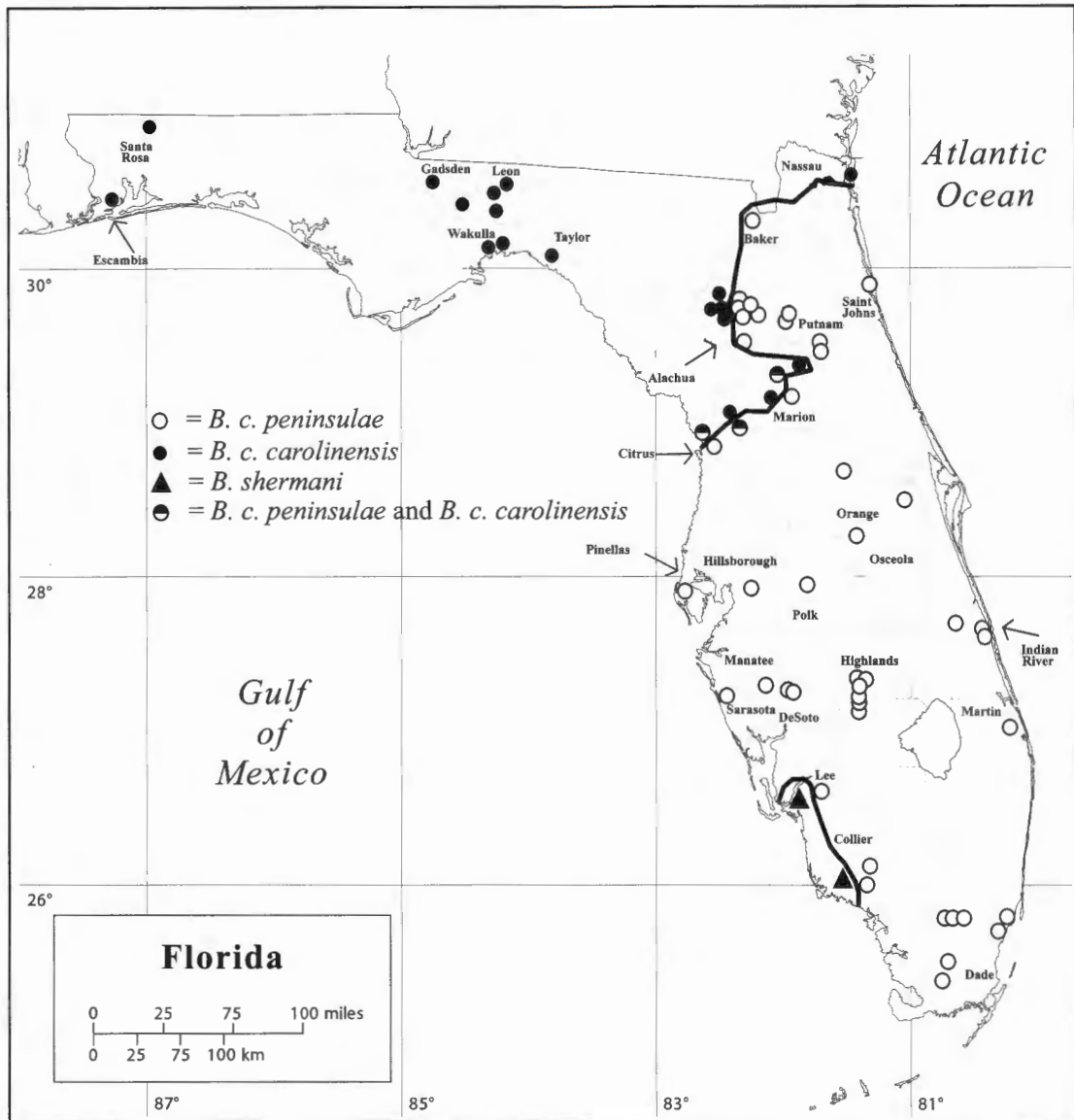


Figure 4. Map of Florida showing distributions of *Blarina carolinensis carolinensis* (closed circles north and west of the heavy line through the northern peninsula), *B. c. peninsulae* (open circles south and east of the heavy line), and *Blarina shermani* (two localities indicated by black triangles in Lee and Collier counties). Counties mentioned in text are labeled. Both subspecies of *B. carolinensis* were identified at localities indicated by circles that are black above and white below. Localities shown on the map are identified in the lists of Specimens Examined. To avoid crowding, nearby localities are covered by one symbol.

