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Systematic Revision of the Northern Short-tailed Shrew, *Blarina brevicauda* (Say)

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Virginia Museum
of Natural History
Memoir 10

Systematic Revision of the Northern Short-tailed Shrew, *Blarina brevicauda* (Say)



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WM. DAVID WEBSTER, NANCY D. MONCRIEF,
JERRY R. CHOATE, AND HUGH H. GENOWAYS

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**Systematic Revision of the Northern
Short-tailed Shrew, *Blarina brevicauda* (Say)**

It's never finished... it's just published.

— Jerry R. Choate
21 March 1943 – 9 December 2009

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Short-tailed Shrew, *Blarina brevicauda* (Say)**

Wm. David Webster, Nancy D. Moncrief,
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Virginia Museum of
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Systematic Revision of the Northern Short-tailed Shrew, *Blarina brevicauda* (Say)

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Nancy D. Moncrief²,
Jerry R. Choate^{3*},
Hugh H. Genoways⁴

Short-tailed shrews, genus *Blarina*, are common inhabitants of a variety of terrestrial habitats in most of eastern North America. Of the 4 species currently recognized, the northern short-tailed shrew, *Blarina brevicauda* (Say, 1823), is the most widely distributed, occurring from southern Canada southward to the central Great Plains and the Appalachian Mountains into Georgia and Alabama and along the East Coast as far south as southeastern North Carolina. It has been more than 65 years since geographic variation within this species has been studied. Accordingly, the objectives of this study were to examine geographic variation in *Blarina brevicauda* and to revise its intraspecific taxonomy as needed.

A total of 12,390 Holocene specimens of *Blarina brevicauda* from throughout the geographic range of the species and the fossil material of *Blarina fossilis*, *B. ozarkensis*, and *B. simplicidens* were examined during the course of this study. Nine cranial and mandibular measurements were taken from 2,736 Holocene specimens, which were grouped into 114 operational taxonomic units (OTUs) for statistical analysis. We used a single classification ANOVA to test for significant differences among means of OTUs and a principal component analysis (PCA) to extract eigenvectors and generate a 2-dimensional plot of OTUs.

Our analysis demonstrates that *B. brevicauda* consists of 7 well-defined subspecies. Two subspecies, the large-bodied *B. b. brevicauda* and the medium-sized *B. b. talpoides*, occupy almost the entire geographic range of the species, with restricted gene flow between these 2 subspecies where their geographic ranges abut in the vicinity of the Mississippi River and its valley. The other 5 subspecies occupy small to modest geographic ranges at the periphery of the range of the species and in isolated geographic areas—an undescribed subspecies on the Cumberland Plateau in Tennessee and adjacent

Kentucky, *B. b. knoxjonesi* along the southeastern coast of North Carolina, another undescribed subspecies on the southern two-thirds of the Delmarva Peninsula, *B. b. aloga* on Martha's Vineyard and Nantucket Island, and a third undescribed subspecies in the Kaw River Valley in northeastern Kansas. In each of these geographic areas, gene flow has been stopped or greatly restricted. We have chosen to recognize these 7 subspecies because we believe that each has begun to follow its own evolutionary path. These taxa are arranged in a geographic configuration that fits the pattern termed centrifugal speciation, or the development of small isolated peripheral and sometimes relictual populations as the parent taxon undergoes normal population expansion and contraction cycles. The fact that at least 3 of these peripheral populations are now partially in contact with the parental populations and have not been swamped out genetically indicates to us that they are adapting to their local conditions and are able to maintain their genetic identities. Our morphological data and mitochondrial DNA analyses by other workers indicate that these peripheral subspecies, with the possible exception of the 1 along the Kaw River valley, are derived from *B. b. talpoides*. These data also indicate that *B. b. brevicauda* and *B. b. talpoides* are semi-species.

INTRODUCTION

Short-tailed shrews, genus *Blarina*, are common inhabitants of a variety of terrestrial habitats in most of eastern North America. Historically, extant short-tailed shrews were placed in 2 species (Hall, 1981; Merriam, 1895)—*B. brevicauda* (Say), considered to be wide-ranging and polytypic, and *B. telmalestes* Merriam, thought to be confined to the Great Dismal Swamp region of southeastern Virginia and northeastern North Carolina. Three nominal fossil taxa—*B. fossilis*, *B.*

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ozarkensis, and *B. simplicidens*—also were recognized (Brown, 1908; Cope, 1899; Hibbard, 1943). More recently, beginning in 1972 (Genoways and Choate, 1972), 3 modern populations within *B. brevicauda* have been recognized as separate species—*B. carolinensis*, *B. hylophaga*, and *B. shermani* (Benedict et al., 2006; Genoways and Choate, 1972; Genoways et al., 1977; George et al., 1981, 1982, 1986; Jones et al., 1984; Moncrief et al., 1982). Also, *B. telmalestes* has been placed in the synonymy of *B. brevicauda* (George et al., 1986; Handley, 1979; Webster, 1996). Finally, the 3 nominal fossil taxa have been placed in the synonymy of *B. brevicauda* (Jones et al., 1984), leaving a total of 4 species of *Blarina* (Benedict et al., 2006).

The 4 species of *Blarina* exhibit geographic parapatry and interspecific relationships unlike those of most other closely related species of mammals, possibly because they underwent speciation as a result of chromosomal changes (George et al., 1982) rather than selection for unique morphological characters. Therefore, the 4 species are extremely similar to each other in external appearance, and they exhibit few morphological differences other than size, although they have different karyotypes (Genoways et al., 1977; George et al., 1982). Populations of *B. brevicauda* are characterized by the karyotype of $2N = 48-50$ and $FN = 48$, with the variation being attributable to a Robertson fission/fusion. The karyotype of *B. shermani* is not known. The karyotype of *B. hylophaga* populations is $2N = 52$ and $FN = 60-62$, whereas that of *B. carolinensis* is $2N = 46$ and $FN = 48$ throughout most of its geographic distribution, but $2N = 50-52$ and $FN = 52$ in *B. c. peninsulae* and $2N = 31-41$ and $FN = 41-45$ in *B. c. minima* in southwestern Tennessee (Beck et al., 1991; Elrod et al., 1996; Genoways et al., 1977; George et al., 1982; Qumsiyeh et al., 1997, 1999; M. L. Kennedy, pers. comm.). In addition, recent molecular and parasite studies have demonstrated monophyly of the genus *Blarina* and monophyly of the species *B. brevicauda*, *B. hylophaga*, and *B. carolinensis* (Benedict, 1999a; Brant and Ortí, 2002, 2003b). Moreover, analyses of the cytochrome-*b* and 16S rRNA mitochondrial DNA (mtDNA) genes have revealed 2 well-differentiated and reciprocally monophyletic east-west clades of *B. brevicauda*, separated by the Mississippi River (Brant and Ortí, 2002). The eastern clade consists of 2 subclades: 1 centered in the Ohio River and Great Lakes region and the other extending north to south along the Appalachian Mountains and East Coast (Brant and Ortí, 2003a).

Of the 4 species currently recognized, the northern short-tailed shrew, *Blarina brevicauda* (Say, 1823), is

the most widely distributed, occurring in bogs, swamps, grasslands, and coniferous and deciduous woodlands from southern Canada southward to the central Great Plains and the Appalachian Mountains into northern Georgia and Alabama (George et al., 1986; Trani et al., 2007) and along the East Coast as far south as southeastern North Carolina (Webster et al., 1985, 1996). In agricultural areas of the Great Plains, northern short-tailed shrews are confined mostly to riparian or otherwise mesic habitats and to grassy roadsides and fence rows in which ground cover and leaf litter are present (George et al., 1986, and references cited therein). Although *B. brevicauda* is ubiquitous over much of its geographic range, local distribution apparently is limited by moisture, temperature, and friability of the soil. Ground cover also is important, especially when vegetation is sparse. Northern short-tailed shrews seldom are found in areas where the moisture content of the soil is insufficient to keep the litter saturated (George et al., 1986, and references cited therein).

Several studies (e.g., Benedict et al., 2006; Braun and Kennedy, 1983; Ellis et al., 1978; French, 1981; Genoways and Choate, 1972; Jones and Findley, 1954; Moncrief et al., 1982; Rippey, 1967; Tate et al., 1980; Webster, 1996) included regional samples of short-tailed shrews to define characteristics of local populations and to identify contact zones between species on the local level, but no recent study has examined morphologic variation throughout the entire geographic range of *B. brevicauda*. The most recent study that examined geographic variation throughout the range of *B. brevicauda* was conducted by Bole and Moulthrop (1942) before the modern arrangement of species was recognized. They recognized 12 subspecies of *B. brevicauda* in the United States and Canada and *B. telmalestes* in the Great Dismal Swamp of southeastern Virginia and northeastern North Carolina. Twelve subspecies of *B. brevicauda* currently are recognized (Hall, 1981; George et al. 1986; Webster 1996) within the restricted geographic range of the species, which includes *B. b. telmalestes* Merriam, 1895, reflecting the notable variation in size exhibited by this species (Fig. 1). Because it has been more than 65 years since geographic variation within *B. brevicauda* has been studied, and because confusion exists as to the status of several nominal taxa in the genus *Blarina*, we judged that an intensive study of geographic variation was needed. Accordingly, the objectives of this study were 1) to examine morphologic and morphometric variation in *B. brevicauda* throughout its geographic range, 2) to relate that variation to geographic location, and 3) to revise the intraspecific taxonomy of this species.

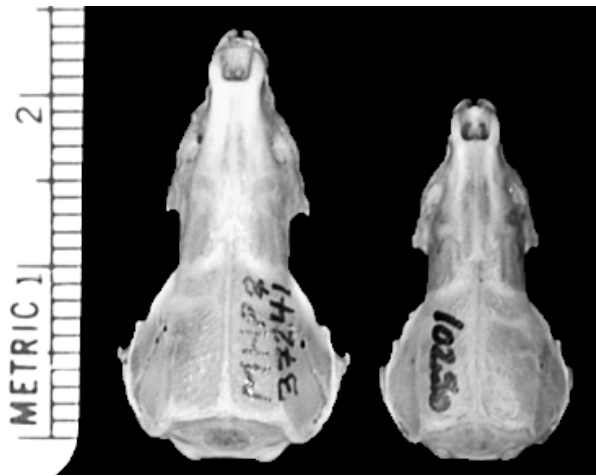


Fig. 1. Dorsal view of crania of *Blarina brevicauda brevicauda* (left, MHP 37241) and an undescribed taxon from the Cumberland Plateau of Tennessee (right, OMNH 37146, formerly UM 10250), demonstrating size variation in the species.

MATERIALS AND METHODS

A total of 12,390 Holocene specimens of *B. brevicauda* from throughout the geographic range of the species and from near the type locality of each nominal subspecies (Anderson, 1947; Hall, 1981; Webster, 1996) were examined during the course of this study. In addition, we examined the fossil material of *B. fossilis* (Pleistocene locality #5, Rezabek gravel pit, Irvingtonian Mammal Age, Lincoln County, Kansas, $n = 1$), *B. ozarkensis* (Conard Fissure, Irvingtonian Mammal Age, Newton County, Arkansas, $n =$ approximately 150), and *B. simplicidens* (Port Kennedy Cave, Irvingtonian Mammal Age, Montgomery County, Pennsylvania, $n = 1$). Only individuals with complete sets of cranial and mandibular measurements ($n = 2,736$) were used in the statistical analyses of geographic variation. For each individual, 9 cranial and mandibular measurements (Fig. 2) were taken with dial or digital calipers to the nearest 0.1 mm as described by Choate (1972): occipito-premaxillary length, P⁴-M³ length, maxillary breadth, width of zygomatic plate, interorbital breadth, cranial breadth, mandibular length, mandibular height, and articular width.

Specimens were assigned to age classes on the basis of amount of wear to teeth and condition of pelage (Choate, 1972). The sex of each animal was recorded from the specimen tag; however, it is likely that the sex of many museum specimens is reported incorrectly. No consistent pattern of significant differences among age and sex classes in *Blarina* has been reported (Choate, 1972; Moncrief et al., 1982). We performed a preliminary 2-way analysis of variance (ANOVA) to test for age and

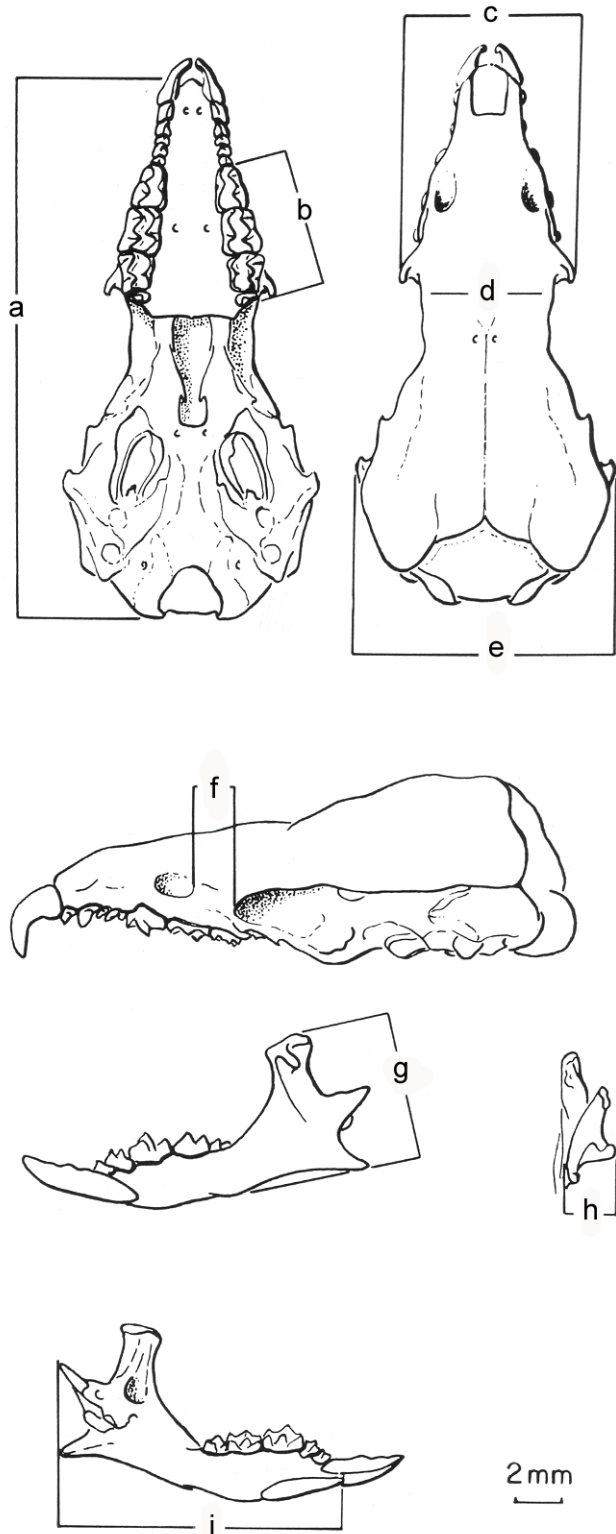


Fig. 2. Cranial and mandibular characters measured for this study were: a) occipito-premaxillary length; b) P⁴-M³ length; c) maxillary breadth; d) interorbital breadth; e) cranial breadth; f) width of zygomatic plate; g) mandibular height; h) articular width; and i) mandibular length.

sex differences in a sample of 322 *B. brevicauda* from Tompkins County, New York (operational taxonomic unit [OTU] 89). These analyses revealed no pattern of significant differences among age and sex classes; therefore, we pooled all age and sex classes for statistical analyses in this study.

Specimens were grouped by county, and sometimes specimens from proximate counties were pooled to insure adequate sample sizes from localities throughout the entire range of the species (Fig. 3, Appendix 1). For each OTU, standard statistics (mean, standard deviation, range, and coefficient of variation) were computed for each mensural character. We used a single classification ANOVA (*F*-test, significance level 0.05) to test for significant differences among means of OTUs. When means were significantly different, a Duncan's multiple-range test was used to determine maximally non-significant subsets. A principal components analysis

(PCA) was performed by deriving a product-moment correlation matrix from variance-standardized character means for each OTU, extracting eigenvectors, and generating a 2-dimensional plot of OTUs.

