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Taxonomy of Short-Tailed Shrews (Genus *Blarina*) in Florida

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

RUSSELL A. BENÉDICT, HUGH H. GENDORS, AND JERRY R. CROATE

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 renauleses 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 1999a).

These studies prompted several investigators to reevaluate taxonomic relationships within the genus. Based on morphometric (Benedict 1999a; Basar and Kennedy 1983; Ellis et al. 1978; French 1981; George et al. 1982; 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. rexlandsteeri 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 in far north as Illinois (Genoways and Choate 1998). Elliot’s short-tailed shrew (B. hylaphaga) 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. hylaphaga 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 reassess taxonomic relationships between B. c. shermani and B. c. peninsulare 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,
We recorded eight cranial measurements, selected from those used by Choate (1972), Genoways and Choate (1972), Tate et al. (1980), George et al. (1981), Moncreif 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 toothrow, 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).

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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).

Reference samples of the three taxa differed in size (Table I). The nominal taxon peninsulae averaged 7.8% larger than carolinensis 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 toothrow 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>
<thead>
<tr>
<th>Trait</th>
<th>X</th>
<th>SD</th>
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<th>SD</th>
<th>range</th>
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<tr>
<td>OCPM</td>
<td>18.87</td>
<td>0.35</td>
<td>18.31-19.60</td>
<td>20.63</td>
<td>0.35</td>
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<td>MOLAR</td>
<td>5.25</td>
<td>0.10</td>
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<td>5.57</td>
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<td>5.34-5.77</td>
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<td>0.33</td>
<td>9.01-10.50</td>
<td>10.60</td>
<td>0.26</td>
<td>10.13-11.02</td>
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<tr>
<td>ZYGPL</td>
<td>2.31</td>
<td>0.12</td>
<td>2.13-2.54</td>
<td>2.51</td>
<td>0.12</td>
<td>2.30-2.71</td>
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<td>0.17</td>
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<td>4.74-5.23</td>
<td>5.41</td>
<td>0.12</td>
<td>5.18-5.61</td>
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<td>HTMAN</td>
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<td>0.20</td>
<td>4.95-5.80</td>
<td>6.12</td>
<td>0.18</td>
<td>5.76-6.37</td>
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<td>0.08</td>
<td>1.86-2.14</td>
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<td>0.07</td>
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<td>shermani (n = 16)</td>
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<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>OCPM</td>
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<td></td>
<td></td>
<td>19.61</td>
<td>0.43</td>
<td>18.56-20.53</td>
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<tr>
<td>MOLAR</td>
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<td></td>
<td></td>
<td>5.19</td>
<td>0.14</td>
<td>4.80-5.48</td>
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<td>CRRTH</td>
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<td></td>
<td></td>
<td>10.28</td>
<td>0.28</td>
<td>9.69-10.97</td>
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<tr>
<td>ZYGPL</td>
<td></td>
<td></td>
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<td>2.17</td>
<td>0.16</td>
<td>1.80-2.52</td>
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<tr>
<td>MBXTH</td>
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<td>6.64</td>
<td>0.21</td>
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<td></td>
<td>5.17</td>
<td>0.18</td>
<td>4.82-5.71</td>
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<tr>
<td>HTMAN</td>
<td></td>
<td></td>
<td></td>
<td>5.59</td>
<td>0.16</td>
<td>5.15-5.93</td>
</tr>
<tr>
<td>ARBTH</td>
<td></td>
<td></td>
<td></td>
<td>1.99</td>
<td>0.10</td>
<td>1.39-2.29</td>
</tr>
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</table>

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 carolinensis, the average discriminant score was -194.50 for shermani (range =-187.42 to -199.92) and -172.79 for carolinensis (range =-163.83 to -182.82). Length of molariform toothrow, 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 wa =-27.17 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 >95.0%. 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 carolinensis, and 35 individuals could not be identified to taxa with a probability value >75.0%. The two specimens identified as carolinensis (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 20931), captured in Lee County about

bread, maxillary breadth, interorbital breadth, and height of mandible, and were significant at P=0.01 for breadth of zygomatic plate. Length of molariform toothrow and articular breadth did not differ between the two taxa (P=0.05).
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 *peninsulata* (n = 44).