The zone of contact appears to enter southwestern Marion County near Dunnellon. A specimen from Dunnellon was assigned to *carolinensis* (UF 16865, 95.0%), as was one of four specimens from 0.5 mi S, 4 mi E Dunnellon (UF 13518, 99.1%). The other three

specimens from the latter location were assigned to *peninsulae* (UF 13517, 100%; UF 13516, 99.9%; UF 13509, 98.9%). From there, the zone of contact appears to pass just east of Ocala—three specimens from Shady (just south of Ocala) were assigned to *carolinensis* (UF

16854, 99.2%; UF 16857, 83.7%; UF 16859, 79.0%), whereas two specimens from Lynne (east of Ocala) were assigned to *peninsulae* (UF 16855, 97.4%; UF 16862, 92.5%). The zone of contact then runs almost straight north from east of Ocala to Fort McCoy, where one specimen was assigned to each subspecies (UF 16863, 99.9% *carolinensis*; UF 16861, 98.7% *peninsulae*). Farther north and east, at Eureka Dam, the two available specimens were assigned to *carolinensis* (UF 16853, 90.4%; UF 16864, 83.3%).

From Eureka Dam, the zone of contact bends west into Alachua County to include a specimen from Micanopy within *peninsulae*. This placement of the line of contact puts all specimens from Putnam County within the geographic range of *peninsulae*, which, for the most part, is appropriate. Of six specimens examined from the vicinity of Welaka, four clearly are *peninsulae* (UF 2539, 99.8%; UF 2552, 98.7%; UF 649, 98.2%; UF 2527, 83.9%). One specimen (UF 655) most closely resembled *peninsulae* but only at the 63.4% probability level. The sixth specimen resembled *carolinensis* (UF 650, 97.1%), but we assigned it to *peninsulae* on geographic grounds. Three specimens taken between Melrose and Putnam Hall in northwestern Putnam County demonstrate the need for additional study in that area. UF 23585, from 3 mi E Melrose, Alachua County, resembled *peninsulae* at the 95.7% level. UF 28965, from the Katharine Ordway Preserve, resembled *carolinensis* at the 89.5% level. Finally, UF 28976, from that same location, is an intergrade with probability values of 53.5% *carolinensis* and 46.5% *peninsulae*.

Alachua County presents as many challenges as all other areas combined when assessing the course of the zone of contact between *carolinensis* and *peninsulae*. Several specimens lack precise locations of capture, and the zone of contact apparently passes, or passed, through the city of Gainesville where environmental alterations make interpretation difficult at best. Three specimens assigned to *peninsulae* give only Alachua County as the locality (UF 2532, 100%; UF 11083, 87.1%; UF 11082, 81.5%). Of four specimens that simply state "Gainesville" as their geographic origin, one (UF 11098) was assigned to *carolinensis* at the 99.9% level, whereas the other three were assigned to *peninsulae* on geographic

grounds but had low probability values (UF 5017, 70.3%; UF 6464, 69.5%; UF 226, 59.6%).

Beginning at Micanopy (UF 28282, 99.9% *peninsulae*), the zone of contact appears to pass west of Payne's Prairie at the southeast edge of Gainesville, where a specimen (UF 2114) was assigned to *peninsulae* at the 80.9% probability level. From this point, the line of contact may divide Gainesville nearly in half in a north-south direction. Placing the line in this position would classify as *peninsulae* the specimens used in our analyses from the following localities (which are from Gainesville and eastward in Alachua County): Tiger Bay [on Newnan's Lake Road on the west side of the lake just east of Gainesville] (UF 2529, 99.9%); 1/2 mi N Paradise [on the northern edge of Gainesville] (UF 2533, 99.2%); Gracie's Crossing [= Gracy's, 2 mi NW Paradise] (UF 2535, 99.8%; UF 2531, 78.1%; UF 17, 75.4%); and 5 mi towards Waldo from Gainesville [probably along Florida State Highway 24] (UF 10237, 89.6%).

Two specimens from the University of Florida campus in Gainesville are particularly interesting. UF 2530, from the east side of Lake Alice on campus, has a probability value of 88.0% of being *carolinensis*. UF 15, with a locality of "University Campus," has intermediate probability values 52.0% *peninsulae* and 48.0% *carolinensis*. We assigned both to *carolinensis*. Three specimens from northern Alachua County were available for our study. Two specimens from 8 mi N Gainesville are unquestionably *carolinensis* (UF 5545 and 5544, 99.8 and 99.5%, respectively). The third specimen (UF 19161), from 7 mi N, 7 mi E Gainesville, is best assigned to *peninsulae* (72.8%). We draw the line of contact of the two subspecies between these two locations. The final specimen from Alachua County is from Fort Clarke (UF 5018), located in western Gainesville just to the west of Interstate Highway 75. As we have drawn the line of contact, this specimen is in the geographic range of *B. c. carolinensis*, to which we have assigned it, but its probability values of 77.7% *peninsulae* and 22.3% *carolinensis* argue for assignment to *peninsulae*. Clearly, the distribution of short-tailed shrews in the vicinity of Gainesville is complex and probably changing with urban and suburban development. Resolution of questions about *Blarina* in and around Gainesville awaits a more thorough survey of short-tailed shrews in the area.