In addition, we used the sagittal and lambdoidal crests, pelage coloration, and dental pigmentation as qualitative characters in describing geographic variation, although the character states for these characters are not described in detail. The cranial crests develop as an individual matures, but even specimens of apparently the same age from widely separated regions of the eastern United States exhibit patterns of geographic variation in the development of the sagittal and lambdoidal crests that appear to be phylogenetically meaningful. Pelage coloration and the amount of contrast between dorsal and ventral pigmentation have been used in past taxonomic studies of *Blarina* (Anderson, 1943, 1947; Bole and Moulthrop, 1942; Handley and Varn, 1994;

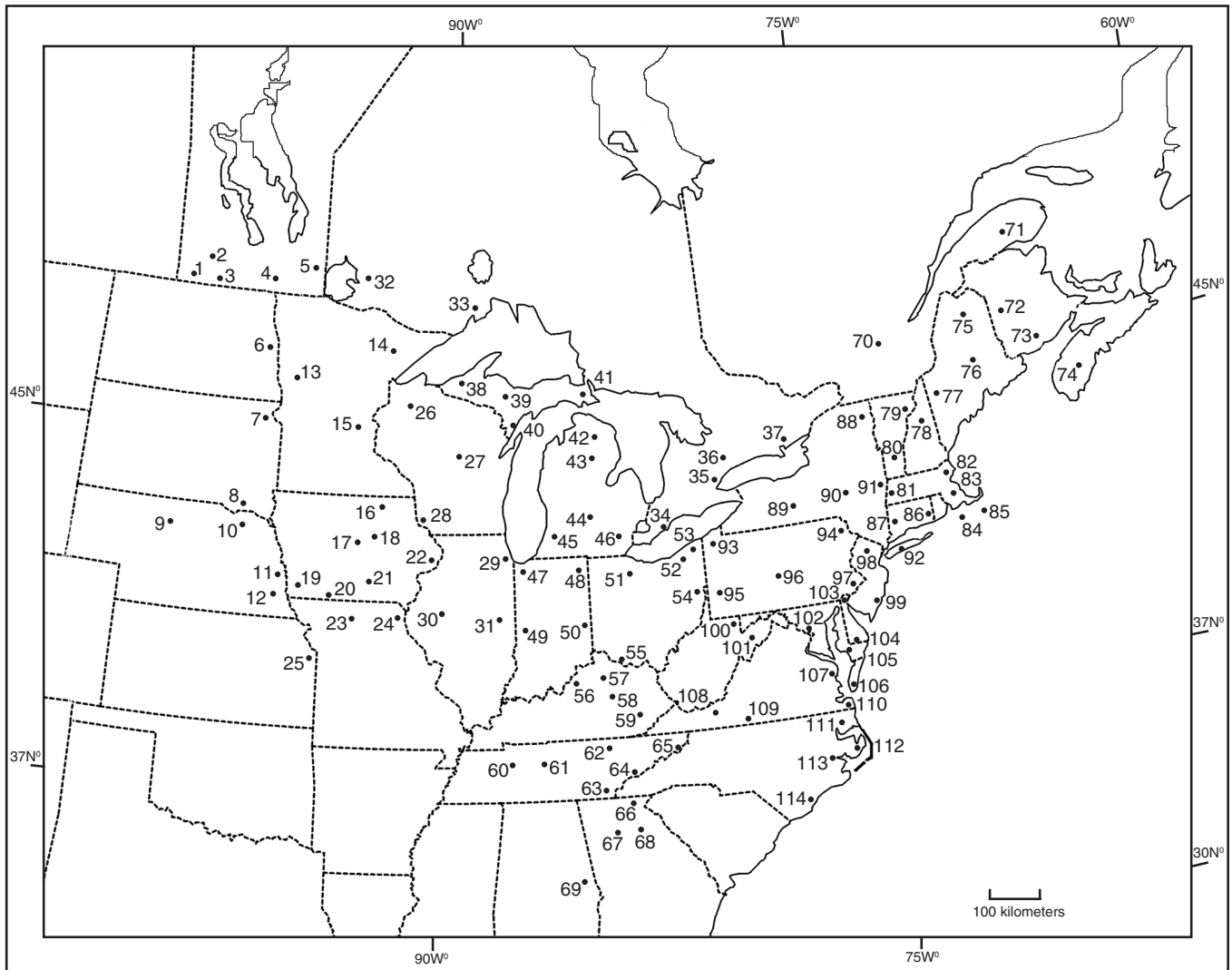


Fig. 3. Geographic distribution of operational taxonomic units (OTUs) of *Blarina brevicauda* used in this study. See Appendix 1 for OTU localities.

Merriam, 1895; Smith, 1940; Webster, 1996), and it was appropriate to use them here. Likewise, the amount of dental pigmentation has been shown to have some taxonomic usefulness in *Blarina* (Bole and Moulthrop, 1942; Merriam, 1895; Webster, 1996), although it seems to vary nongeographically more than geographically in Palearctic *Sorex* (Dannelid, 1994). Dental pigmentation results from the deposition of iron to harden the enamel, and the iron concentration varies predictably among cusps and teeth in *B. brevicauda* (Strait and Smith, 2006), which suggests that it is under genetic control and therefore might be a useful character in assessing geographic variation. Indeed, Webster (1996) found significant variation in dental pigmentation in 15 OTUs from throughout the geographic distribution of *B. brevicauda*.

We do not feel that strictly clinal patterns of geographic variation are meaningful from the standpoint of evolution in *Blarina*. However, abrupt changes in size or morphological features between populations of *B. brevicauda* were judged to indicate evolutionary significance and to warrant taxonomic recognition. This criterion was used throughout this study with respect to recognition of subspecies and relegation of others to synonymy. Accounts of subspecies include detailed synonymies. The first entry in a synonymy is the name originally applied to the taxon and its type locality. Subsequent entries, in chronological order, include all junior synonyms of the original name. Holotypes are identified, and those that we examined are indicated. A list of Specimens Examined concludes each subspecies account; if fractions were used on the original specimen tag, locality data were converted (i.e., $\frac{1}{2}$ mi was converted to 0.5 mi).

RESULTS

Univariate analysis

Standard statistics for all characters for each OTU are provided in Appendix 2. For most characters, coefficients of variation (CVs) are less than 4%; however, CVs for both width of zygomatic plate and articular width typically exceed 5%, reflecting the fact that small dimensions require greater precision (more significant digits) in taking those measurements, greater variability in those characters, or perhaps the difficulty in taking those measurements. Sample sizes for the 114 OTUs range from 5 to 173 (Appendix 2), with an average of 24, a mode of 11, and a median of 18.5. Character means appear to be unaffected by small sample sizes; in other words, standard deviations and coefficients of

variation for individual measurements appear similar among OTUs, regardless of sample size.

For each cranial character, there are highly significant differences ($P \leq 0.0001$) among means of OTUs, and results of the Duncan's multiple-range tests (representative measurements in Tables 1 and 2) are highly congruent. In the following paragraphs, we note geographic patterns in size variation (see Fig. 3, Tables 1 and 2, and Appendix 2). Consistently, there is a group of shrews from west of the Mississippi River (OTUs 1-13, 15-24) and immediately east of the Mississippi River in southwestern Wisconsin (28) whose means are significantly larger than those of shrews from other OTUs. In particular, shrews from southeastern South Dakota (8), northeastern Nebraska (9-11), and central Iowa (17-18) are the largest of all specimens examined in most cranial measurements. Shrews from much of Minnesota (13, 15) and the remainder of the Dakotas (6-7) and Iowa (16, 19-21) also are much larger than average for the species, and those from southern Manitoba (1-5) and northern Missouri (23-24) are almost as large.

Shrews from a small area of northeastern Kansas (25) are significantly smaller than shrews from all other OTUs from west of the Mississippi River, and in most cranial measurements they are most similar in size to shrews from east of the Mississippi River. In particular, shrews from the Kaw River Valley in northeastern Kansas are disproportionately short in occipito-premaxillary length and narrow in zygomatic plate width, relative to the remaining 7 cranial measurements.

Shrews from central Tennessee (60-62) and southeastern North Carolina (113-114) are significantly smaller than shrews from all other OTUs. In particular, specimens from southeastern North Carolina (113-114) are especially diminutive in maxillary breadth, cranial breadth, mandibular length, mandibular height, and articular width, whereas those from central Tennessee (60-62) are especially diminutive in occipito-premaxillary length and interorbital breadth. Shrews from OTUs immediately adjacent to those mentioned above—112 in eastern North Carolina and 63 in southeastern Tennessee—have cranial measurements that also are smaller than average, and they clearly are intermediate in size between the extremely small shrews from southeastern North Carolina (113-114) and central Tennessee (60-62) and the larger shrews from adjacent populations in the Great Dismal Swamp region of southeastern Virginia (110) and northeastern North Carolina (111) and the southern Appalachian Mountains (64-66) and central Kentucky (56-59), respectively.

Shrews from Martha's Vineyard (84) and Nantucket

Table 1. Results of Duncan's multiple-range test of geographic variation in 114 operational taxonomic units (OTUs) of *Blarina brevicauda* for 2 measurements: occipito-premaxillary length and P⁴-M³ length. Vertical lines to the right of sample means connect maximally non-significant subsets at the 0.05 probability level. Sample sizes and standard deviations are in Appendix 2.

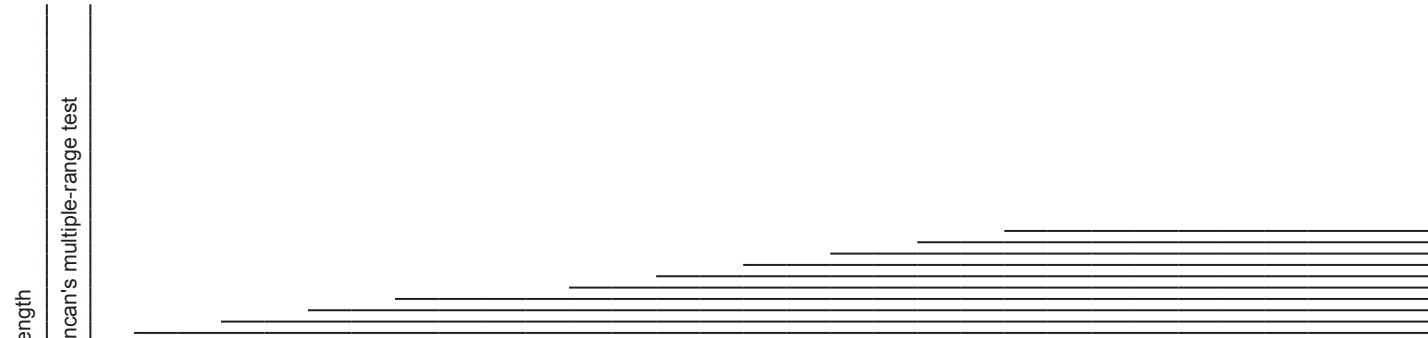
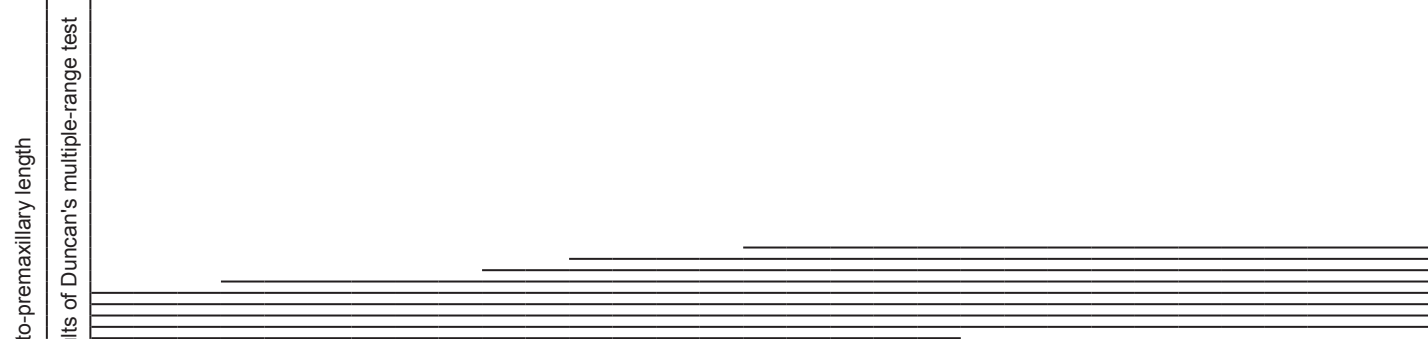
Occipito-premaxillary length		P ⁴ -M ³ length	
OTU	Mean	OTU	Mean
9	24.13	18	6.59
10	23.91	10	6.58
18	23.88	9	6.53
17	23.86	11	6.52
11	23.84	17	6.50
1	23.83	22	6.46
7	23.70	15	6.46
8	23.69	12	6.46
21	23.59	6	6.46
6	23.55	19	6.46
19	23.51	21	6.45
15	23.45	20	6.43
22	23.44	8	6.43
12	23.44	7	6.42

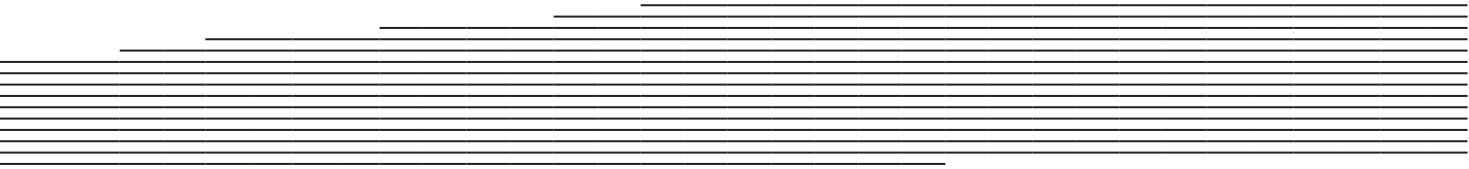
16 6.40
13 6.35
1 6.35
31 6.35
5 6.32
3 6.30
29 6.29
4 6.27
24 6.26
30 6.25
14 6.25
33 6.24
25 6.24
28 6.24
23 6.21
32 6.19

20 23.41
13 23.41
16 23.32
5 23.22
3 23.08
4 23.03
24 22.97
23 22.97
14 22.96
2 22.87
71 22.83
32 22.79
70 22.78
28 22.74
31 22.71
33 22.70

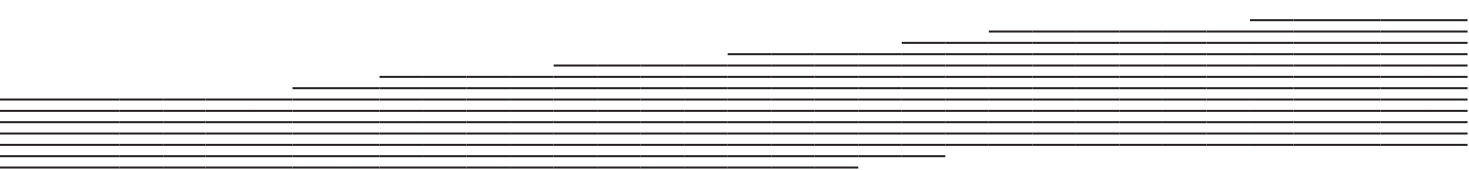
Table 1. *continued.*

Occipito-premaxillary length		P ⁴ -M ³ length	
OTU	Mean	OTU	Mean
29	22.68	2	6.19
73	22.59	98	6.16
26	22.59	69	6.13
44	22.56	91	6.12
91	22.50	67	6.12
36	22.49	26	6.12
27	22.47	64	6.10
64	22.46	95	6.09
40	22.46	71	6.09
30	22.45	82	6.08
98	22.43	44	6.07
82	22.43	27	6.06
81	22.40	68	6.06
88	22.40	37	6.06





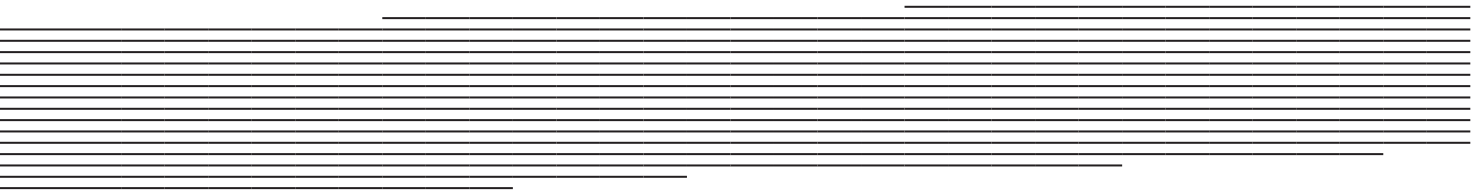
107	6.05
36	6.05
47	6.05
70	6.04
89	6.04
87	6.03
79	6.03
65	6.02
96	6.02
110	6.01
81	6.01
40	6.01
100	6.01
77	6.00
99	6.00
53	6.00



72	22.40
74	22.39
25	22.36
77	22.34
79	22.34
90	22.28
87	22.28
41	22.26
76	22.25
95	22.24
96	22.20
39	22.19
93	22.18
110	22.18
35	22.18
89	22.16

Table 1. *continued.*

Occipito-premaxillary length		P ⁴ -M ³ length	
OTU	Mean	OTU	Mean
80	22.11	76	5.99
94	22.11	88	5.99
46	22.10	97	5.98
38	22.08	109	5.98
100	22.07	54	5.98
65	22.07	108	5.98
97	22.01	94	5.97
69	22.01	102	5.97
34	22.00	35	5.96
78	21.99	90	5.96
101	21.99	66	5.96
53	21.98	74	5.95
37	21.96	80	5.94
47	21.94	73	5.94



68	21.92	92	5.94
63	21.83	49	5.94
75	21.83	86	5.93
67	21.82	38	5.93
108	21.82	101	5.93
54	21.80	46	5.92
111	21.76	41	5.92
52	21.76	93	5.91
66	21.73	78	5.91
112	21.71	85	5.91
43	21.69	103	5.91
86	21.66	52	5.91
48	21.65	83	5.91
109	21.64	39	5.91
50	21.62	48	5.91
51	21.61	50	5.89

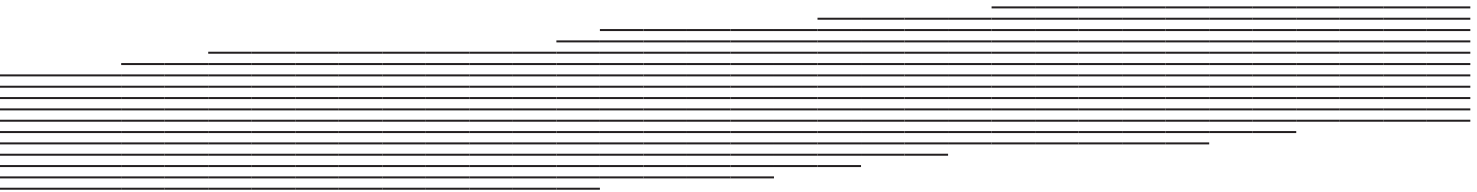


Table 1. continued.