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

<table>
<thead>
<tr>
<th>Measurement</th>
<th><em>carolinensis</em></th>
<th><em>peninsulata</em></th>
<th><em>shermani</em></th>
<th><em>shermani</em></th>
<th><em>peninsulata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Occipital-premaxillary length</td>
<td>-7.406 (-144.5)</td>
<td>-7.578 (-148.9)</td>
<td>-8.09 (-16.1)</td>
<td>-7.457 (-146.1)</td>
<td>-8.09 (-16.1)</td>
</tr>
<tr>
<td>Length of molariform toothrow</td>
<td>21.330 (111.1)</td>
<td>7.076 (38.3)</td>
<td>-12.886 (-67.1)</td>
<td>-7.457 (80.3)</td>
<td></td>
</tr>
<tr>
<td>Cranial breadth</td>
<td>0.497 (5.1)</td>
<td>7.120 (73.0)</td>
<td>7.744 (80.3)</td>
<td>7.744 (80.3)</td>
<td></td>
</tr>
<tr>
<td>Breadth of zygomatic plate</td>
<td>6.292 (14.0)</td>
<td>-9.264 (-22.3)</td>
<td>-15.562 (-35.2)</td>
<td>-14.619 (-34.6)</td>
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<tr>
<td>Maxillary breadth</td>
<td>-0.734 (-4.8)</td>
<td>-14.105 (-95.6)</td>
<td>-12.899 (-87.7)</td>
<td>-13.591 (-77.9)</td>
<td></td>
</tr>
<tr>
<td>Interorbital breadth</td>
<td>-9.033 (-46.1)</td>
<td>-3.899 (-20.1)</td>
<td>3.658 (19.2)</td>
<td>3.658 (19.2)</td>
<td></td>
</tr>
<tr>
<td>Height of mandible</td>
<td>-8.285 (-45.6)</td>
<td>-19.591 (-112.1)</td>
<td>-13.591 (-77.9)</td>
<td>-13.591 (-77.9)</td>
<td></td>
</tr>
<tr>
<td>Articular breadth</td>
<td>7.458 (34.6)</td>
<td>17.232 (35.3)</td>
<td>2.928 (5.9)</td>
<td>2.928 (5.9)</td>
<td></td>
</tr>
</tbody>
</table>

* Multiplier is number that an individual’s measurement is multiplied by to compute discriminant score.
* * 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% peninsulae, 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% peninsulae, 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% peninsulae and 10.9% shermani.

Comparison of carolinensis and peninsulae.—Discriminant scores of the reference samples of carolinensis and peninsulae did not overlap (Figure 2). The average discriminant score was -68.11 for carolinensis (range -64.17 to -73.19) and -79.71 for peninsulae (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 peninsulae, 38 were identified as peninsulae 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 peninsulae were 74.8, 64.6, 55.6, 45.1, 42.4, and 37.3%). The average probability value of peninsulae reference specimens was 92.4%.

Discriminant function analysis identified 217 of 281 unknowns as peninsulae and 25 as carolinensis. The remaining 29 could not be assigned to a taxon with certainty.
a probability -75.0%. Specimens with morphometric attributes of *peninsulae* were found 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 specimen 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 3.5% 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 2091) 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 2091 likely represents an atypical *peninsulae* rather than an intergrade between *peninsulae* and *shermani*. Our analyses also revealed that two specimens (NMNH 300000 and 300005) collected as part of the original type series but not included in our reference sample had probabilities 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 206680) 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 99.5% 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 (Woodes 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 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.
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 *peninsularis* 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 *peninsularis*. 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 *peninsularis* 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. peninsularis* 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 *peninsularis* (probability level 99.8%). South of this location in Citrus County, a sample of 11 specimens from Homassa Springs and one specimen from 1 mi SW Homassa Springs were available for analysis. Of these 12 specimens, six classified as *peninsularis* 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 *peninsularis* 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. peninsularis* except the one from Crystal River State Preserve, and we drew the line of contact between *carolinensis* and *peninsularis* 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, 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 peninsulae (UF 16855, 93.3%; 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 Wekiva, 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.