From Alachua County, the line of contact turns northeastward to accommodate a specimen from Glen St. Mary, Baker County (NMNH 262340), which resembled *peninsulae* with a probability level of 99.9%. East of Baker County, we drew the line directly eastward to meet the St. John's River where it turns east and flows into the Atlantic Ocean. This places specimens from Amelia Island, Nassau County, in the geographic range of *carolinensis* and a specimen from Anastasia Island, St. John's County (AMNH 269338), which resembled *peninsulae* with a probability value 98.0%, in the geographic range of *peninsulae*. Of two Amelia Island specimens, one resembled *carolinensis* (AMNH 240257, 97.6%) and the other (AMNH 240255) was intermediate (51.3% *carolinensis*, 48.7% *peninsulae*). It is tempting from a physiographic standpoint to place the line of contact for these taxa along the St. John's River to the east of Putnam and Clay counties as it runs northward into Duval County, but for now this seems inappropriate.

The remaining issue to be addressed concerning *B. c. carolinensis* and *B. c. peninsulae* relates to the misassigned individuals that were caught well within the geographic range of the other taxon. For example, in southern Florida, individuals in three counties were misassigned to *carolinensis*. These misassigned individuals include 10 of 147 specimens (6.8%) from Highlands County (probability of being *carolinensis* 97.8%, 97.1%, 95.8%, 95.2%, 95.0%, 90.1%, 83.6%, 81.3%, 80.5%, and 77.9%), 4 of 38 specimens (10.5%) from Indian River County (probability of being *carolinensis* 99.2%, 93.2%, 89.8%, and 79.8%), and one specimen from Sarasota County (probability of being *carolinensis* 61.0%). With regard to Indian River County, fossil specimens from the Late Wisconsinan Vero 2 and 3 sites were assigned to *B. carolinensis* by Jones et al. (1984; Genoways and Choate 1998), but examination of Figure 17 (in Jones et al. 1984) shows these specimens are most similar to *B. c. peninsulae*.

In northern Florida, in the geographic range we ascribe to *B. c. carolinensis*, four specimens were misassigned to *peninsulae*. These include individual specimens from Escambia (82.8%) and Gadsden (75.2%) counties and two specimens from Leon County with

probability values of 99.6% and 88.1%. We believe these specimens represent large individuals of *B. c. carolinensis* rather than misplaced *B. c. peninsulae*.

Contact Zones, the Fossil Record, and Karyotypic Variation in Blarina.—It is informative to compare the contact zone between *B. c. carolinensis* and *B. c. peninsulae* in peninsular Florida to the contact zone between *B. brevicauda* and *B. hylophaga* in Nebraska. Genoways and Choate (1972) described the abrupt boundary between *B. brevicauda* and *B. hylophaga* in Nebraska using multivariate analyses of morphometric data. Within the region of contact, they found both parental phenotypes and possible hybrids. Based on these findings, they proposed that speciation between these two taxa had occurred through a stasipatric mechanism (Key 1968; White 1968; White et al. 1967) by which chromosomal changes occurring in small populations led to reproductive isolation. This contact zone later was examined in detail by Benedict (1999a, 1999b) using mitochondrial DNA data and multivariate analysis of morphometric data. The line of contact between *B. brevicauda* and *B. hylophaga* in Nebraska is sharp, with the zone of sympatry ranging from 0.64 to 2.90 km in width. Only two of 1300 specimens studied were captured >2 km inside the geographic range of the other species. The number of hybrids identified was relatively low, with parental individuals greatly outnumbering hybrids. Furthermore, mtDNA analyses indicated that F₁ hybrids were fertile because probable F₂ individuals were present. The line of contact is a fairly straight line when viewed on a large scale and is not associated with any obvious ecotone. On a local scale, however, the line of contact between *B. brevicauda* and *B. hylophaga* wanders, apparently in response to structures in the environment. In particular, the line of contact often coincides with streams or highways that may trap it by intensifying the numerical disadvantage faced by any shrew that crosses the structure into the geographic range of the other species. The line of contact between these two species in Nebraska is capable of rapid movement, having shifted 2.4 km southward in 22 months at one site; however, the overall position of the line of contact has remained fairly stable since 1968 (Benedict 1999b).

The zone of contact between *B. brevicauda* and *B. hylophaga* in Nebraska may be a tension zone—a hybrid zone whose width is determined by the strength of selection acting against hybrids and the rate of dispersal of parental individuals into the zone (Barton and Hewitt 1985). If so, the paucity of hybrids indicates strong selection against hybrids, assortative mating, and/or a low rate of dispersal of parental individuals into the zone.

The zone of contact between *carolinensis* and *peninsulae* in Florida differs from the pattern described above in that there is no abrupt step in the morphometric cline that defines the taxa and there are misassigned individuals of both taxa well within the presumed geographic range of each taxon. Furthermore, the zone of contact between *carolinensis* and *peninsulae* appears to follow a more circuitous path than the boundary in Nebraska.