Occipito-premaxillary length		P ⁴ -M ³ length	
OTU	Mean	OTU	Mean
103	21.61	34	5.88
107	21.60	111	5.88
83	21.56	51	5.87
99	21.56	63	5.86
45	21.54	112	5.85
42	21.47	106	5.85
49	21.46	56	5.82
92	21.40	57	5.81
58	21.36	58	5.80
102	21.31	72	5.79
104	21.30	75	5.78
59	21.28	45	5.77
55	21.26	43	5.77
85	21.23	105	5.76
57	21.21	55	5.74

56	21.20	113	5.72
106	21.15	59	5.69
113	20.95	42	5.68
62	20.86	62	5.67
105	20.79	84	5.65
114	20.68	61	5.60
84	20.64	104	5.58
60	20.44	60	5.51
61	20.29	114	5.50

Table 2. Results of Duncan's multiple-range test of geographic variation in 114 operational taxonomic units (OTUs) of *Blarina brevicauda* for 2 measurements: cranial breadth and inter-orbital breadth. Vertical lines to the right of sample means connect maximally non-significant subsets at the 0.05 probability level. Sample sizes and standard deviations are in Appendix 2.

Cranial breadth		Interorbital breadth	
OTU	Mean	OTU	Mean
9	13.74	9	6.34
8	13.49	7	6.30
17	13.45	18	6.25
10	13.39	11	6.18
11	13.37	22	6.18
18	13.36	10	6.17
19	13.22	1	6.15
6	13.21	19	6.14
20	13.19	17	6.13
22	13.19	8	6.13
21	13.17	20	6.12
16	13.16	6	6.11
1	13.10	21	6.11
12	13.07	15	6.10

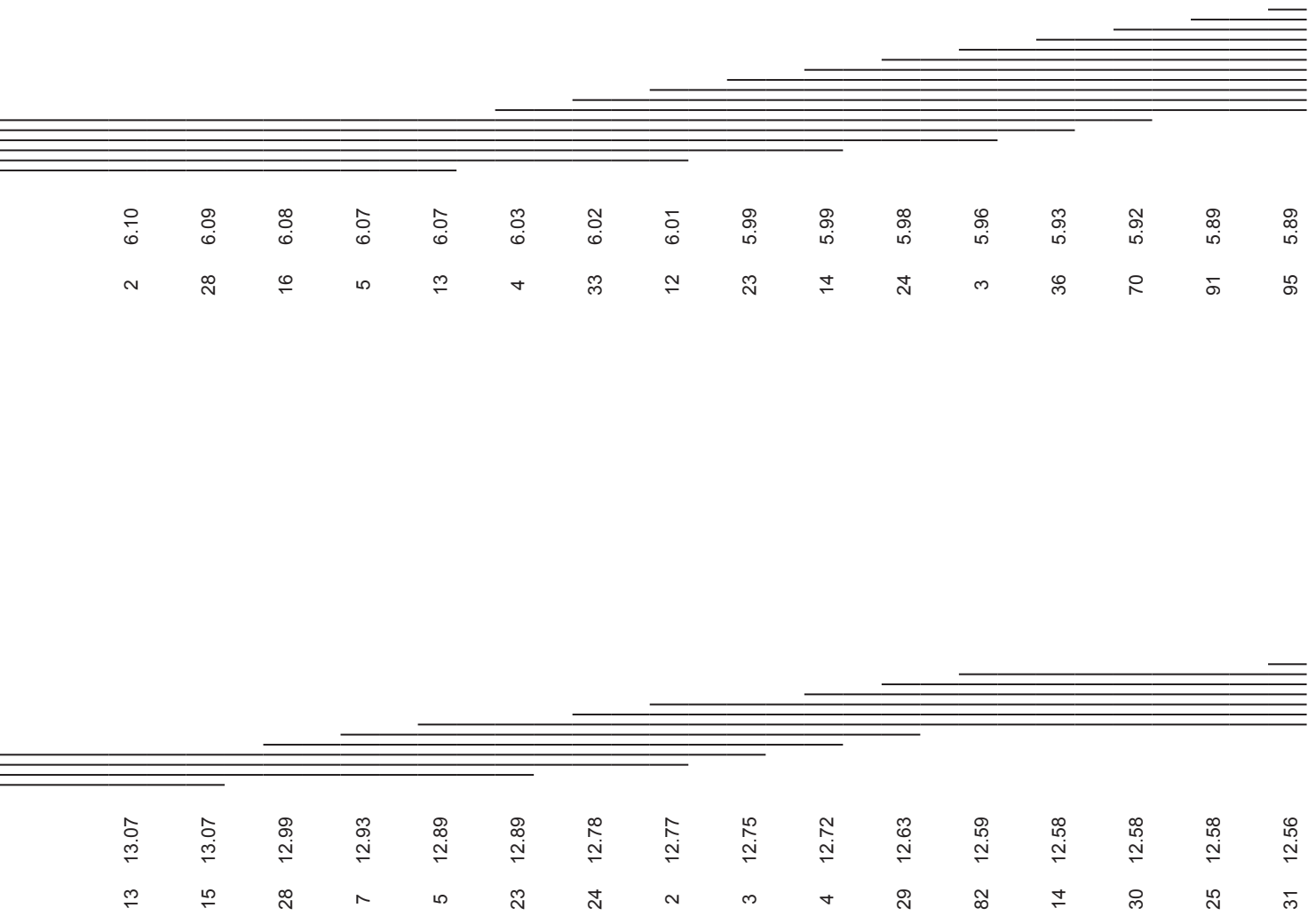
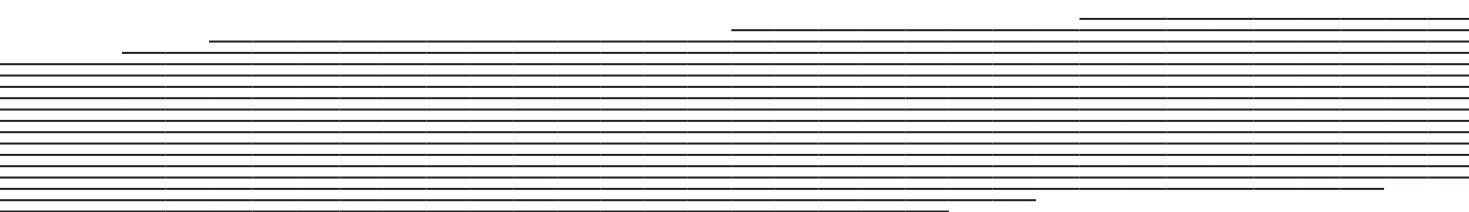


Table 2. continued.

Cranial breadth		Interorbital breadth	
OTU	Mean	OTU	Mean
87	12.54	82	5.87
44	12.53	98	5.87
70	12.52	32	5.86
27	12.51	64	5.86
32	12.51	41	5.85
81	12.50	94	5.85
95	12.47	26	5.85
36	12.47	81	5.84
91	12.47	25	5.84
98	12.45	88	5.84
88	12.43	27	5.83
71	12.43	76	5.83
90	12.39	69	5.83
89	12.38	79	5.83



26	12.38	38	5.83
80	12.37	96	5.82
76	12.36	67	5.82
65	12.36	44	5.82
48	12.35	68	5.81
47	12.32	40	5.81
94	12.31	74	5.81
64	12.30	35	5.81
35	12.29	77	5.80
73	12.29	37	5.80
79	12.29	47	5.80
96	12.28	57	5.79
74	12.28	108	5.79
93	12.27	58	5.79
100	12.26	90	5.79
46	12.25	31	5.78

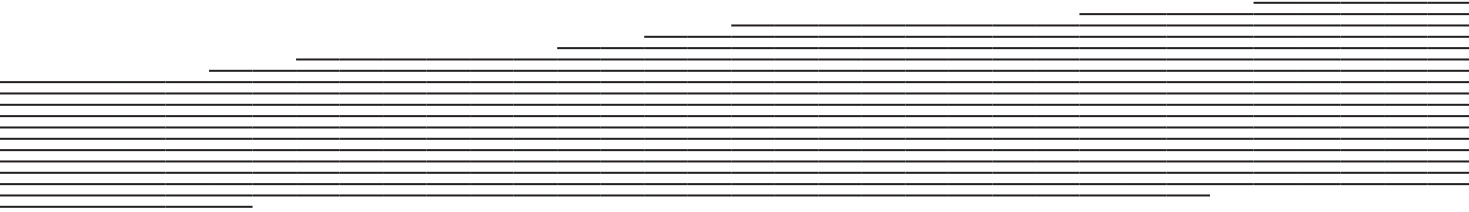


Table 2. continued.

Cranial breadth		Interorbital breadth	
OTU	Mean	OTU	Mean
68	12.25	29	5.78
97	12.24	89	5.78
54	12.24	80	5.77
34	12.24	30	5.76
72	12.23	87	5.76
51	12.22	66	5.76
41	12.22	71	5.76
108	12.21	97	5.74
40	12.21	73	5.73
53	12.20	83	5.73
77	12.20	65	5.73
78	12.18	78	5.72
101	12.16	48	5.71
83	12.14	84	5.71

85 5.70
34 5.70
43 5.70
46 5.69
50 5.69
110 5.69
53 5.69
101 5.69
92 5.68
72 5.67
102 5.66
75 5.66
86 5.65
93 5.65
100 5.65
107 5.65

86 12.14
39 12.11
50 12.11
33 12.10
99 12.09
52 12.08
75 12.07
38 12.07
66 12.07
37 12.06
63 12.06
102 12.05
67 12.04
103 12.03
111 12.03
109 12.02

Table 2. continued.

Cranial breadth		Interorbital breadth	
OTU	Mean	OTU	Mean
55	12.00	54	5.63
92	11.99	59	5.63
49	11.98	42	5.63
57	11.96	39	5.63
69	11.94	49	5.61
110	11.94	52	5.60
42	11.92	99	5.59
43	11.92	45	5.58
58	11.92	55	5.58
107	11.90	51	5.58
106	11.85	111	5.51
45	11.84	105	5.50
56	11.80	103	5.49
59	11.72	56	5.43

84	11.69	106	5.43
62	11.67	112	5.41
104	11.63	109	5.41
112	11.59	104	5.28
85	11.54	63	5.26
60	11.53	113	5.24
105	11.53	114	5.23
61	11.40	62	5.08
114	11.33	61	5.06
113	11.05	60	5.03

Island (85) also are small in many cranial measurements, including occipito-premaxillary length, cranial breadth, mandibular length, and mandibular height, but they average in the middle of the range for the species in interorbital breadth. Shrews from adjacent mainland OTUs (83, 86) are similar in size to these insular shrews in interorbital breadth, but they are much larger in all other measurements and more similar overall to shrews from other mainland OTUs.

Shrews from much of the Delmarva Peninsula (104-106) also are distinctly smaller than average for the species in most cranial measurements, especially mandibular length and mandibular height, but generally not to the extent seen in those shrews from southeastern North Carolina (113-114) and the Cumberland Plateau of Tennessee (60-62). Shrews from adjacent OTUs—District of Columbia (102), northern Delmarva Peninsula (103), and southern New Jersey (99)—typically are intermediate in size between the smaller shrews from the remainder of the Delmarva Peninsula (104-106) and larger shrews from populations in northern New Jersey (98) and eastern Pennsylvania (94, 97).

Shrews from the remainder of the geographic range of the species, a broad area extending from southwestern Ontario eastward to the Gaspé Peninsula and Nova Scotia and southward to the Ohio River, southern Appalachian Mountains, and the Great Dismal Swamp (14, 26-27, 29-59, 63-83, 86-103, 107-112), average in the middle of the range for the species in most cranial measurements. However, there is noticeable variability within this group, and consistent patterns in cranial variation are not always apparent. In general, however, shrews from the Lower Peninsula of Michigan (42-43, 45), southern Ohio (55) and central Kentucky (56-59), and the swamps of southeastern Virginia (110) and northeastern North Carolina (111-112) tend to be smaller than average for the species, whereas shrews from southwestern Ontario (32-33), most of Wisconsin (26-27), northeastern Minnesota (14), Illinois (29-31), and the southern Appalachian Mountains of eastern Tennessee and western North Carolina (64-65) tend to be larger than average. Considering individual measurements, shrews from the Upper Peninsula of Michigan (38-41) have zygomatic plates that are wider than average and articular widths that are smaller than average for the species, shrews from southeastern Tennessee (63) have zygomatic plates that are narrower than average and interorbital breadths that are much narrower than average for the species, and shrews from

east-central North Carolina (112) are much narrower than average in maxillary breadth.

Multivariate analysis

The first 2 principal components for the 114 OTUs explain 94.0% of the variation in the morphometric data set (Table 3). Principal component I (PC I) explains 90.3% and principal component II (PC II) explains 3.7% of the variation. All 9 measurements load positively and are weighted similarly on PC I, although the loading value for width of zygomatic plate is slightly lower. Width of zygomatic plate and interorbital breadth load positively on PC II and articular width loads negatively. The first principal component, therefore, is an indicator of overall size, whereas the second principal component is an indicator of shape, especially in the interorbital region and in characters associated with the anterior masticatory musculature (width of zygomatic plate and articular width).

The plot of PC I versus PC II (Fig. 4) revealed 4 assemblages of OTUs—a moderately large cluster of OTUs located at the top of the 2-dimensional plot (A), 2 small clusters of OTUs at the bottom of the plot (F and G), and a large cluster of OTUs in the middle of the plot (B, C, D, and E). Shrews from southeastern Wisconsin (28) and all sites west of the Mississippi River (1-13, 15-24), save for those from the Kaw River Valley in northeastern Kansas (25), form the distinct assemblage of OTUs (A) at the top of the plot (Figs. 3 and 4). These shrews are massive (relatively speaking) in all cranial dimensions and much larger than shrews from all other OTUs. There is a moderate amount of geographic variation within this assemblage. First, there is a subtle

Table 3. Principal component loadings for 9 cranial and mandibular measurements in 2736 specimens of *Blarina brevicauda*.

Measurement	PC I	PC II	PC III
Occipito-premaxillary length	0.337	0.009	-0.383
P ⁴ -M ³ length	0.337	-0.069	-0.210
Maxillary breadth	0.339	-0.229	0.248
Width of zygomatic plate	0.306	0.707	0.581
Interorbital breadth	0.321	0.480	-0.474
Cranial breadth	0.343	-0.135	-0.024
Mandibular length	0.343	-0.151	-0.159
Mandibular height	0.344	-0.132	0.066
Articular width	0.329	-0.394	0.395
Percent of variance explained	90.329	3.666	2.184

north to south cline in cranial size, with slightly smaller shrews in much of southern Manitoba (2-5) and larger shrews in southeastern South Dakota (8), northeastern Nebraska (9-11), and central Iowa (17-18). However, the cline does not extend farther south, as shrews from northern Missouri (23-24) are slightly smaller and similar to those from southern Manitoba and southeastern Wisconsin (28) in size (Figs. 3 and 4).

Two assemblages of OTUs—one from southeastern North Carolina (113-114) and another from the Cumberland Plateau region of Tennessee (60-62)—are located at the bottom of the plot, reflecting both the small overall size and shape in specimens from these regions (Figs. 3 and 4). Shrews from OTUs 113-114 (G) have crania that are especially narrow, and their mandibles average smaller than those in shrews from all other OTUs, whereas those from OTUs 60-62 (F) have short crania that are especially narrow in the interorbital region (Fig. 4). Shrews from these 2 assemblages are widely separated geographically and their similarity in size in many measurements appears to be the result of convergence rather than relatedness.