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. We assign 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 269338), which resembled *peninsulæ* with a probability level of 98.0%. The probability values of 99.6% and 88.1% of two specimens from Amelia Island, Nassau County, in the geographic range of *carolinensis* and a specimen from Anastasia Island, St. John’s County (AMNH 269294) resembled *peninsulæ* 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 *peninsulæ* with a probability value of 98.0%, in the geographic range of *peninsulæ*. Of two Amelia Island specimens, one resembled *carolinensis* (AMNH 240257, 97.6%) and the other (AMNH 240255) was intermediate (51.3% *carolinensis*, 48.7% *peninsulæ*). 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. peninsulæ* 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%, 80.3%, 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. c. 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. peninsulæ*.

In northern Florida, in the geographic range we ascribe to *B. c. carolinensis*, four specimens were misassigned to *peninsulæ*. These include individual specimens from Escambia (82.8%) and Gauley (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. peninsulæ*.

Contact Zones, the Fossil Record, and Karyotypic Variation in Blarinina. It is informative to compare the contact zone between *B. c. carolinensis* and *B. c. peninsulæ* 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 phena and possible hybrids. Based on these findings, they proposed that speciation between these two taxa had occurred through a stasispatric mechanism (Key 1968; White 1968; Whitt 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 analyses 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 F₁ individuals were present. The line of contact is a fairly straight line when viewed on a large scale but 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 structurint 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. brevicatrda* 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 morphometriccline 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 may be forming a parapatric model where a continuous population diverges into genetically distinct taxa across an 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 unicuspids 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 of many of the species is 2N = 46 and FN = 44 (George et al. 1986). 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)


Neotype.—NMNH 574157, adult male skin and skull, from beside Awendaw Creek, 3.2 km E of 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 (FSU); 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.: Encoquina [= En-confina] 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, Rainbow Bay, 1 (UGAMNH); Savannah River Plant, Sun Bay, 4 (UGAMNH).

*Blarina carolinensis peninsulae* Merriam 1895


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

Distribution.—Confinned to Florida, primarily in peninsular parts of the state, excepting the southwesterm 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 Duval and Highlands counties, B. c. peninsularis has a unique karyotype with 2N = 50-52 and FN = 52 (George et al. 1982). If the distinctively different karyotypes of carolinensis and peninsularis 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); Gainesville, 3 (UF); Gainesville, Payne’s Prairie, 1 (UF); 0.5 mi N Paradise, 1 (UF); Tiger Bay, 1 (UF); Micamy, 1 (UF); no locality specified, 3 (UF). Baker Co.: Glen St. Mary, 1 (AMNH). Citrus Co.: Crystal River State Preserve, 1 (UF); Homosassa Springs, 11 (6 AMNH, 5 UF); 1 mi SW Homosassa Springs, 1 (AMNH). Collier Co.: Deep Lake [26°02'32"N, 81°20'39"W], 1 (AMNH); 4.5 mi E Royal Palm [= Royal Palm Hammock; site of settlement is at 25°59'38"N, 81°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, 4 (AMNH); 4 mi W Kendall, 1 (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 E Fort Myers, 1 (UF). 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). 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, Tosohatchee [= Tosohatchee] State Preserve, 1 (UF); 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 Reserve, 1 (UF); Ordway Reserve, 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


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, serve[s] 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 peninsularis, 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°59'38"N, 81°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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