The differences between the parapatric boundaries in Nebraska and Florida may indicate that the process of speciation/divergence is at a different stage or following a different mechanism in these two regions. If speciation/divergence is following an allopatric model in both states, then the boundary between *carolinensis* and *peninsulae* in Florida may have arisen when two weakly differentiated populations reestablished contact. It is possible that the two taxa in Nebraska had reached a level of differentiation in which widespread genetic exchange no longer could occur after contact between the two populations was reestablished. Alternatively, the divergence process in Florida may be following a parapatric model where a continuous population diverges into genetically distinct taxa across an environmental gradient (Endler 1977; Turelli et al. 2001). If true, then the contact zone in Florida is characterized by weak selection across the environmental gradient and/or has been in existence for a short period of time so that substantial divergence has not occurred. Unfortunately, distinguishing allopatric from parapatric divergence is difficult if not impossible (Hewitt 1989).

The fossil record provides only limited insight into speciation in *Blarina*. Jones et al. (1984) examined fossils of *Blarina* from 82 sites across eastern North America. Only six sites contained more than one species of *Blarina*, and three of those were located near the present boundary between those same two species (Jones et al. 1984; Benedict 1997). The remaining three sites cannot be evaluated in this context—two are in areas currently uninhabited by *Blarina*, and the third is so old that it cannot be compared to present-day contact areas. The relative scarcity of sites containing more than one species of *Blarina* is what would be expected from either allopatric or parapatric speciation occurring across an abrupt environmental gradient.

Another important and unanswered question pertains to the karyotypic characteristics of *carolinensis* and *peninsulae*. George et al. (1982) karyotyped seven *carolinensis* and 15 *peninsulae* and found substantial differences between the two subspecies. If these karyotypic differences are consistent throughout the geographic ranges of these two taxa, then chromosomal differences could lead to a reduction in gene flow by causing meiotic problems in hybrids (Baker and Bickham 1986) or by “suppressing recombination and extending the effects of linked isolation genes” (Rieseberg 2001:351). According to this model, morphometric differences would accumulate at the boundary between the two chromosomal types (Key 1974, 1982). The contact zone between *carolinensis* and *peninsulae* in Florida, therefore, may provide a valuable site to study speciation. Furthermore, the presence of several different contact zones within *Blarina*, involving taxa that differ in how closely related they are to each other, makes this genus an ideal system for studying divergence and speciation. Thus, the contact zone between *carolinensis* and *peninsulae* in Florida needs to be analyzed with karyotypic and genetic data and compared to specific boundaries elsewhere in the genus *Blarina*.

SYSTEMATICS OF FLORIDA *BLARINA**Blarina carolinensis* (Bachman 1937)

Diagnosis.—Like other species of *Blarina*, *B. carolinensis* is a robust, short-tailed shrew with five unicuspidate teeth in each upper jaw. Features of the dentition and details of the dental formula in *Blarina* were illustrated and described by George et al. (1986) and Genoways and Choate (1998). Pelage coloration is silver to nearly black, and in some individuals the hairs have faint brown tips. The two most diagnostic features of this species are its small size and distinctive karyotypes. *Blarina carolinensis* is the smallest of the four species currently recognized in the genus (Genoways and Choate 1998). The karyotype over much of the range of the species is $2N = 46$ and $FN = 44$ (George et al. 1982). However, a population in Shelby County, Tennessee, exhibits a highly variable karyotype with $2N = 34-41$ and $FN = 41-45$ (Beck et al. 1991; Elrod 1992; Elrod et al. 1996; George et al. 1982). Based on study of G-banded chromosomes, Qumsiyeh et al. (1997) reported that this variability could be accounted for by five Robertsonian translocations (Genoways and Choate 1998). A detailed diagnosis of other features of the species was published by Genoways and Choate (1998).

Blarina carolinensis carolinensis (Bachman 1837)

1837. *Sorex carolinensis* Bachman. Some remarks on the genus *Sorex*, with a monograph of the North American species. *Journal of the Academy of Natural Sciences of Philadelphia* 7(2):366.

Neotype.—NMNH 574157, adult male skin and skull, from beside Awendaw Creek, 3.2 km E Awendaw Post Office, Charleston Co., South Carolina. Obtained on 27 July 1989 by C. O. Handley, Jr., and M. Varn (Handley and Varn 1994).

Distribution.—Gulf and Atlantic Coastal Plain, including all or parts of the following states: Alabama, Arkansas, Florida, Georgia, Mississippi, North Carolina, South Carolina, and Virginia (Genoways and Choate 1998).