The large assemblage of OTUs in the center of Fig. 4 (B, C, D, and E) includes specimens that vary considerably in size and shape across the remainder of the geographic range of the species, and trends in geographic variation are not apparent without detailed comparisons with adjacent OTUs. For example, shrews from northeastern Kansas (25, B) are much smaller than those from other sites west of the Mississippi River (1-13, 15-24), and they are more similar in size to shrews from Illinois (29-31) and northeastern Minnesota (14, Figs. 3 and 4).

In addition, shrews from Martha's Vineyard (84)

and Nantucket Island (85), which collectively form group D, are much smaller than those from the adjacent mainland (82-83, 86-87) in most cranial measurements, although they are similar in interorbital breadth (Figs. 3 and 4). When compared to shrews from Nantucket Island (85), shrews from Martha's Vineyard (84) have wider zygomatic plates and shorter P⁴-M³ tooththrows; however, these differences are minor in comparison to the more pronounced differences between insular and mainland shrews in all cranial measurements except interorbital breadth (Tables 1 and 2).

Moreover, shrews from the southern two-thirds of the Delmarva Peninsula (104-106, E) are distinctly and consistently smaller than those from adjacent regions in eastern Pennsylvania (94, 97), New Jersey (98-99), northern Delaware (103), and the District of Columbia (102, Figs. 3 and 4). Shrews from southern Delaware (104) and the Eastern Shore of Maryland (105) are virtually indistinguishable in size, whereas those from the Eastern Shore of Virginia (106) are slightly larger in maxillary breadth and cranial breadth (Table 2).

Finally, shrews from some OTUs in the Lower Peninsula of Michigan (42-43, 45) and those from south-central Ohio and Kentucky (55-59) also are smaller than average in most cranial measurements (Figs. 3 and 4), but there are no patterns that suggest a lack of gene flow among them and adjacent populations.

Given the clearly defined patterns of geographic variation in *B. brevicauda* described in this analysis and given that these patterns differ substantially from those espoused by Bole and Moulthrop (1942) and Hall (1981), the following revision summarizes the results of our investigation.

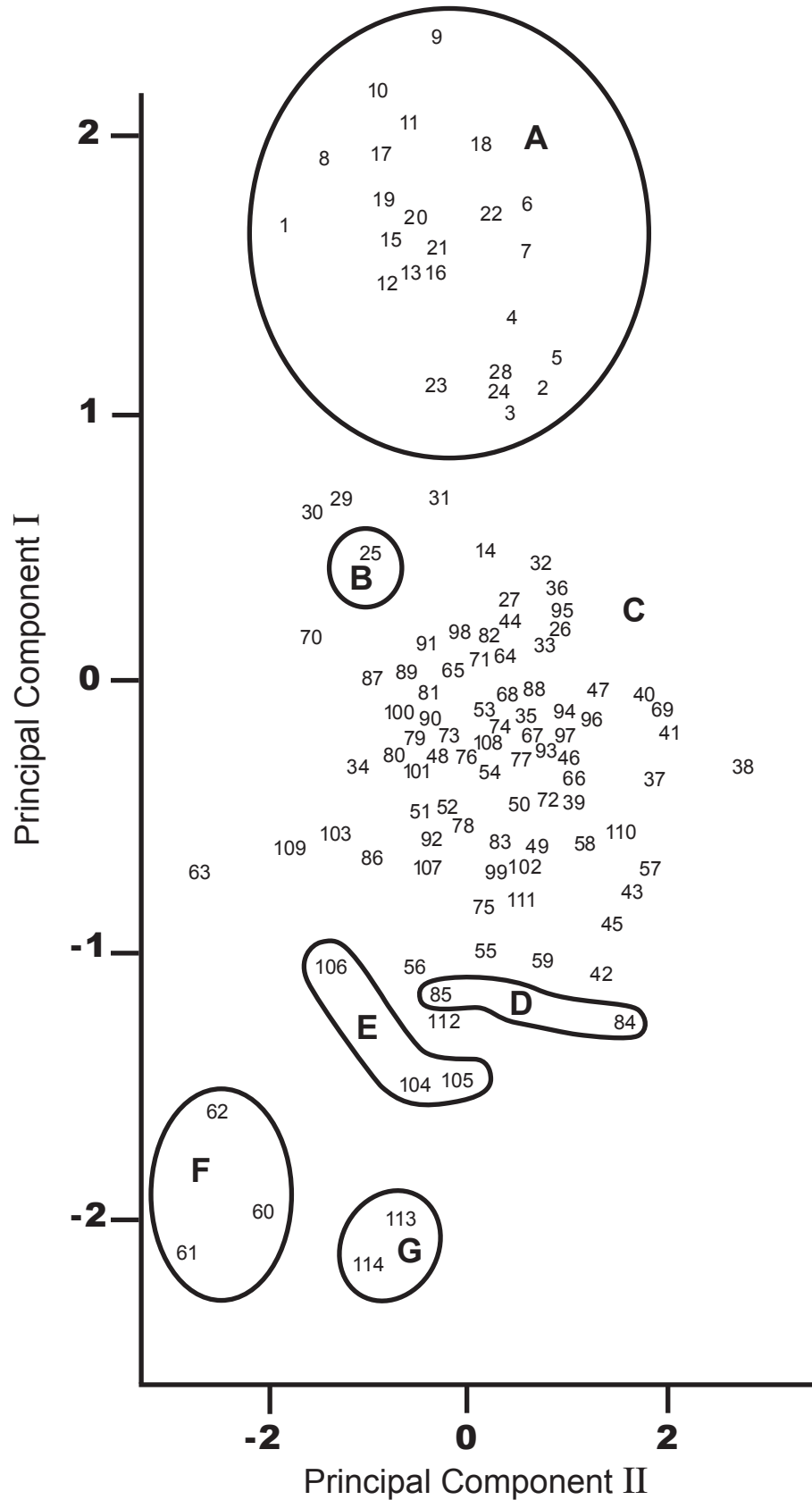


Fig. 4. Two-dimensional plot of principal components I and II for 114 operational taxonomic units (OTUs) of *Blarina brevicauda*. Letters A-G refer to groupings of OTUs as indicated in text. See Fig. 3 and Appendix 1 for OTU localities.

SYSTEMATIC ACCOUNTS

Blarina brevicauda brevicauda (Say)

1823. *Sorex brevicaudus* Say, in Long, Account of an expedition ... to the Rocky Mountains, 1:164. Type locality: Engineer Cantonment, which was shown by Carlson et al. (2004) and Genoways and Ratcliffe (2008) to be in the extreme southeastern corner of modern Washington County, Nebraska, at a place 3 miles south and 4 miles east of the town of Fort Calhoun (41°24'43" N, 95°57'00.6" W). The site is approximately 305 meters in elevation. Holotype evidently destroyed (see remarks below and Woodman, 2009).
1891. *Blarina costaricensis* J. A. Allen, Bulletin of the American Museum of Natural History, 3:205, 17 April. Type locality: likely the upper Mississippi Valley (perhaps Iowa, see Merriam, 1895:10, and Bole and Mouthrop, 1942:113), although allegedly from La Carpintera, Costa Rica (Allen, 1897). Holotype examined (AMNH 3642; see *Acknowledgments* for institutional abbreviations), a fluid-preserved specimen with skull, numbered 2800, removed, but not included in the Specimens Examined because its location of capture is unknown.
1943. *Blarina fossilis* Hibbard, University of Kansas Science Bulletin, 29:238, 15 October. Holotype examined (KUVP 6675), a fragmentary right ramus bearing M₃ from the Rezabek Fauna (Pleistocene locality #5, Rezabek gravel pit), Irvingtonian Mammal Age, Lincoln County, Kansas, but not included in the Specimens Examined.
1947. *Blarina brevicauda manitobensis* Anderson, Bulletin of the National Museum of Canada, 102:23, 24 January. Type locality: Max Lake, Turtle Mountains, Manitoba, Canada. Elevation 2100 ft. Holotype not examined (CMN 8549).

Neotype: Adult female, skin and skull, Sternberg Museum of Natural History 37241, obtained at the original type locality (3 mi S, 4 mi E Fort Calhoun, Washington County, Nebraska, 41°24'43" N, 95°57'00.6" W) on 2 October 2006 by C. W. Thompson, original field number 268. Skin in excellent condition. Total length, 128; length of tail, 27; length of hind foot, 14; weight, 25.5. Skull in excellent condition; teeth moderately worn. Occipito-premaxillary length, 24.6; P⁴-M³ length, 6.4; width of zygomatic plate, 2.5; interorbital breadth, 6.5; cranial breadth, 13.6. A dorsal view of the cranium is shown in Fig. 1.

Topotypes: Adult female, skin and skull, Sternberg

Museum of Natural History 37239 and juvenile female, skin and skull, Sternberg Museum of Natural History 37240, both obtained at the type locality on 2 October 2006 by C. W. Thompson, original field numbers 266 and 267, respectively.

Distribution: Southern Saskatchewan and southern Manitoba southward to Nebraska and northern Missouri, and eastward to the counties immediately east of the Mississippi River in western Wisconsin and northwestern Illinois (OTUs 1-13, 15-24, 28; Fig. 5).

Description: The largest subspecies of *B. brevicauda* in all dimensions; the nasal and premaxillary bones are inflated anteriorly where they form the external nares; well-developed sagittal and lambdoidal crests, resulting in a strongly sculptured appearance; relatively large, darkly pigmented teeth; rich blackish-gray to gray pelage, with scant contrast in dorsal and ventral coloration. The karyotype of the neotype and 1 topotype, both females from the type locality, was 2N=50 and FN=48. (Thompson and Hoffman, 2009).

Diagnosis: Specimens of *B. b. brevicauda* have cranial measurements that are consistently larger on average than those of all other subspecies (Appendix 2, Tables 1 and 2, Fig. 4). For example, occipito-premaxillary length, interorbital breadth, and cranial breadth average greater than 22.9, 6.0, and 12.6 in specimens of *B. b. brevicauda*, respectively, but smaller in specimens of other subspecies.

Comparisons: Specimens of *B. b. brevicauda* (1-13, 15-24, 28) are much larger than those of other subspecies, especially in dimensions that reflect cranial width (Appendix 2, Tables 1 and 2, Fig. 4). These differences are especially pronounced when comparing specimens of *B. b. brevicauda* with those from peripheral populations found in central Tennessee (60-62), southeastern North Carolina (113-114), the southern Delmarva Peninsula (104-106), Martha's Vineyard (84), and Nantucket Island (85). Specimens of *B. b. brevicauda* are robust and large overall, and they exhibit little overlap in cranial dimensions with those from the latter groups (Appendix 2, Figs. 3 and 4). Comparisons with the undescribed subspecies from northeastern Kansas (25) are discussed in that account.

Another species in the genus, *B. hylophaga*, is found to the south of *B. b. brevicauda* in southern Nebraska, southwestern Iowa, and northern Missouri (Bowles, 1975; Moncrief et al., 1982; Thompson, 2008). Although there is some overlap in cranial measurements when comparing individuals, specimens of *B. hylophaga* from central Kansas average 21% smaller than specimens of *B. b. brevicauda* from northeastern Nebraska (Benedict, 1999a), respectively: occipito-premaxillary length, 20.9

and 23.8; cranial breadth, 11.4 and 13.4; mandibular height, 6.2 and 7.7; and articular width, 2.3 and 2.9. Moreover, *B. hylophaga* (2N = 52 and FN = 60-62) and *B. brevicauda* (2N = 48-50 and FN = 48) have different karyotypes (George et al., 1982), although there is an extremely narrow zone of hybridization between these 2 species in southern Nebraska, based on an analysis of morphological and cytochrome-b mtDNA data (Benedict, 1999a).

Remarks: The holotype of *B. brevicauda* is not known. It likely was destroyed when a portion of the Peale Museum in Philadelphia, which had been purchased by P. T. Barnum, burned in 1851. It is clear from the description by Say (1823) that the species was based on a single specimen, and images of that individual are available among the Titian Ramsay Peale Sketches (B P31.15d, images 47-48; see cover of this monograph) at the American Philosophical Society (Woodman, 2009). Woodman (2009) provided evidence that the specimen depicted in the Peale sketches was *Blarina brevicauda* based on its overall size, shape of rostrum, length of tail, pelage coloration, and long foreclaws. The type locality of *B. brevicauda* is located approximately 70 km north of a contact zone (Benedict, 1999b) with another species of short-tailed shrew, *B. hylophaga*, which has similar characteristics. However, *B. hylophaga* is smaller and has paler pelage, characteristics that are not easily discernable in the Peale sketches. Because Peale's sketches cannot serve as the name-bearing type (ICZN, 1999: Article 74.4) and because the sketches do not by themselves unequivocally identify the specimen as *B. brevicauda* (a karyotype is required for confirmation) we designate as the neotype for *B. brevicauda* a specimen from the original type locality that has the 2N = 50, FN = 48 chromosomal arrangement of *B. brevicauda* (Thompson and Hoffman, 2009).

The exact site of the Engineer Cantonment has been the source of much discussion (see, for example, James, 1823; Jackson, 1951; and Jones, 1964), as it serves as the type locality of *Blarina brevicauda brevicauda*, *Cryptotis parva parva*, *Canis latrans latrans*, and *Canis lupus nubilus*. Jones (1964) opined that the site was located on the west bank of the Missouri River, 3 miles above the mouth of Boyer River, approximately 2 miles east of Fort Calhoun, near Blair, Washington County, Nebraska. Recent historical archeological research (Carlson et al., 2004; Genoways and Ratcliffe, 2008) has shown that the site is actually located 3 miles south and 4 miles east of Fort Calhoun, Washington County, Nebraska (41°24'43" N, 95°57'00.6" W).

There is noticeable variation in size in *B. b. brevicauda*. The largest individuals occur in southern

South Dakota (8), northern and east-central Nebraska (9-11), and central Iowa (17, 18), but specimens become progressively smaller to the north in southern Manitoba (1-5) and to the south in northern Missouri (23-24; Appendix 2, Figs. 3 and 4). Specimens from southern Manitoba, originally described (Anderson, 1947) as slightly larger in size and darker in pelage coloration than those from eastern Nebraska and therefore allocated to *B. b. manitobensis* Anderson, are remarkably similar to those from Nebraska and Iowa, except for being slightly darker and smaller overall, and, therefore, they do not warrant recognition as a separate subspecies. In addition, Brant and Ortí (2002, 2003a), demonstrated that *B. b. brevicauda* and *B. b. manitobensis* are not differentiated at the molecular level. In their analysis of cytochrome-*b* and 16S rRNA mtDNA sequence data (Brant and Ortí, 2002, 2003a), specimens of *B. brevicauda* from 1 site in southern Manitoba, 3 counties in Nebraska, and 2 counties in eastern Iowa formed a monophyletic clade distinct from a second monophyletic clade that included specimens of *B. brevicauda* from 12 states located east of the Mississippi River.

Specimens of *B. b. brevicauda* also are smaller to the east, where intergradation with an adjacent subspecies (as discussed beyond) is evident. This line of intergradation begins in southern Canada between Manitoba and Ontario, it extends across northeastern Minnesota, and then it continues on the east side of the Mississippi River from northwestern Wisconsin (Burnett County) southward to northwestern Illinois (Rock Island County). For example, specimens from just east of the Mississippi River in southwestern Wisconsin (28) are slightly smaller than those from west of the Mississippi River in Iowa (16, 18, 22) in external and cranial dimensions, their teeth are less darkly pigmented, and they are charcoal-gray in coloration. However, overall the northern short-tailed shrews in southwestern Wisconsin (28) are more similar to specimens of *B. brevicauda* from the west side of the river (16, 18, 22) than to specimens from northern and central Wisconsin (26-27) and Illinois (29-31; Appendix 2, Figs. 3 and 4). Therefore, we assign specimens from southwestern Wisconsin (28) to *B. b. brevicauda*.

As classified herein, the extinct taxon originally named *Blarina fossilis* by Hibbard (1943), later relegated as *B. brevicauda fossilis* by Hibbard (1957), and subsequently placed in synonymy with *B. b. brevicauda* by Graham and Semken (1976), is retained as a synonym of *B. b. brevicauda*. Jones et al. (1984) found no differences between *B. fossilis* and Holocene specimens of *B. brevicauda* and noted that the fossils most closely resembled the subspecies *B. b. brevicauda*.

Blarina brevicauda brevicauda

Specimens Examined (1,128) See *Acknowledgments* for institutional abbreviations.

MANITOBA, CANADA (182). Seddon's Corner, Agassiz (1 CMN); Aweme (1 ROM); 17 mi SE Brandon (1 CMN); Caddy Lake (1 UAMZ); 3 mi SW Clarkleigh, T18, R5 (2 ROM); Whitshell Park, Caddy Lake (3 MMMN); Dauphin (1 ROM); Dauphin Lake (3 MMMN); northwest shore Mossy River, Dauphin Lake (6 UAMZ); Delta (3 MUMZ, 8 MMMN); 1 mi E Delta, T14, R7 (1 ROM); Bluff Point, Dog Lake (1 UAMZ); Spruce Woods Forest Reserve, Douglash (1 UAMZ); Watjask Lake, Duck Mountain (2 UAMZ); Glenboro (2 MMMN); Lake St. Martin Res., Gypsumville (1 ROM); Holland (1 MMMN); Island Lake (2 MMMN); Cat Lake, Lac du Bonnet (1 MMMN); Lake Manitoba (1 MMMN); 4 mi SE Elm Point, Lake Manitoba (5 UAMZ); Lake Francis, Lake Manitoba (1 UAMZ); Lake Winnipeg (1 NMNH); Dawson Bay, Lake Winnipegosis (3 UAMZ); Margret (3 MMMN); Middlebro (1 MMMN); North Kidonan (1 MMMN); Oak Lake (10 MMMN); 5 mi S Oak Lake, 49°42' N, 100°39' W (2 CMN); Ochre River (1 ROM); Onanole (1 MMMN); Pinawa (1 MMMN); Pine Falls (2 CMN); Portage la Prairie (1 MMMN); Pratt (2 MMMN); Rennie (8 CMN); near Rennie, Red Rock Lake (26 CMN, 4 MMMN); Deep Lake, Riding Mountain National Park (3 MMMN); east shore Edwards Creek, 12.3 mi S Dauphin, Riding Mountain National Park (1 ROM); Edwards Lake, Riding Mountain National Park (1 UAMZ); Moon Lake, Riding Mountain National Park (1 MMMN); Norgate, Riding Mountain National Park (3 MMMN); Whirlpool Lake, T20, R17, 6 mi NE Wasagaming, Riding Mountain National Park (2 ROM); Rock Lake (2 UAMZ); Rossburn (1 MMMN); Sandilands Forest Reserve (3 CMN); West-Central Sandilands Forest Reserve (1 UAMZ); Whitemouth River, Sandilands Forest Reserve (1 UAMZ); Red River, Selkirk Settlement (1 NMNH); Sprague (1 MMMN); 0.25 mi N Swan River City, 1200 ft (1 KU); 0.25 mi N Swan River City, 1220 ft (1 KU); Telford (4 CMN, 4 UAMZ); Brea-don Lake, Turtle Mountain (1 UAMZ); Lake William, Turtle Mountain (2 MMMN, 3 UAMZ); Max Lake, Turtle Mountains (4 CMN); Wasagaming (3 CMN); Swanson Creek, Wasagaming (5 MMMN); Whitewater Lake (1 MMMN); Winnipeg (1 CMN, 2 MMMN, 1 ROM); Fort Garry, Winnipeg (1 MMMN, 1 TCWC, 10 UAMZ).

ILLINOIS, UNITED STATES (4). *Rock Island Co.*: 2 mi S, 5 mi E Moline (4 KU).

IOWA, UNITED STATES (443). *Adams Co.*: 4 mi N, 0.75 mi W Nodaway (1 KU). *Allamakee Co.*: New Albin (2 UWSP); Yellow River Forest, 1 mi N, 2 mi W Waukau Junction (1 CUI). *Black Hawk Co.*: Cedar Falls (11 CUI); Hartman Reserve, Waterloo (1 CUI). *Boone Co.*: 3.5 mi S Boone (2 KU); 3.5 mi S, 0.5 mi W Boone (1 KU).

Buchanan Co.: T88N, R9W, Sec 23 (1 KU). *Buena Vista Co.*: 0.25 mi N, 2 mi W Alta (2 KU). *Butler Co.*: 0.5 mi S, 3 mi E Greene (6 KU); T91N, R15W, Sec 5 (1 KU). *Cerro Gordo Co.*: Meservey (1 CUI); 0.5 mi E Meservey (2 CUI). *Chickasaw Co.*: 1 mi S, 1 mi W North Washington (10 KU). *Clayton Co.*: Osborn (2 CUI). *Clinton Co.*: 0.5 mi S Clinton (7 KU); 0.5 mi S, 0.5 mi W Clinton (2 KU). *Decatur Co.*: 1 mi N Davis City (1 CM); 4.5 mi NW Pleasanton (3 CM, 3 MHP); 3 mi NW Pleasanton (1 CM, 1 MHP); 3.25 mi N, 0.25 mi E Woodland (1 KU). *Delaware Co.*: Plum Spring (1 NMNH). *Dickinson Co.*: T99N, R36W, Sec 24 (2 KU). *Dubuque Co.*: Sageville (2 CUI). *Fremont Co.*: 2 mi S, 3 mi E Tabor (1 CM, 2 MHP); 2 mi S, 4 mi E Tabor (3 CM, 2 MHP). *Greene Co.*: 4 mi W Jefferson (4 KU). *Grundy Co.*: 5.25 mi W Grundy Center (2 KU); 4 mi S, 1.5 mi W Wellsburg (2 KU); 5 mi S, 0.5 mi E Wellsburg (11 KU); 5 mi S, 1.5 mi W Wellsburg (5 KU); 5 mi S, 3.5 mi W Wellsburg (1 KU). *Guthrie Co.*: Springbrook State Park (2 ROM). *Hamilton Co.*: Jewell (5 NMNH). *Hancock Co.*: Forest City (1 UMMZ); 2 mi N, 4.5 mi W Meservey [*in Cerro Gordo Co.*] (2 CUI). *Hardin Co.*: 0.5 mi W Eldora (9 KU); 1 mi N, 1.5 mi E New Providence (5 KU); 1.5 mi N, 1 mi E New Providence (1 KU). *Henry Co.*: Hillsboro (2 NMNH). *Howard Co.*: T98N, R11W, Sec 1 (4 CUI); T98N, R11W, Sec 2 (10 CUI). *Johnson Co.*: Iowa City (1 AMNH, 3 NMNH). *Keokuk Co.*: Sigourney (4 KU); 6.5 mi S, 1 mi W Sigourney (2 KU). *Linn Co.*: 2 mi N Marion (2 ROM). *Lucas Co.*: 2.5 mi S, 2.5 mi E Chariton (1 CUI); 2.5 mi N, 2.5 mi E Russell (1 KU); 1 mi N, 2.5 mi E Russell (1 KU). *Lyon Co.*: 1 mi N, 4 mi W Inwood (1 CUI). *Mahaska Co.*: Oskaloosa (2 KU); 2 mi N, 2.5 mi E Oskaloosa (1 KU); 2 mi N, 3 mi E Oskaloosa (1 KU); 5 mi N Oskaloosa (1 KU); 5.5 mi N Oskaloosa (2 KU); 5 mi E Oskaloosa (1 KU); 2 mi S, 10 mi W Oskaloosa (1 KU); 2.5 mi S, 4 mi W Oskaloosa (2 KU); 3 mi S, 9 mi W Oskaloosa (1 KU); 3.5 mi SW Oskaloosa (2 KU); 1 mi W Oskaloosa (1 KU); 5 mi E [William] Penn College (1 KU). *Marion Co.*: 1.25 mi N, 2.25 mi W Bussey (2 KU); Knoxville (2 NMNH); 4.5 mi N Knoxville (4 KU); 5.75 mi N Knoxville (1 KU); 5.5 mi N, 3 mi W Pella (3 CUI); 0.25 mi S, 3 mi W Pella (1 CUI); 1 mi S Pella (1 CUI); 1 mi S, 3 mi W Pella (2 CUI); 1.5 mi S, 0.25 mi W Pella (54 CUI); 2.5 mi S Pella (1 CUI); 2.5 mi S, 1.5 mi E Pella (1 CUI); 0.5 mi W Tracy (1 KU). *Mills Co.*: 0.5 mi S, 3 mi W Henderson (7 KU); 3 mi S, 2.5 mi W Hillsdale (1 CUI); 2 mi N, 0.5 mi E Tabor [*in Fremont Co.*] (1 CM, 1 MHP); 2 mi N, 1.5 mi E Tabor [*in Fremont Co.*] (1 CM); 3.5 mi N, 2 mi E Tabor [*in Fremont Co.*] (3 CM, 4 MHP). *Monona Co.*: Loess Hills Wildlife Area, 2 mi N, 3 mi W Castana (5 CUI); 0.5 mi S, 2 mi W Moorhead (1 KU); 1 mi S, 3.5 mi W Moorhead (3 KU). *Monroe Co.*: 1 mi N, 2 mi E Albia (2 CUI); 5.5 mi N, 3.5 mi E Albia (1 KU); 5 mi S Albia (3 CUI); 1.5 mi N Melrose (2 KU). *Montgomery Co.*: 1.5 mi S, 2 mi E Wales (4 KU). *Page Co.*: 1 mi W Bethesda (1 MHP); 1 mi N, 2 mi E Imogene

[in Fremont Co.] (1 MHP); 1 mi N, 6 mi E Imogene [in Fremont Co.] (1 CM). *Plymouth Co.*: 2 mi N Le Mars (10 KU). *Polk Co.*: Des Moines (1 NMNH). *Pottawattamie Co.*: Council Bluffs (7 NMNH). *Poweshiek Co.*: 1 mi S, 2 mi W Grinnell (1 KU). *Ringgold Co.*: 2 mi N Blockton (1 CM, 2 MHP); 1 mi S Blockton (1 CM, 2 MHP); 3 mi S Blockton (1 CM); 0.5 mi N, 2 mi E Mount Ayr (3 KU). *Sioux Co.*: Ireton (2 UMMZ). *Story Co.*: Ames (1 KU); 4 mi W Ames (2 KU); T82N, R22W, Sec 22 (1 KU); T84N, R23W, NW 1/4, Sec 12 (1 KU); T84N, R24W, Sec 23 (1 KU); T84N, R24W, NE 1/4, Sec 27 (9 HMNH). *Tama Co.*: 1 mi N, 1.5 mi W Lincoln (14 KU); Tama (2 UMMZ). *Taylor Co.*: 0.5 mi S, 1 mi E Lenox (2 CM, 1 MHP); 2 mi S, 1 mi E Lenox (1 CM); 4.5 mi S, 1 mi E Lenox (1 CM, 1 MHP); 5 mi S, 1 mi E Lenox (1 CM); 6 mi S, 1 mi E Lenox (2 CM, 3 MHP); 10 mi S Lenox (1 CM, 1 MHP); 12 mi S Lenox (8 CM, 8 MHP); 14 mi S Lenox (1 CM, 1 MHP); 17 mi S, 1 mi E Lenox (1 CM, 1 MHP); 19 mi S, 1 mi E Lenox (1 CM, 2 MHP). *Union Co.*: 1.75 mi N, 0.5 mi E Thayer (4 KU). *Van Buren Co.*: T68N, R10W, Sec 3 (1 CUI). *Webster Co.*: 2.5 mi S, 3.5 mi E Dayton (1 KU); Fulton (1 HMNH); Brushy Creek State Recreation Area, 2 mi N, 3 mi E Lehigh (3 CUI); Brushy Creek State Recreation Area, 1.5 mi E Lehigh (5 CUI). *Winnebago Co.*: 0.5 mi N, 3.5 mi W Thompson (2 KU). *Winneshiek Co.*: Conover (10 UMMZ); Decorah (12 HMNH, 6 UMMZ); Ridgeway (5 UMMZ). *Woodbury Co.*: T86, R44, Sec 25 (5 CUI).

MINNESOTA, UNITED STATES (234). *Anoka Co.*: Cedar Creek Forest, 4 mi E Bethel (2 MMNH); T31N, R23W, NE 1/4 Sec 12, Blaine (1 MMNH); Carlos Avery Game [Wildlife] Management Area (2 MHP); Carlos Avery Game Refuge [Wildlife Management Area] (1 MMNH); Carlos Avery Game Refuge [Wildlife Management Area], 6 mi E [W] Forest Lake (1 MMNH); 4 mi N Lino Lakes (2 MMNH); no specific locality (1 MMNH). *Benton Co.*: T38N, R30W, SE 1/4 Sec 18 (6 MMNH); T38N, R30W, SW 1/4 Sec 18 (1 MMNH). *Brown Co.*: T110N, R31W, SW 1/4 Sec 7 (4 MMNH). *Carver Co.*: T114N, R25W, NE 1/4 Sec 5 (6 MMNH); T116N, R25W, NW 1/4 Sec 5 (8 MMNH). *Clay Co.*: T141N, R46W, NW 1/4 Sec 24 (1 MMNH). *Clearwater Co.*: Itasca State Park (3 MMNH). *Dakota Co.*: Fort Snelling (1 MMNH). *Douglas Co.*: T129N, R37W, NE 1/4 Sec 30 (1 MMNH); T129N, R37W, SE 1/4 Sec 30 (1 MMNH). *Faribault Co.*: T102N, R25W, SW 1/4 Sec 11 (1 MMNH). *Freeborn Co.*: Big Island State Park, Albert Lea (1 MMNH); T104N, R19W, SE 1/4 Sec 22 (1 MMNH); T104N, R19W, NW 1/4 Sec 22 (2 MMNH). *Fillmore Co.*: Forestville (1 MMNH). *Goodhue Co.*: Pine Island, T109N, R15W, Sec 20 (1 MMNH); T110N, R17W, SW 1/4 Sec 16 (4 MMNH); T112N, R13W, SW 1/4 Sec 9 (1 MMNH); T112N, R15W, SE 1/4 Sec 9 (2 MMNH). *Greenwood Co.*: Hamilton (1 MMNH). *Hennepin Co.*: Brooklyn Township (1 MMNH); Brooklyn Center (1 MMNH); southeast end of Haydens Lake, Champlin (1 MMNH); Edina (2 MMNH);

Theo Wirth Park, Minneapolis (1 MMNH); Robbinsdale (2 MMNH); T119N, R23W, NE 1/4 Sec 32 (7 MMNH). *Houston Co.*: 2 mi N, 4 mi W Caledonia (1 MMNH); La Crescent (2 MMNH); 2 mi S Reno (2 MMNH). *Hubbard Co.*: Island Lake, 6 mi S Nevis (1 MMNH); T139N, R33W, SE 1/4 Sec 17 (1 MMNH). *Isanti Co.*: T34N, R24W, SE 1/4 Sec 21 (1 MMNH). *Jackson Co.*: Heron Lake (2 MMNH); T102N, R38W, NW 1/4 Sec 23 (2 MMNH). *Kandiyohi Co.*: 2 mi E Sibley State Park (1 MMNH); T118N, R34W, SE 1/4 Sec 2 (1 MMNH); T121N, R33W, SE 1/4 Sec 32 (2 MMNH). *Kittson Co.*: Skane Township (2 MMNH). *Lac Qui Parle Co.*: Sec 6, Manfred Township (1 MMNH); Sec 32, Mehurin Township (1 MMNH); T118N, R46W, SE 1/4 Sec 14 (3 MMNH). *Le Sueur Co.*: T110N, R23W, SW 1/4 Sec 8 (3 MMNH). *Lincoln Co.*: Sec 32, Diamond Lake Township (1 MMNH); Sec 1, Verdi Township (1 MMNH). *Lyon Co.*: Lynd (1 MMNH); T110N, R40W, SW 1/4 Sec 14 (2 MMNH); T112N, R40W, NE 1/4 Sec 14 (1 MMNH); T112N, R42W, SW 1/4 Sec 14 (2 MMNH). *Mahnomen Co.*: T143N, R42W, NW 1/4 Sec 13 (3 MMNH); T143N, R42W, Sec 33 (1 MMNH). *Marshall Co.*: T156N, R41W, NE 1/4 Sec 31 (1 MMNH); T156N, R45W, SE 1/4 Sec 32 (1 MMNH); T156N, R45W, SW 1/4 Sec 32 (2 MMNH). *Martin Co.*: 5 mi NW Fairmont (1 MMNH). *Meeker Co.*: Litchfield (2 MMNH); T121N, R31W, NE 1/4 Sec 30 (1 MMNH). *Mille Lacs Co.*: T42N, R25W, NW 1/4 Sec 7 (2 MMNH); T42N, R26W, SW 1/4 Sec 11 (1 MMNH). *Morrison Co.*: Clough Township (1 MMNH); Green Prairie Township (1 MMNH); 6 mi S Little Falls (1 MMNH). *Mower Co.*: T104N, R17W, NW 1/4 Sec 22 (1 MMNH). *Nicollet Co.*: T110N, R29W, NW 1/4 Sec 7 (2 MMNH). *Nobles Co.*: T104N, R40W, NW 1/4 Sec 23 (2 MMNH); T104N, R42W, SE 1/4 Sec 22 (3 MMNH). *Norman Co.*: T143N, R44W, NE 1/4 Sec 13 (1 MMNH); T145N, R44W, NW 1/4 Sec 13 (3 MMNH). *Olmsted Co.*: Pleasant Grove Township (1 MMNH); T106N, R11W, SW 1/4 Sec 23 (1 MMNH). *Ottertail Co.*: Parker's Prairie (3 MMNH); T133N, R40W, NE 1/4 Sec 25 (1 MMNH); T135N, R42W, NW 1/4 Sec 26 (3 MMNH). *Pipestone Co.*: Split Rock State Park, Ihlen (3 MMNH); 2 mi N Jasper (1 MMNH); T108N, R46W, NW 1/4 Sec 22 (2 MMNH). *Polk Co.*: T151N, R39W, SE 1/4 Sec 6 (1 MMNH); T153N, R50W, NE 1/4 Sec 12 (4 MMNH); T153N, R50W, NW 1/4 Sec 12 (1 MMNH). *Pope Co.*: 6.5 mi SSE Glenwood (1 MMNH). *Ramsey Co.*: Lake Josephine (3 MMNH); 0.5 mi E Lake Josephine (1 MMNH); Roseville, T29N, R23W, NE 1/4 Sec 11 (2 MHP); St. Paul (1 MMNH); St. Anthony Park, St. Paul (1 MMNH); T30N, R22W, NE 1/4 Sec 30 (5 MMNH); 1 mi NE Lake Valentine (1 MMNH); 1 mi E Valentine [Lake] (2 MMNH). *Redwood Co.*: T112N, R38W, SE 1/4 Sec 12 (1 MMNH). *Renville Co.*: 1 mi N, 5 mi W Morton (1 MHP); 2 mi N, 1 mi E Morton, T113N, R34W, SE 1/4 Sec 17 (1 MMNH); 3 mi N, 0.5 mi E Morton (1 MHP); T114N, R36W, NW