Comparisons.—This subspecies is intermediate in size for the three subspecies currently recognized

in *Blarina carolinensis*. It is larger than *B. c. minima* but smaller than *B. c. peninsulae*, as described herein. However, all external and cranial measurements show overlap among the subspecies. The only karyotype yet reported for this subspecies in Florida was $2N = 46$ and $FN = 44$ (George et al. 1982).

Specimens examined.—FLORIDA. Alachua Co.: 8 mi NW Gainesville, 2 (UF); Fort Clark, 1 (UF); Gainesville, 1 (UF); E Side of Lake Alice, 1 (UF); University [of Florida] Campus, 1 (UF). Citrus Co.: Crystal River State Preserve, 1 (UF). Escambia Co.: Pensacola, 1 (AMNH). Gadsden Co.: Chattahoochee, 1 (AMNH). Leon Co.: 11 mi NE Tallahassee, 1 (AMNH); 1 mi N Tallahassee, 1 (FSUM); Holland, 1 (CM); St. Mark's River, Natural Bridge, 10 mi SE Tallahassee, 2 (AMNH). Marion Co.: Eureka Dam, 2 (UF); Fort McCoy, 1 (UF); Shady, 3 (UF); Dunnellon, 1 (UF); 0.5 mi S, 4 mi E Dunnellon, 1 (UF). Nassau Co.: Amelia Island, 2 (AMNH). Santa Rosa Co.: Blackwater State Forest, 1 (UGAMNH). Taylor Co.: Encanjina [= Encanfina] River, 4 mi N of mouth, 1 (UF). Wakulla Co.: Panacea Unit, St. Mark's National Wildlife Refuge, 1 (AMNH); Spring Creek, 1 (UF).

SOUTH CAROLINA. Aiken Co.: 2 mi N, 1.5 mi W Jackson, 1 (MHP); Savannah River Plant, Bullfrog Pond, 12 (UGAMNH); Savannah River Plant, Linda Pond, 2 (UGAMNH); Savannah River Plant, Rainbow Bay, 1 (UGAMNH); Savannah River Plant, Sun Bay, 4 (UGAMNH).

Blarina carolinensis peninsulae Merriam 1895

1895. *Blarina carolinensis peninsulae* Merriam. Revision of the shrews of the American genera *Blarina* and *Notiosorex*. *North American Fauna* 10:14.

Holotype.—NMNH 70874, adult male, from Miami River, Dade Co., Florida. Obtained on 2 March 1895 by J. A. Loring.

Distribution.—Confined to Florida, primarily in peninsular parts of the state, excepting the southwestern coast.

Comparisons.—This is the largest of the three subspecies currently recognized in the species. It averages

slightly larger than the geographically adjacent *B. c. carolinensis* in all cranial measurements except length of molariform toothrow and breadth of zygomatic plate (Table 1). However, all external and cranial measurements exhibit extensive overlap. Based on specimens from Dade and Highlands counties, *B. c. peninsulae* has a unique karyotype with $2N = 50-52$ and $FN = 52$ (George et al. 1982). If the distinctively different karyotypes of *carolinensis* and *peninsulae* hold up across Florida, it should be possible to distinguish the taxa by this criterion alone.

Specimens examined.—FLORIDA. Alachua Co.: 7 mi N, 7 mi E Gainesville, 1 (UF); Gainesville, 5 mi towards Waldo, 1 (UF); Grace's Crossing, 3 (UF); Gainesville, 3 (UF); Gainesville, Payne's Prairie, 1 (UF); 0.5 mi N Paradise, 1 (UF); Tiger Bay, 1 (UF); Micanopy, 1 (UF); no locality specified, 3 (UF). Baker Co.: Glen St. Mary, 1 (AMNH). Citrus Co.: Crystal River State Preserve, 1 (UF); Homasassa Springs, 11 (6 AMNH, 5 UF); 1 mi SW Homasassa Springs, 1 (AMNH). Collier Co.: Deep Lake [$26^{\circ}02'32''N$, $81^{\circ}20'39''W$], 1 (AMNH); 4.5 mi E Royal Palm [= Royal Palm Hammock; site of settlement is at $25^{\circ}59'38''N$, $81^{\circ}35'31''W$], 1 (KU). Dade Co.: 22 mi W Miami, 1 (KU); 21 mi W Miami, 2 (KU); 20 mi W Miami, 1 (KU); 19 mi W Miami, 1 (KU); 15 mi W Miami, 2 (KU); 15 mi W Miami, Bird Road and Palmetto Drive, 1 (KU); Miami, 2 (AMNH); 4 mi W Kendall, 2 (KU); 1 mi W Chekika SRA, 27 (24 CM, 3 MHP); Everglades National Park, 1 (UF); Everglades National Park, Island 1, 1 (KU); Everglades National Park, Island 6, 3 (KU). De Soto Co.: 9.75 mi NW Arcadia, 1 (AMNH); 7.5 mi NW Arcadia, 1 (AMNH). Highlands Co.: 4 mi N Lake Placid, 1 (AMNH); Estates Highlands Park [=Highlands Park Estates], 4.5 mi NE Lake Placid, 1 (AMNH); Lake Placid, 1 (CM); 6 mi S Lake Placid, 12 (8 AMNH, 3 CM, 1 MHP); Archbold Biological Station, 8 mi S Lake Placid, 129 (AMNH); Archbold Biological Station, Red Hill, 10 mi S Lake Placid, 3 (AMNH). Hillsborough Co.: no locality specified, 5 (UF). Indian River Co.: 3 mi N Vero Beach, 8 (3 AMNH, 5 UF); Vero Beach, 2 (UF); ICSM, 10 (UF); ICSM 06-001, 17 (UF); no specific locality, 1 (UF). Lee Co.: 9 mi E Fort Myers, 1 (UF). Manatee Co.: 9.5 mi S Myakka City, 1 (AMNH). Marion Co.: Fort McCoy, 1 (UF); Lynn, 2 (UF); 0.5 mi S, 4 mi E Dunnellon, 3 (UF). Martin Co.: Jonathan Dickinson State Park, 2 (UF). Orange Co.: Wekiva Springs State Park, 1 (UF);