1/4 Sec 12 (2 MMNH). *Rock Co.*: Mound Township (1 MMNH); Rosedell Township (2 MMNH); T102N, R44W, NE 1/4 Sec 28 (1 MMNH); T102N, R46W, SE 1/4 Sec 27 (2 MMNH). *Roseau Co.*: Warroad (4 MMNH). *Scott Co.*: Savage (2 MMNH). *Sherburne Co.*: Elk River (6 MMNH); 6 mi S, 5 mi W Princeton [*in Mille Lacs Co.*], T35N, R27W, NE 1/4 Sec 33 (2 MMNH). *Sibley Co.*: 0.25 mi SE Gibbon (1 MMNH). *Stearns Co.*: T125N, R29W, SE 1/4 Sec 31 (1 MMNH). *Steele Co.*: T106N, R19W, NE 1/4 Sec 16 (2 MMNH); T106N, R21W, NW 1/4 Sec 16 (2 MMNH). *Stevens Co.*: T124N, R42W, SE 1/4 Sec 3 (1 MMNH); T124N, R44W, NW 1/4 Sec 2 (6 MMNH). *Swift Co.*: T120N, R42W, SE 1/4 Sec 2 (4 MMNH); T122N, R42W, SE 1/4 Sec 2 (2 MMNH); no specific locality (1 MMNH). *Todd Co.*: 0.5 mi S, 1 mi E Long Prairie, T129N, R33W, SE 1/4 Sec 21 (1 MMNH). *Waseca Co.*: T106N, R23W, NW 1/4 Sec 17 (1 MMNH). *Washington Co.*: 3 mi WNW Afton (1 MMNH); Birchwood (1 MMNH); T32N, R20W, SE 1/4 Sec 24 (1 MMNH). *Wilkin Co.*: Rothsay (2 MMNH). *Winona Co.*: Altura (1 MMNH); Dresbach (1 MMNH); Homer (1 MMNH). *Wright Co.*: T121N, R23W, SW 1/4 Sec 33 (4 MMNH).

MISSOURI, UNITED STATES (34). *Adair Co.*: 0.5 mi W Brashear, Hwy 6 (2 CM, 3 MHP); 3 mi N Connelleville (1 CM). *Clark Co.*: 1.5 mi N, 3 mi W Antioch, T64N, R8W, NW 1/4 Sec 14 (1 MHP). *Grundy Co.*: 3.5 mi S Modena [*in Mercer Co.*] (1 CM); 6.5 mi S Modena [*in Mercer Co.*] (2 CM); 2.5 mi S Tindall (3 CM). *Lewis Co.*: 1.5 mi N Canton, T62N, R5W, SE 1/4 Sec 23 (1 CM); 0.5 mi S, 2.5 mi E Deer Ridge, T62N, R9W, E 1/2 Sec 2 (1 CM); 0.5 mi S, 3 mi E Deer Ridge, T62N, R9W, E 1/2 Sec 1 (1 MHP); 2 mi S, 2 mi E Deer Ridge, T62N, R9W, SE 1/4 Sec 11 (1 CM); 2.5 mi S, 2 mi E Deer Ridge, T62N, R9W, E 1/2 Sec 14 (1 MHP). *Mercer Co.*: 14.5 mi N Goshen (2 CM, 2 MHP); 11 mi N Goshen (1 MHP); 9 mi N Goshen (1 MHP); 3 mi N Goshen (1 CM); 1 mi N Goshen (2 CM, 2 MHP); 1.5 mi S Goshen (1 MHP); 5.5 mi S Goshen (1 MHP). *Ralls Co.*: Hannibal (1 MUMZ). *Randolph Co.*: Moberly (2 MUMZ).

NEBRASKA, UNITED STATES (138). *Antelope Co.*: Neligh (1 NMNH). *Boyd Co.*: 5 mi WNW Spencer (1 KU); 5 mi S, 2 mi E Spencer (2 KU). *Buffalo Co.*: Kearney (2 NMNH). *Burt Co.*: 1 mi E Tekamah (2 KU). *Butler Co.*: Platt River, 2 mi E Columbus (1 KU); 4 mi E Rising City (2 KU); 5 mi E Rising City (4 KU). *Cass Co.*: Louisville (5 KU); 1 mi S Louisville (1 KU); 0.5 mi N Manley (1 KU); 0.5 mi W Manley (3 KU); 0.4 mi N, 2 mi W Weeping Water (1 KU); 1 mi N, 2 mi W Weeping Water (1 KU); 2 mi N, 2 mi W Weeping Water (3 KU); 1 mi S, 1.5 mi W Weeping Water (1 KU). *Cedar Co.*: 4 mi SE Laurel (7 KU). *Cherry Co.*: Valentine (3 NMNH); 4 mi E Valentine (1 KU); 3 mi SSE Valentine (2 KU). *Clay Co.*: 1 mi N, 1 mi W Saronville (1 KU); 1 mi N, 2 mi W Saronville (1

KU); 1 mi N, 3 mi W Saronville (1 KU). *Cuming Co.*: 1 mi S Beemer (1 KU). *Dawson Co.*: 5 mi S Gothenburg (1 KU). *Hall Co.*: 6 mi S Grand Island (3 KU). *Holt Co.*: 1 mi S Atkinson (1 KU); 6 mi N Midway (1 KU). *Keya Paha Co.*: 12 mi NNW Springview (1 KU). *Knox Co.*: 1 mi SE Niobrara (1 KU); 3 mi W Niobrara (2 KU). *Lancaster Co.*: Lincoln (1 KU); 0.5 mi N Lincoln (1 KU); 5 mi N Lincoln (1 KU); 1 mi S Lincoln (1 KU); 3 mi W Lincoln (1 KU). *Merrick Co.*: Platte River, 1.5 mi S Central City (2 KU). *Platte Co.*: Columbus (3 NMNH). *Polk Co.*: 15 mi W Osceola (2 KU). *Rock Co.*: Perch [Post Office (historical)] (4 AMNH). *Saline Co.*: 2 mi NE Crete (4 KU). *Sarpy Co.*: Fort Crook (1 AMNH); 1 mi W Meadow (3 KU); 3 mi S Springfield (1 KU). *Saunders Co.*: 2 mi NE Ashland (4 KU). *Seward Co.*: 1 mi N Pleasant Dale (4 KU). *Stanton Co.*: 4.5 mi SSE Norfolk [*in Madison Co.*] (1 KU). *Thurston Co.*: 1 mi S Winnebago (3 KU). *Valley Co.*: 2.5 mi N Ord (2 KU). *Washington Co.*: Blair (1 NMNH, 8 UMMZ); 1 mi E Blair (2 KU); 3 mi SE Blair (2 KU); 6 mi SE Blair (8 KU); 3 mi S, 4 mi E Fort Calhoun (3 MHP). *Wayne Co.*: 0.5 mi W Wayne (4 KU); Wayne (10 KU). *Washington Co.*: 3 mi S, 4 mi E Fort Calhoun (3 MHP, including the neotype of *B. b. brevicauda*).

NORTH DAKOTA, UNITED STATES (45). *Barnes Co.*: Valley City (2 NMNH). *Benson Co.*: Pleasant Lake (3 UMMZ). *Dickey Co.*: Oakes (3 NMNH). *Grand Forks Co.*: 3 mi S Grand Forks, T151N, R50W, SE 1/4 Sec 26 (1 MMNH). *McLean Co.*: Fort Berthold (1 NMNH). *Pembina Co.*: Pembina (1 NMNH); T163N, R55W, Sec 31 (1 MSB); Walhalla (1 NMNH). *Ramsey Co.*: Sweetwater Lake (2 NMNH). *Richland Co.*: Fairmont (2 NMNH); 5 mi NE Fairmont (2 NMNH); Wahpeton (11 NMNH). *Rolette Co.*: Fish Lake [=Belcourt Lake] (1 NMNH); Turtle Mountains (1 NMNH). *Traill Co.*: Portland (10 NMNH). *Walsh Co.*: Grafton (3 AMNH).

SOUTH DAKOTA, UNITED STATES (23). *Bon Homme Co.*: Sand Creek Park (1 KU); 3 mi SW Springfield (4 KU). *Clay Co.*: 1 mi S, 1 mi E Burbank (2 MSB); 0.5 mi W Vermillion (2 MSB). *Day Co.*: Waubay National Wildlife Refuge, Waubay (1 NMNH). *Grant Co.*: 6 mi N Milbank (3 KU). *Marshall Co.*: Roy Lake State Park (4 KU). *Roberts Co.*: Hartford Beach [State] Park (1 KU). *Union Co.*: Union County [State] Park, 1200 feet (5 KU).

WISCONSIN, UNITED STATES (25). *Burnette Co.*: Danbury (2 NMNH); 10 mi N Grantsburg (1 LACM). *Crawford Co.*: Lynxville (2 NMNH). *Grant Co.*: Cassville (1 NMNH); Platteville (1 AMNH, 5 NMNH); Wauzeka (3 NMNH). *La Crosse Co.*: La Crosse (2 NMNH). *Pepin Co.*: Pepin (1 NMNH). *Richland Co.*: Gotham (1 UWSP); Richland Center (1 UWSP); Viola (1 UWSP). *St. Croix Co.*: Roberts (1 UWSP). *Trempealeau Co.*: Trempealeau (2 NMNH). *Vernon Co.*: Hillsboro (1 UWSP).

***Blarina brevicauda aloga* Bangs**

1902. *Blarina brevicauda aloga* Bangs, Proceedings of the New England Zoological Club, 3:76, 31 March. Type locality: West Tisbury, Martha's Vineyard, Dukes County, Massachusetts. Holotype examined (MCZ B9727; see *Acknowledgments* for institutional abbreviations).
1902. *Blarina brevicauda compacta* Bangs, Proceedings of the New England Zoological Club, 3:77, 31 March. Type locality: Nantucket Island, Nantucket County, Massachusetts. Holotype examined (MCZ B9705).

Holotype: Young adult, sex unknown, skin and skull, Museum of Comparative Zoology 9727, obtained on 25 June 1899 by O. Bangs, original number 2 (for that date of collection). Skin in excellent condition, slightly foxed; molting on head, shoulders, and rump. Total length, 120; length of tail, 24; length of hind foot, 14. Skull in good condition; mandibles disarticulated; teeth moderately worn; annular tympanic bones missing. Occipito-premaxillary length, 21.7; P⁴-M³ length, 5.7; interorbital breadth, 5.9; cranial breadth, 11.9.

Distribution: Known only from Martha's Vineyard (84) and Nantucket Island (85), Massachusetts (Fig. 5).

Description: Relatively small in external and cranial dimensions, especially when compared to specimens from the adjacent Cape Cod mainland, except in interorbital breadth where the insular and mainland populations average nearly the same; moderately developed sagittal and lambdoidal crests; moderately pigmented teeth; grayish in pelage coloration above, noticeably paler below.

Diagnosis: Northern short-tailed shrews from Martha's Vineyard and Nantucket Island (84-85) are smaller on average than those from the adjacent mainland (Appendix 2, Tables 1 and 2, Fig. 4). By way of example, the occipito-premaxillary length, cranial breadth, and mandibular length in specimens from Martha's Vineyard and Nantucket Island (84-85) average 20.9, 11.6, and 11.8, respectively, whereas the same measurements in shrews from the adjacent mainland (83, 86) average 21.9, 12.3, and 12.4, respectively. The same sample groups do not differ in interorbital breadth (5.7).

Comparisons: Specimens from Martha's Vineyard and Nantucket Island (84-85) are distinctly smaller than those from the adjacent mainland (83, 86) in all dimensions except interorbital breadth, their teeth are pigmented less, and they are paler in pelage coloration, with more contrast in dorsal and ventral coloration. Individuals from Nantucket Island average slightly

larger than those from Martha's Vineyard, but the differences between them are much less pronounced than the differences among the insular forms and specimens from the mainland. Comparisons with other subspecies are provided in those accounts.

Remarks: Throughout the New England region, there is a slight but noticeable cline in the size of the cranium in *B. brevicauda* (for example, Choate, 1972). Specimens from southeastern Massachusetts, Rhode Island, and eastern Connecticut (83, 86) are smaller than those from the remainder of the New England mainland (75-82). Northern short-tailed shrews on Martha's Vineyard and Nantucket Island (84-85), however, are distinctly smaller than would be predicted on the basis of this cline, and they demonstrate a clearly defined step in variation that suggests a reduction in gene flow between the insular and mainland populations. In addition, there appears to be an "island effect" (Foster, 1964; Lomolino, 1985) in the Cape Cod area, whereby northern short-tailed shrews on Martha's Vineyard and Nantucket Island (84-85) are smaller than those at more inland New England sites (75-83). This pattern will be described in more detail in the Discussion and in subsequent Systematic Accounts because it is evident in other parts of the range of the northern short-tailed shrew.

Bangs (1902) named *Blarina brevicauda aloga* from Martha's Vineyard (Bangs, 1902:76) and *Blarina brevicauda compacta* from Nantucket Island (Bangs, 1902:77) in the same publication, distinguishing the 2 subspecies on the basis of pelage characteristics but not size. *B. b. aloga* was characterized as being brown above and pale gray below, with a well-defined line of demarcation along the sides, whereas *B. b. compacta* was characterized by the absence of a well-defined line of demarcation separating the dorsal and ventral pelage, with grayish ventral pelage extending up the flanks and onto the dorsum. Our analyses indicate that individuals from Nantucket Island are slightly larger than those from Martha's Vineyard, but the differences between them are minor when compared to northern short-tailed shrews from the adjacent mainland and across the range of the species. For example, occipito-premaxillary length, maxillary breadth, and mandibular length average 21.2, 7.5, and 11.8 in specimens from Nantucket Island (85) and 20.6, 7.4, and 11.7 in specimens from Martha's Vineyard (84), respectively, whereas the same measurements average 22.4, 7.7, and 12.6 in specimens from western Massachusetts (81) and 22.3, 7.7, and 12.6 in specimens from western Connecticut (87). In addition, we found scant differences in cranial morphology, dental pigmentation, or pelage coloration in shrews from the 2 islands. Because there is no compelling

counterargument, we apply the name *B. b. aloga* to this taxon because it has page priority.

Blarina brevicauda aloga

Specimens Examined (182) See *Acknowledgments* for institutional abbreviations.

MASSACHUSETTS, UNITED STATES (182). *Dukes Co.*: Holmes Hole (1 NMNH); Martha's Vineyard (3 NMNH, 1 UMMZ); Edgartown, Martha's Vineyard (1 NMNH); North Tisbury, Martha's Vineyard (2 NMNH); West Tisbury, Martha's Vineyard (1 MCZ [the holotype of *B. b. aloga*], 1 NMNH, 132 UCONN); 1 mi NE West Tisbury, Martha's Vineyard (2 UCONN); 0.3 mi SW West Tisbury, Martha's Vineyard (1 UCONN); Martha's Vineyard Island (12 UMMZ). *Nantucket Co.*: Nantucket (1 MCZ [the holotype of *B. b. compacta*], 5 NMNH); 4 mi E Nantucket (1 UCONN); 4 mi N Siasconset, Nantucket Island (4 UCONN); Nantucket Island (9 UCONN, 5 UMMZ).