Christmas, Tosahatchee [= Tosohatchee] State Preserve, 1 (UCF). Osceola Co.: Kissimmee, 1 (AMNH). Pinellas Co.: no locality specified, 3 (UF). Polk Co.: near Winterhaven, 2 (CM). Putnam Co.: 3 mi E Melrose, 1 (UF); Ordway Preserve, 1 (UF); Ordway Preserve, One Shot Pond, 1 (UF); Welaka, 4 (UF); Welaka Reserve, 2 (UF). Sarasota Co.: Osprey, 1 (UF). St. Johns Co.: Anastasia Island, 1 (AMNH).

Blarina shermani Hamilton 1955

1955. *Blarina brevicauda shermani* Hamilton. A new subspecies of *Blarina brevicauda* from Florida. Proceedings of the Biological Society of Washington 68:37.

Holotype.—Cornell University Mammal Collection 8026, adult female, from 2 mi N Fort Myers, Lee Co., Florida. Obtained on 13 February 1954 by W. J. Hamilton, Jr.

Distribution.—Confined to the southwestern coast of Florida from just north of Fort Myers to the vicinity of Royal Palm (the latter based on the existence of a possible hybrid).

Diagnosis.—The two most diagnostic features of this species are its size and color. External and cranial size of *B. shermani* are about intermediate for the genus but are larger than in other taxa of *Blarina* in Florida. As noted by Hamilton (1955:37), "The dark pelage, without a trace of brown, combined with the larger size, both in body proportions and skull, serves to distinguish this *Blarina* from other Florida races." The karyotype of *B. shermani* is not known, and no other genetic data are available for the species.

Comparisons.—This species comes into geographic contact with only one other taxon of *Blarina*, *B. carolinensis peninsulae*, from which it can be distinguished by its larger size and slightly darker color (Hamilton 1955). Its relationship with *B. brevicauda* awaits further study.

Specimens examined.—FLORIDA. Collier Co.: 4.5 mi E Royal Palm [= Royal Palm Hammock; $25^{\circ}59'38''N$, $81^{\circ}35'31''W$], 1 (KU). Lee Co.: 2 mi N Fort Myers, 18 (1 AMNH, 14 CUVC, 2 NMNH, 1 UF).

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LITERATURE CITED

- Bachman, J. 1837. Some remarks on the genus *Sorex*, with a monograph of North American species. *Journal of the Academy of Natural Sciences of Philadelphia* 7:262-402.
- Baker, R. J., and J. W. Bickham. 1986. Speciation by monobrachial centric fusions. *Proceedings of the National Academy of Science, USA* 83:8245-8248.
- Barton, N. H., and G. M. Hewitt. 1985. Analysis of hybrid zones. *Annual Review of Ecology and Systematics* 16:113-148.
- Beck, M. L., C. J. Biggers, and J. A. Huggins. 1991. Variation in chromosome number in the southern short-tailed shrew *Blarina carolinensis*. *Mammalia* 55:623-625.
- Benedict, R. A. 1997. Morphological and genetic analyses of a hybrid zone between short-tailed shrews (*Blarina*) in Nebraska. Ph.D. dissertation, University of Nebraska-Lincoln.
- Benedict, R. A. 1999a. Morphological and mitochondrial DNA variation in a hybrid zone between short-tailed shrews (*Blarina*) in Nebraska. *Journal of Mammalogy* 80:112-134.
- Benedict, R. A. 1999b. Characteristics of a hybrid zone between two species of short-tailed shrews (*Blarina*). *Journal of Mammalogy* 80:135-141.
- Bole, B. P., Jr., and P. N. Moulthrop. 1942. The Ohio Recent mammal collection in the Cleveland Museum of Natural History. *Scientific Publication, Cleveland Museum of Natural History* 5:83-181.
- Bowles, J. B. 1975. Distribution and biogeography of mammals of Iowa. *Special Publications of the Museum, Texas Tech University* 9:1-184.
- Braun, J. K., and M. L. Kennedy. 1983. Systematics of the genus *Blarina* in Tennessee and adjacent areas. *Journal of Mammalogy* 64:414-425.
- Choate, J. R. 1972. Variation within and among populations of short-tailed shrews in Connecticut. *Journal of Mammalogy* 53:116-128.
- Ellis, L. S., V. E. Diersing, and D. F. Hoffmeister. 1978. Taxonomic status of short-tailed shrews (*Blarina*) in Illinois. *Journal of Mammalogy* 59:305-311.
- Elrod, D. A. 1992. Genetic studies of *Odocoileus virginianus* and *Blarina carolinensis*: I. Temporal assessment of genetic variability in a population of white-tailed deer (*Odocoileus virginiana*); II. Chromosomal variation in the southern short-tailed shrew (*Blarina brevicauda*). M. S. thesis, Memphis State University, Memphis, Tennessee.