***Blarina brevicauda cumberlandensis*, new subspecies
Webster, Moncrief, Choate, and Genoways**

Holotype: Adult female, skin and skeleton, Sam Noble Oklahoma Museum of Natural History 37146 (formerly University of Memphis Mammal Collection 10250), obtained 7 June 1979 by J. A. Huggins, original number 1112. Skin in good condition except that a small patch of fur is missing on both sides of the abdomen. Total length, 107; length of tail, 23; length of hind foot, 15. Skull in good condition; left annular tympanic bone missing; mandibles separated at mandibular symphysis; teeth moderately worn. Occipito-premaxillary length, 20.4; P⁴-M³ length, 5.6; maxillary breadth, 7.3; width of zygomatic plate, 2.3; interorbital breadth, 5.7; cranial breadth, 11.4. A dorsal view of the cranium is shown in Fig. 1.

Type locality: Murfreesboro, Rutherford County, Tennessee.

Distribution: Cumberland Plateau region of central Tennessee (60-62) and adjacent parts of western and south-central Kentucky (Fig. 5). *B. b. cumberlandensis* likely occurs in northern Alabama, north of the Tennessee River.

Description: Extremely small in external and cranial dimensions, especially in occipito-premaxillary length and interorbital breadth; poorly developed sagittal and lambdoidal crests; teeth scantily to moderately pigmented; pelage grayish to brownish-gray in color, slightly darker above than below.

Diagnosis: Specimens of *B. b. cumberlandensis* (60-62) average 20.5, 5.1, and 11.5 in occipito-premaxillary length, interorbital breadth, and cranial

breadth, respectively; whereas, other specimens of *B. brevicauda* from adjacent parts of eastern Tennessee (63-65) average 21.7, 5.4, and 12.0, and those from eastern Kentucky (56-59) average 21.3, 5.7, and 11.9 for the same cranial measurements (Appendix 2, Fig. 4).

Comparisons: Specimens of *B. b. cumberlandensis* are small in all cranial and external dimensions, and individuals of this taxon are among the smallest northern short-tailed shrews. *B. b. cumberlandensis* is much smaller than *B. b. brevicauda*, the largest of the northern short-tailed shrews, as well as an undescribed subspecies of moderately-large shrews from northeastern Kansas (OTU 25, Appendix 2). Also, the teeth in individuals of *B. b. cumberlandensis* are moderately pigmented on average; whereas, those in most other subspecies of *B. brevicauda* are more darkly pigmented.

In terms of its diminutive size, specimens of *B. b. cumberlandensis* warrant close comparisons only with specimens of *B. b. aloga* from Martha's Vineyard and Nantucket Island, Massachusetts (84-85), specimens from southeastern North Carolina (113-114), and specimens of an undescribed subspecies from the Delmarva Peninsula (104-106). Occipito-premaxillary length, maxillary breadth, interorbital breadth, and cranial breadth in specimens of *B. b. cumberlandensis* (60-62) average 20.5, 7.3, 5.1, and 11.5, respectively; specimens of *B. b. aloga* (84-85) average 20.9, 7.5, 5.7, and 11.6; specimens from southeastern North Carolina (113-114) average 20.8, 7.0, 5.2, and 11.2; and specimens from the Delmarva Peninsula (104-106) average 21.1, 7.3, 5.4, and 11.7 for the same cranial measurements, respectively (Appendix 2, Figs. 3 and 4). Thus, *B. b. cumberlandensis* is the smallest of the northern short-tailed shrews in cranial length, but its cranium is slightly wider than that of specimens from southeastern North Carolina (113-114).

Another species in the genus, *B. carolinensis*, is found to the east, south, and west of the Cumberland Plateau on the south side of the Tennessee River, but it is much smaller than *B. b. cumberlandensis*. By way of example, selected cranial measurements for 42 specimens of *B. b. cumberlandensis* (60-62), followed by those of 22 *B. carolinensis* from southeastern North Carolina (Appendix 3), are: occipito-premaxillary length, 20.5 and 18.4; P⁴-M³ length, 5.6 and 5.0; interorbital breadth 5.1 and 4.9; and cranial breadth, 11.5 and 9.9. In addition, specimens of *B. carolinensis* have a karyotype of 2N = 46 and FN = 48 throughout most of the geographic range, with exceptions in Florida and western Tennessee (Beck et al., 1991; Elrod et al., 1996; Qumsiyeh et al., 1997, 1999; M. L. Kennedy, pers. comm.), whereas the karyotype of *B. brevicauda* is 2N = 48-50 and FN = 48

(George et al., 1982).

Etymology: Along its eastern, southern, and western boundaries, the geographic distribution of *B. b. cumberlandensis* coincides with the Cumberland Plateau, as delineated by the Tennessee River, including the Land Between the Lakes region, hence the epithet *cumberlandensis*.

Remarks: There is little geographic variation in *B. b. cumberlandensis*, except along the northeastern limit of its range in Tennessee and Kentucky. For example, specimens of *B. b. cumberlandensis* from west-central Tennessee (60) average 20.4 in occipito-premaxillary length, 7.3 in maxillary breadth, and 11.5 in cranial breadth, whereas those from central Tennessee (61) average 20.3, 7.3, and 11.4, and those from northern Tennessee (62) average 20.9, 7.4 and 11.7, respectively, for the same measurements. Specimens from north-central Kentucky (56) average 21.2, 7.5, and 11.8, those from eastern Kentucky (59) average 21.3, 7.4, and 11.7, and those from southeastern Tennessee (63) average 21.8, 7.7, and 12.1, respectively. Thus, the geographic range of *B. b. cumberlandensis* coincides with the Cumberland Plateau of central Tennessee and the Pennyroyal Plateau of western Kentucky.

Like *B. b. aloga*, *B. b. cumberlandensis* displays a reduction in body size that may be explained by the “island effect” or “peninsula effect” (Foster, 1964; Lomolino, 1985), although it does so on a larger geographic scale than observed in other subspecies of *B. brevicauda*, because the geographic range of this taxon includes the entire Cumberland Plateau. This will be discussed in more detail beyond.

The southern short-tailed shrew, *B. carolinensis*, occurs to the south and west of the Cumberland Plateau, and the Tennessee River appears to be an isolating mechanism in preventing sympatry on either side of the river.

Blarina brevicauda cumberlandensis

Specimens Examined (96) See *Acknowledgments* for institutional abbreviations.

KENTUCKY, UNITED STATES (10). *Edmonson Co.:* Mammoth Cave (3 NMNH); River Styx [Mammoth Cave National Park] (3 KU). *Trigg Co.:* 8 mi NNE Golden Pond (2 UMMZ). *Wayne Co.:* near mouth of Hine’s Cave, Mill Springs (1 UMMZ); Monticello (1 NMNH).

TENNESSEE, UNITED STATES (86). *Anderson Co.:* Clear Creek (1 UMMZ); Oak Ridge (9 TTU). *Bledsoe Co.:* Cane Creek Bridge, E of south entrance, Fall Creek Falls State Park (1 UM). *Campbell Co.:* Brushy Mountain (west slope), 1 mi SE Caryville, Hwy 25 (6 UM); 4 air mi NW Caryville (9 UM); 1 mi S Jellico, I-75 (4 UM);

Walnut Mountain, 6.5 mi NW La Follette (1 UM); Rock Creek Mountain (west slope), 4.4 mi NNE La Follette (1 UM); E of La Follette (1 NMNH). *Claiborne Co.:* Lincoln Memorial University (1 UM); Newman’s Ridge [in Hancock Co.] (1 UMMZ). *Clay Co.:* fire tower, about 3.5 mi NNE Celina (2 UM). *Cumberland Co.:* Catoosa Wildlife Management Area, about 11.2 mi NNE Crossville (1 UM). *Davidson Co.:* Nashville (west side) (3 UM); Nashville (4 LSUMZ, 1 NMNH); Ashwood Ave, Nashville (1 LSUMZ); 2112 Woodlawn Ave, Nashville (1 LSUMZ). *DeKalb Co.:* Cul-Car-Mac Falls, Fall Creek Gorge (3 UM). *Dickson Co.:* vicinity of golf course, Montgomery Bell State Park (1 UM); Lake Woodhaven, Montgomery Bell State Park (1 UM); 2.2 mi E Tennessee City, 1.2 mi E jct Hwy 70 and CCC St (3 UM). *Fentress Co.:* Northrup Falls, 4.7 mi S, 3.3 mi E Jamestown (1 UM). *Grundy Co.:* about 5 mi NE Collins, Savage Gulf State Park (1 UM); bottom of Savage Gulf, Savage Gulf State Park, about 1200 ft (2 UM); Savage Falls Ranger Station (1 UM); Savage Falls Ranger Station, campground, 1350 ft (1 UM). *Humphreys Co.:* 0.5 mi N jct I-40 and Cuba Landing Rd (3 UM). *Lawrence Co.:* 5 mi W Lawrenceburg (1 LSUMZ). *Lincoln Co.:* 6 mi E Frankewing [in Giles Co.] (1 NMNH). *Marshall Co.:* Henry Horton State Park (1 CM). *Rhea Co.:* 2 mi W Washington, Hwy 30 (1 UM). *Roane Co.:* jct Hwy 95 and Haw Ridge, Oak Ridge (1 CM). *Rutherford Co.:* Murfreesboro (1 OMNH, the holotype of *B. b. cumberlandensis*). *Smith Co.:* Defeated Creek Recreation Area, about 4.3 mi NNE Carthage (1 UM). *Stewart Co.:* Stewart State Forest, East Branch Cross Creek, 3.5 mi S Carlisle (1 UM); 4.5 mi S Carlisle, Hwy 49 (1 UM); Dyer Creek Recreation Area, about 1 mi NE Dover (5 UM); Dover fire tower, 4.8 mi S Dover (1 UM). *Sumner Co.:* Strother Creek, 1.5 mi N Cottontown, Hwy 25 (2 UM). *Wayne Co.:* 8 mi N Waynesboro (1 NMNH). *Williamson Co.:* Burke Branch, 2 mi N Arrington (1 UM); South Harpeth Creek, about 2.4 mi SSW Fernvale (2 UM).

***Blarina brevicauda delmarvensis*, new subspecies Webster, Moncrief, Choate, and Genoways**

Holotype: Adult male, skin and skull, University of Kansas 45447, obtained on 12 January 1926 by Ralph W. Jackson, original number 301 (number 5867 of the Ralph Ellis, Jr., collection). Skin in excellent condition. Total length, 102; length of tail, 24; length of hind foot, 13.5. Skull in good condition, but mandibles separated at mandibular symphysis. Occipito-premaxillary length, 20.6; P⁴-M³ length, 5.7; maxillary breadth, 7.2; width of zygomatic plate, 2.2; interorbital breadth, 5.5; cranial breadth, 11.9.

Type locality: Cambridge, Dorchester County, Maryland.

Distribution: Southern half of Delaware and the

Eastern Shores of Maryland and Virginia (104-106; Fig. 5).

Description: Average cranial measurements for specimens from the southern two-thirds of the Delmarva Peninsula (104-106), followed by those from specimens from eastern Pennsylvania (97), southern New Jersey (99), northern Delaware (103), and the District of Columbia (102) are: occipito-premaxillary length, 21.1, 22.0, 21.6, 21.6, and 21.3; interorbital breadth, 5.4, 5.7, 5.6, 5.5, and 5.7; cranial breadth, 11.7, 12.2, 12.1, 12.0, and 12.1; mandibular length, 11.8, 12.5, 12.2, 12.2, and 12.1; and mandibular height, 6.2, 6.7, 6.5, 6.6, and 6.6. The dorsal pelage of specimens from the southern two-thirds of the Delmarva Peninsula (104-106) is slate-gray in color, slightly paler on the venter, and the teeth are moderately pigmented.

Diagnosis: Shrews from the southern two-thirds of the Delmarva Peninsula are distinctly smaller than average for the species in most cranial measurements, especially mandibular length and mandibular height, and they are clearly smaller than specimens from adjacent regions.

Comparisons: Shrews from the southern Delmarva Peninsula (*B. b. delmarvensis*) are intermediate in size between the extremely small shrews from southeastern North Carolina, the Cumberland Plateau Region of Tennessee (*B. b. cumberlandensis*), and Martha's Vineyard and Nantucket Island (*B. b. aloga*) and the large shrews from west of the Mississippi River (*B. b. brevicauda*), the undescribed subspecies of moderately-sized shrews from northeastern Kansas, and the moderately-sized shrews from the remainder of eastern North America. Average cranial measurements for shrews from southeastern North Carolina (113-114), *B. b. cumberlandensis* (60-62), and *B. b. aloga* (84-85) are: occipito-premaxillary length, 20.8, 20.5, and 20.9; interorbital breadth, 5.2, 5.1, and 5.7; cranial breadth, 11.2, 11.5, and 11.6; mandibular length, 11.4, 11.8, and 11.8; and mandibular height, 6.0, 6.2, and 6.3. Average cranial measurements for *B. b. brevicauda*, the undescribed shrew from northeastern Kansas, and shrews from the remainder of eastern North America are provided in those accounts.

Etymology: The name *delmarvensis* refers to the geographic distribution of this northern short-tailed shrew, which is restricted to the southern two-thirds of the Delmarva Peninsula. The name of the peninsula is an abbreviation formed by the names of the states that compose the peninsula, in alphabetical order—*del*, Delaware; *mar*, Maryland; *va*, Virginia.

Remarks: There is subtle size variation in *B. b. delmarvensis*, as shrews from southern Delaware (104) and the Eastern Shore of Maryland (105) are virtually

indistinguishable in size, whereas those from the Eastern Shore of Virginia (106) are slightly larger in maxillary breadth and cranial breadth (Table 2). Populations from northern Delaware (103), however, demonstrate a clearly defined zone of intergradation with populations of *B. b. delmarvensis* from the southern two-thirds of the Delmarva Peninsula. Evidence of this intergradation extends to populations from southern New Jersey (99) and the District of Columbia (102) as well. Nonetheless, specimens from northern Delaware, southern New Jersey, and the District of Columbia are more similar morphologically to specimens from New York (88-91), Pennsylvania (93-97), and mainland Virginia (107-110) than they are to populations from the southern two-thirds of the Delmarva Peninsula, which we assign to *B. b. delmarvensis*. Thus, the island (or peninsula) effect appears to be evident in northern short-tailed shrews on the Delmarva Peninsula.

The small size of northern short-tailed shrews on the Delmarva Peninsula has caused some confusion among mammalogists working on the genus in the past. For example, prior to the seminal work by Genoways and Choate (1972) and Genoways et al. (1977), which clearly demonstrated that the genus *Blarina* consisted of at least 3 species rather than 1 ubiquitous, highly variable species, it was not uncommon to refer short-tailed shrews from the lower Delmarva Peninsula to *B. brevicauda carolinensis* (see, for example, Bole and Moulthrop, 1942; Gardner, 1950; Jones and Findley, 1954), which would have placed these shrews in the species *B. carolinensis* under the new taxonomic arrangement.

Blarina brevicauda delmarvensis

Specimens Examined (77) See *Acknowledgments* for institutional abbreviations.

DELAWARE, UNITED STATES (11). *Sussex Co.*: Bethany Beach (1 AMNH); Trap Pond State Park (10 DMNH).

MARYLAND, UNITED STATES (23). *Dorchester Co.*: Cambridge (14 KU [including the holotype of *B. b. delmarvensis*], 3 LACM, 1 NMNH, 2 UMMZ); Blackwater Refuge, Cambridge (1 NMNH). *Worcester Co.*: Pocomoke Swamp, 1 mi S Delaware state line (2 UMMZ).

VIRGINIA, UNITED STATES (43). *Accomack Co.*: Belle Haven (1 NMNH); 1.5 mi E Wattsville (2 NMNH); 2.3 mi E Wattsville (1 NMNH). *Northampton Co.*: Cape Charles (16 NMNH); 1 mi S Cape Charles (5 CM); 1 mi S Cape Charles, M T Wells estate (2 CM); 8 mi S, 1.5 mi E Cheriton (9 VMNH); Eastern Shore of Virginia National Wildlife Refuge (4 VMNH); Eastville (3 AMNH).

***Blarina brevicauda jerrychoatei*, new subspecies
Webster, Moncrief, and Genoways**

Holotype: Young adult male, skin and skull, University of Kansas 114306, obtained on 4 November 1967 by Jerry R. Choate, original field number 694. Skin in excellent condition. Total length, 110; length of tail, 23; length of hind foot, 16. Skull in excellent condition, but mandibles separated at mandibular symphysis. Occipito-premaxillary length, 22.5; P⁴-M³ length, 6.3; maxillary breadth, 7.8; width of zygomatic plate, 2.3; interorbital breadth, 6.1; cranial breadth, 12.5.

Type locality: Taken in the “turnpike right-of-way, 1 ½ mi N, 1 ½ mi E Courthouse, Lawrence,” Douglas County, Kansas.

Distribution: Disjunct; currently known only from the valleys of the Kaw River and its tributaries in Douglas, Jefferson, and Leavenworth counties, Kansas (25; Fig. 5).

Description: *B. b. jerrychoatei* is intermediate in external and cranial measurements. The skull is slightly depressed in lateral view, and the sagittal and lambdoidal crests are moderately developed. The dark pelage is slate gray to plumbeous gray above and slightly paler below, and the tail is relatively hairy.