- Elrod, D. A., M. L. Beck, and M. L. Kennedy. 1996. Chromosomal variation in the southern short-tailed shrew (*Blarina carolinensis*). *Genetica* 98:199-203.
- Endler, J. A. 1977. Geographic variation, speciation, and clines. Princeton University Press, Princeton, New Jersey.
- French, T. W. 1981. Notes on the distribution and taxonomy of short-tailed shrews (genus *Blarina*) in the Southeast. *Brimleyana* 6:101-110.
- Genoways, H. H., and J. R. Choate. 1972. A multivariate analysis of systematic relationships among populations of short-tailed shrews (genus *Blarina*) in Nebraska. *Systematic Zoology* 21:106-116.
- Genoways, H. H., and J. R. Choate. 1998. Natural history of the southern short-tailed shrew, *Blarina carolinensis*. Occasional Papers of the Museum of Southwestern Biology, University of New Mexico 8:1-43.
- Genoways, H. H., J. C. Patton III, and J. R. Choate. 1977. Karyotypes of shrews of the genera *Cryptotis* and *Blarina* (Mammalia: Soricidae). *Experientia* 33:1294-1295.
- George, S. B., J. R. Choate, and H. H. Genoways. 1981. Distribution and taxonomic status of *Blarina hyllophaga* Elliot (Insectivora: Soricidae). *Annals of the Carnegie Museum* 50:493-513.
- George, S. B., J. R. Choate, and H. H. Genoways. 1986. *Blarina brevicauda*. *Mammalian Species* 261:1-9.
- George, S. B., H. H. Genoways, J. R. Choate, and R. J. Baker. 1982. Karyotypic relationships within the short-tailed shrews, genus *Blarina*. *Journal of Mammalogy* 63:639-645.
- Graham, R. W., and H. A. Semken. 1976. Paleocological significance of the short-tailed shrew (*Blarina*), with a systematic discussion of *Blarina ozarkensis*. *Journal of Mammalogy* 57:433-449.
- Hall, E. R. 1981. The mammals of North America. John Wiley & Sons, New York.
- Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. Ronald Press Company, New York.
- Hamilton, W. J., Jr. 1955. A new subspecies of *Blarina brevicauda* from Florida. *Proceedings of the Biological Society of Washington* 68:37-39.
- Handley, C. O., Jr., and M. Varn. 1994. Identification of the Carolinian shrews of Bachman 1837. Pp. 393-406 in *Advances in the biology of shrews* (J. F. Merritt, G. L. Kirkland, Jr., R. K. Rose, eds.). Special Publication, Carnegie Museum of Natural History 18:1-458.
- Hewitt, G. M. 1989. Hybrid zones: Natural laboratories for evolutionary studies. *Trends in Ecology and Evolution* 3:158-167.
- Jones, C. A., J. R. Choate, and H. H. Genoways. 1984. Phylogeny and paleobiogeography of short-tailed shrews (genus *Blarina*). Pp. 56-148 in *Contributions in Quaternary vertebrate paleontology: A volume in memorial to John E. Guilday* (H. H. Genoways and M. R. Dawson, eds.). Special Publication, Carnegie Museum of Natural History 8:1-538.
- Key, K. H. L. 1968. The concept of stasipatric speciation. *Systematic Zoology* 17:14-22.
- Key, K. H. L. 1974. Speciation in Australian morabine grasshoppers—taxonomy and ecology. Pp. 43-56 in *Genetic mechanisms of speciation in insects* (M. J. D. White, ed.). Australia and New Zealand Book Company Sydney, Australia.
- Key, K. H. L. 1982. Species, parapatry, and the morabine grasshoppers. *Systematic Zoology* 30:425-458.
- Laerm, J., L. E. Logan, M. E. McGhee, and H. N. Neuhauser. 1981. Annotated checklist of the mammals of Georgia. *Brimleyana* 7:121-135.
- Layne, J. N. 1992. Sherman's short-tailed shrew, *Blarina carolinensis shermani*. Pp. 328-334 in *Rare and endangered biota of Florida. Volume 1* (S. R. Humphrey, ed.). University Press of Florida, Gainesville.
- Lee, M. R., and E. G. Zimmerman. 1969. Robertsonian polymorphism in the cotton rat, *Sigmodon fulviventer*. *Journal of Mammalogy* 50:333-339.
- Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill, New York.
- Merriam, C. H. 1895. Revision of the shrews of American genera *Blarina* and *Notiosorex*. *North American Fauna* 10:1-34.
- Meylan, A. 1967. Formules chromosomiques et polymorphisme Robertsonian chez *Blarina brevicauda* (Say) (Mammalia: Insectivora). *Canadian Journal of Zoology* 45:1119-1127.

- Moncrief, N. D., J. R. Choate, and H. H. Genoways. 1982. Morphometric and geographic relationships of short-tailed shrews (genus *Blarina*) in Kansas, Iowa, and Missouri. *Annals of the Carnegie Museum* 51:157-180.
- Norusis, M. J. 1991. SPSS/PC+ studentware plus, Version 1.0. SPSS Inc., Chicago, Illinois.
- Qumsiyeh, M. B., J. L. Coate, J. A. Peppers, P. K. Kennedy, and M. L. Kennedy. 1997. Robertsonian chromosomal rearrangements in the short-tailed shrew, *Blarina carolinensis*, in western Tennessee. *Cytogenetics and Cell Genetics* 76:153-158.
- Rieseberg, L. H. 2001. Chromosomal rearrangements and speciation. *Trends in Ecology and Evolution* 16:351-358.
- SAS Institute. 1991. The SAS system for Windows, Release 6.11. SAS Institute Inc., Cary, North Carolina.
- Stangl, F. B., Jr., and C. B. Carr. 1997. Status of *Blarina hylophaga* (Insectivora: Soricidae) in North Texas and southern Oklahoma. *Texas Journal of Science* 49:159-162.
- Tate, C. M., J. F. Pagels, and C. O. Handley, Jr. 1980. Distribution and systematic relationship of two kinds of short-tailed shrews (Soricidae: *Blarina*) in south-central Virginia. *Proceedings of the Biological Society of Washington* 93:50-60.
- Turelli, M., N. H. Barton, and J. A. Coyne. 2001. Theory and speciation. *Trends in Ecology and Evolution* 16:330-343.
- Webb, S. D. 1974. Chronology of Florida Pleistocene mammals. Pp. 5-31 in *Pleistocene mammals of Florida* (S. D. Webb, ed.). University Press of Florida, Gainesville.
- Webster, W. D. 1996. Geographic variation in *Blarina brevicauda* (Insectivora: Soricidae) from eastern North Carolina, with description of a new subspecies. Pp. 47-56 in *Contributions in mammalogy: A memorial volume honoring Dr. J. Knox Jones, Jr.* (H. H. Genoways and R. J. Baker, eds.). Museum of Texas Tech University, Lubbock.
- White, M. J. D. 1968. Models of speciation. *Science* 159:1065-1070.
- White, M. J. D., R. E. Blackith, R. M. Blackith, and J. Cheney. 1967. Cytogenetics of the viatica group of morabine grasshoppers. II. The "coastal" species. *Australian Journal of Zoology* 15:263-302.
- Woods, C. A. 1992. Florida saltmarsh vole, *Microtus pennsylvanicus dukecampbelli*. Pp. 131-139 in *Rare and endangered biota of Florida. Volume 1* (S. R. Humphrey, ed.). University Press of Florida, Gainesville.
- Woods, C. A., W. Post, and C. W. Kilpatrick. 1982. *Microtus pennsylvanicus* (Rodentia: Muridae) in Florida: A Pleistocene relict in a coastal saltmarsh. *Bulletin of the Florida State Museum, Biological Science* 28:25-52.

Addresses of authors:

RUSSELL A. BENEDICT

812 University Street
Central College
Pella, IA 50219
benedictr@central.edu

HUGH H. GENOWAYS

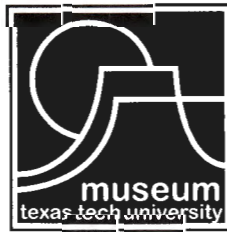
University of Nebraska State Museum
and School of Natural Resource Sciences
W436 Nebraska Hall
University of Nebraska-Lincoln
Lincoln, NE 68588
hgenoway@unl.edu

JERRY R. CHOATE

Sternberg Museum of Natural History
Fort Hays State University
Hays, KS 67601
jchoate@fhsu.edu

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