Diagnosis: Northern short-tailed shrews from northeastern Kansas are similar in most respects to shrews from the Great Lakes and Ohio River Valley. Specimens of *B. b. jerrychoatei* have moderately-sized skulls (Appendix 2) with long, narrow rostra. The bones forming the external nares (nasals and premaxillaries) are not greatly inflated, and the teeth, feet, and tail are darkly pigmented.

Comparisons: Compared to other subspecies, the skull of *B. b. jerrychoatei* is intermediate in most characters, not as massive as in specimens from elsewhere west of the Mississippi River, only slightly smaller than in specimens from the Great Lakes, Ohio River Valley, and New England, and distinctly larger than in specimens from Martha’s Vineyard and Nantucket Island, the Cumberland Plateau of Tennessee and adjacent Kentucky, the southern Delmarva Peninsula, or southeastern North Carolina. For example, average cranial measurements for *B. b. jerrychoatei* (25), followed by those for *B. b. brevicauda* from eastern Nebraska (11-12), animals from Indiana (47-50), *B. b. aloga* from Martha’s Vineyard and Nantucket Island (84-85), *B. b. cumberlandensis* from central Tennessee (60-62), *B. b. delmarvensis* from the southern Delmarva Peninsula (104-106), and specimens from southeastern North Carolina (113-114), respectively, are: occipito-premaxillary length, 22.4, 23.6, 21.7, 20.9, 20.5, 21.1,

and 20.8; interorbital breadth, 5.8, 6.1, 5.7, 5.7, 5.1, 5.4, and 5.2; cranial breadth, 12.6, 13.2, 12.2, 11.6, 11.5, 11.7, and 11.2; and mandibular height, 7.1, 7.6, 6.8, 6.3, 6.2, 6.2, and 6.0.

The size of the teeth and the amount of dental pigmentation follows a similar pattern—specimens of *B. b. jerrychoatei*, on average, have teeth that are not as large and dark as those in *B. b. brevicauda* but not as small and pale as those in *B. b. aloga*, *B. b. cumberlandensis*, *B. b. delmarvensis*, or animals from southeastern North Carolina (113-114). Specimens of *B. b. jerrychoatei* have dental pigmentation most similar to animals from the Great Lakes, Ohio River Valley, and New England, paler than in specimens from the southern Appalachian Mountains, but darker than in specimens from the Great Dismal Swamp of southeastern Virginia (110) and northeastern North Carolina (111). When viewed in lateral profile, the slope of the skull in specimens of *B. b. jerrychoatei* is somewhat depressed as in specimens from the Great Lakes and Ohio River Valley regions, and not inflated as in specimens from New England, the southern Appalachian Mountains, the Great Dismal Swamp, or southern Wisconsin.

Etymology: It is a pleasure to name this isolated population of northern short-tailed shrew for our colleague, mentor, and friend, the late Professor Jerry R. Choate. Jerry was an eminent mammalogist who authored 5 books, more than 150 refereed journal articles, and 55 un-refereed and technical publications. One of his areas of expertise was New World shrews. He successfully chaired the graduate committees of 55 students who received their Masters of Science at Fort Hays State University. Professor Choate holds the distinction of winning 3 of the most prestigious awards of the American Society of Mammalogists: the C. Hart Merriam Award (for research), the Grinnell Award (for education), and Honorary Membership (for outstanding contributions to the Society).

Remarks: The disjunct geographic distribution of *B. b. jerrychoatei* is unusual in that *B. brevicauda* is continuously distributed throughout most of its geographic range; the only other disjunct populations in this species occur on islands (for example, Nova Scotia, Martha’s Vineyard, and Nantucket Island). It is clear that *B. brevicauda* was more widely distributed in the southern and eastern United States during the Illinoian and Wisconsinian glacial maxima (Jones et al., 1984); however, there are Irvingtonian records of *B. fossilis* [= *B. b. brevicauda* see account for that subspecies] from Lincoln County, Kansas (Hibbard, 1943), and *B. ozarkensis* from Newton County, Arkansas (Brown, 1908). Later, during the warm moist Hypsithermal

Period, the geographic distribution of *B. brevicauda* also moved northward and westward into the Great Plains (Jones, 1964; Jones et al., 1984). Then, during the warm, dry Xerothermic Period, species that prefer mesic conditions found refugia along permanent watercourses. We hypothesize that 1 such species, *B. brevicauda*, became isolated in the floodplains and adjacent uplands of the Kaw River valley, differentiating over time to become *B. b. jerryrchoatei*.

The geographic range of another species in the genus, *B. hylophaga*, completely surrounds that of *B. brevicauda jerryrchoatei* (Thompson 2008). To date, there is no indication that these taxa are anywhere sympatric, although a Douglas County, Kansas, specimen of *B. hylophaga* from 5.2 mi W, 0.5 mi S Clinton (KU 18560) is in close proximity to a Douglas County, Kansas, specimen from Rock Creek (KU 1738) and 2 Douglas County, Kansas, specimens from 7.5 mi SW Lawrence (KU 4732 and 6173). Specimens of *B. hylophaga* that we examined were collected in Doniphan, Brown, Nemaha, western Atchison (Muscotah), Jackson, Shawnee, Osage, and Anderson counties, Kansas, and they completely surround the population of *B. b. jerryrchoatei* in northeastern Kansas. There is some overlap in cranial measurements when comparing individuals, but specimens of *B. hylophaga* from central Kansas (Ellis, Osborne, Phillips, Rooks, Rush, Russell, and Trego counties; Moncrief et al., 1982) consistently average smaller than specimens of *B. b. jerryrchoatei* (25) from northeastern Kansas, respectively, as follows: occipito-premaxillary length, 20.9 and 22.4; cranial breadth, 11.5 and 12.6; mandibular height, 6.3 and 7.1; and articular width, 2.3 and 2.6. In addition, *B. hylophaga* (2N = 52 and FN = 60-62) and *B. brevicauda* (2N = 48-50 and FN = 48) have different karyotypes (George et al., 1982). Jones and Glass (1960) identified the clearly defined steps in size of *Blarina* in the Great Plains: large in the Dakotas and northern Nebraska, distinctly smaller in southern Nebraska and most of Kansas and Oklahoma, and intermediate in size in northeastern Kansas. We refer specimens in these 3 geographic regions to *B. b. brevicauda*, *B. hylophaga*, and *B. b. jerryrchoatei*, respectively.

The area occupied by *B. b. jerryrchoatei* and *B. hylophaga* in northeastern Kansas was glaciated during the Pleistocene about 600,000 years ago, but no other major geological events have occurred in this area since that time. The escarpment marking the southern rim of the Wakarusa River south of Lawrence was the southernmost extension of the ice. The original distribution and relationship of *B. b. jerryrchoatei* and *B.*

hylophaga in the Kaw River valley and its environs are impossible to reconstruct. The original forests and tall grass prairie of the area have been removed, and much of the land has been converted to agricultural purposes. The current forests are a mixture of native and introduced species (Charlton, 2002). However, it appears that *B. b. jerryrchoatei* is confined to the valleys of the Kaw and Wakarusa rivers in the vicinity of Lawrence eastward to near the Missouri River. This may indicate that *B. b. jerryrchoatei* prefers more overhead cover and a more mesic habitat than *B. hylophaga*, but in reality, research on the comparative habitat requirements of these 2 species is inadequate to make this final judgement.

Blarina brevicauda jerryrchoatei

Specimens Examined (169) See *Acknowledgments* for institutional abbreviations.

KANSAS, UNITED STATES (169). *Douglas Co.*: 1.25 mi N Baldwin (1 KU); East 1600 Rd, south I-70, north railroad, T12S, R20E, SE 1/4 Sec 20 (12 KU); 0.5 mi W Eudora (2 KU); Lawrence (2 AMNH, 22 KU); 2 mi N Lawrence (1 KU); 5 mi N Lawrence (3 KU); 0.5 mi N, 1 mi E Lawrence (1 KU); 1.5 mi N, 1.2 mi E Lawrence, turnpike right-of-way (12 KU, including the holotype of *B. b. jerryrchoatei*); 1.5 mi N, 1.75 mi E Lawrence courthouse, sandpits (3 KU); 1.9 mi N, 1.6 mi E Lawrence (2 KU); 2 mi N, 1.67 mi E Lawrence, T12S, R20E, SE 1/4 Sec 20 (2 MHP); 2 mi N, 2 mi E Lawrence courthouse (2 KU); 2.2 mi N, 0.8 mi E Lawrence courthouse (2 KU); 2.5 mi N, 0.5 mi E Lawrence, T12S, R20E, W 1/2 Sec 20 (2 MHP); 4 mi N, 2 mi E Lawrence (1 KU); 4.8 mi N, 0.7 mi E Lawrence, 900 ft (1 KU); 5.5 mi N, 3 mi E Lawrence (2 KU); 6 mi ENE Lawrence (*in* Leavenworth Co.) (1 KU); 6.4 mi S Lawrence (1 KU); 0.8 mi S, 2.5 mi W Lawrence (1 KU); 1 mi S, 8 mi W Lawrence (2 KU); 3.9 mi S, 2.6 mi E Lawrence courthouse (1 KU); 5.75 mi S, 0.75 mi W Lawrence courthouse (1 KU); 7 mi SW Lawrence (4 KU); 7.5 mi SW Lawrence (5 KU); 1 mi W Lawrence (7 KU); 2.5 mi W Lawrence (1 KU); 3.5 mi W Lawrence (12 KU); 1 mi N, 4 mi W Lawrence (1 KU); 2.5 mi N, 2 mi W Lawrence (1 KU); 0.5 mi S, 0.5 mi E Pleasant Grove (1 KU); 1 mi S, 1.25 mi W Vinland (1 KU); west of KU campus (1 KU); no specific locality, 855 ft (2 KU); no specific locality (15 KU). *Jefferson Co.*: 7 mi NNE Lawrence (2 KU); 14 km NE Lawrence, Nelson Environmental Study Area (4 KU); 17 km NE Lawrence, Nelson Environmental Study Area (21 KU); Nelson Environmental Study Area (5 KU); Rock Creek (1 KU); Rockefeller Tract (1 KU). *Leavenworth Co.*: Bonner Springs, 1 mi N, 4 mi W Hwys 40 and 7 (2 KU); 2.5 mi N, 3 mi E Lawrence (*in* Douglas Co.) (1 KU); no specific locality (1 KU).

Blarina brevicauda knoxjonesi Webster

1996. *Blarina brevicauda knoxjonesi* Webster, in Contributions in mammalogy, a memorial volume honoring Dr. J. Knox Jones, Jr., Museum of Texas Tech University, Lubbock. p. 52, 5 September. Type locality: Carolina Beach, New Hanover County, North Carolina. Holotype examined (NMNH 567349, formerly UNCW 486; see *Acknowledgments* for institutional abbreviations).

Holotype: Adult male, skin and skull, National Museum of Natural History 567349, obtained on 16 November 1982 by W. D. Webster, original field number 1294. Skin in excellent condition except for a small patch of fur missing from the right side of the abdomen. Total length, 114; length of tail, 23; length of hind foot, 14; weight, 11.0. Skull in excellent condition. Occipito-premaxillary length, 20.3; P⁴-M³ length, 5.6; maxillary breadth, 6.7; width of zygomatic plate, 2.2; interorbital breadth, 5.4; cranial breadth, 10.8.

Distribution: Eastern North Carolina, south of the Pamlico River (113-114).

Description: In most dimensions, individuals of *B. b. knoxjonesi* are among the smallest of *B. brevicauda*, especially measurements of cranial breadth (maxillary breadth, cranial breadth, and articular width) and mandibular dimensions (length and height; Appendix 2, Tables 1 and 2, Fig. 4). Teeth with scant dental pigmentation; molariform teeth relatively small; poorly developed sagittal and lambdoidal crests; pelage brownish-gray, with little frosting on the tips of the individual hairs in the chin and throat region.

Diagnosis: Specimens of *B. b. knoxjonesi* are small, and their gracile skulls are extremely narrow when compared to skulls of other northern short-tailed shrews. To the north of the distribution of this subspecies, specimens are larger in all dimensions, as described in more detail below, and size is the primary character that can be used to separate these taxa in the zone of intergradation.

Comparisons: Given its diminutive size and scantily pigmented teeth, specimens of *B. b. knoxjonesi* are easily distinguished from those of *B. b. brevicauda*, *B. b. jerrychoatei*, and specimens from northeastern North Carolina, all of which are much larger in size and have more richly pigmented teeth. Compared to specimens of *B. b. aloga* and *B. b. delmarvensis*, specimens of *B. b. knoxjonesi* are smaller overall and their teeth have less pigmentation, and compared to specimens of *B. b. cumberlandensis*, specimens of *B. b. knoxjonesi*

are smaller in maxillary breadth, cranial breadth, mandibular length, mandibular height, and articular width but larger in occipito-premaxillary length and interorbital width. Average cranial measurements for *B. b. knoxjonesi* (113-114), followed by those for *B. b. aloga* (84-85), *B. b. cumberlandensis* (60-62), and *B. b. delmarvensis* (104-106), respectively, are: occipito-premaxillary length, 20.8, 20.9, 20.5, and 21.1; maxillary breadth, 7.0, 7.4, 7.3, and 7.3; interorbital breadth, 5.2, 5.7, 5.1, and 5.4; cranial breadth, 11.2, 11.6, 11.5, and 11.7; mandibular length, 11.4, 11.8, 11.8, and 11.8; mandibular height, 6.0, 6.3, 6.2, and 6.2; and articular width, 2.2, 2.3, 2.3, and 2.4.

Remarks: The geographic distribution of *B. brevicauda* extends southward from the Great Dismal Swamp in southeastern Virginia along the east coast of North Carolina. *B. b. knoxjonesi* exhibits the “peninsula effect” or “island effect” (Foster, 1964; Lomolino, 1985), which is discussed in more detail beyond. *B. b. knoxjonesi* has a broad zone of intergradation with another subspecies north of the Pamlico River in eastern North Carolina. Along this zone of intergradation, moving from the Pamlico River (112) northward into the Great Dismal Swamp region of northeastern North Carolina (111) and southeastern Virginia (110), specimens are larger, primarily in external measurements and those of cranial length. Continuing northward beyond the Great Dismal Swamp, specimens from eastern Virginia (107) and District of Columbia (102) have moderately pigmented teeth, a continued increase in cranial length and external measurements, but with a sudden increase in measurements reflecting cranial width. Average cranial measurements for specimens of *B. b. knoxjonesi* (114-115), followed by specimens from eastern North Carolina (112), the Great Dismal Swamp (110-111), and eastern Virginia and District of Columbia (102, 107), respectively, are: occipito-premaxillary length, 20.8, 21.7, 22.0, and 21.4; maxillary breadth, 7.0, 7.3, 7.4, and 7.6; interorbital breadth, 5.2, 5.4, 5.6, and 5.7; and cranial breadth, 11.2, 11.6, 12.0, and 12.0.

The geographic ranges of *B. brevicauda* and *B. carolinensis* overlap more in eastern North Carolina than anywhere else along their lengthy zone of contact (Webster et al., 1985; Webster, 1996; Trani et al., 2007). In eastern North Carolina these 2 species are broadly sympatric, but not syntopic. Specimens of *B. brevicauda* are found in mesic to wet pocosins (poorly-drained higher ground between streams that are dominated by wetland vegetation), river floodplains, and associated wetlands with organic soils. On the other hand, specimens of *B. carolinensis* are found in upland fields, oak-hickory

forests, and hardwood-pine forests on well-drained sandy soils (Webster, 1996).

Throughout this zone of sympatry these 2 species differ in size and karyotype; furthermore, hybridization between these 2 species has not been documented (Webster, 1996). Selected cranial measurements for 22 specimens of *B. brevicauda* from southeastern North Carolina (114-115), followed by those of 22 *B. carolinensis* from southeastern North Carolina (Appendix 3), are: occipito-premaxillary length, 20.8 and 18.4; P⁴-M³ length, 5.6 and 5.0; interorbital breadth, 5.2 and 4.9; and cranial breadth, 11.2 and 9.9.

Blarina brevicauda knoxjonesi

Specimens Examined (119) See *Acknowledgments* for institutional abbreviations.

NORTH CAROLINA, UNITED STATES (119). *Beaufort Co.*: 4 mi N Aurora (19 UNCW). *Bladen Co.*: 2 mi S Rowan, Colly Creek at Hwy 210 (4 UNCW); Salters Lake (1 NCSM). *Carteret Co.*: 5.5 mi ESE Harlowe (1 NCSM); about 2 mi WSW Harlowe (1 NCSM); Straits (1 UNCW). *Craven Co.*: about 7 mi WSW Croatan (1 NCSM); about 8.9 mi SW Croatan (4 NCSM); about 1.25 mi WSW Havelock (1 NCSM); about 11.25 mi WSW Havelock (1 NCSM). *Columbus Co.*: no specific locality (1 NCSM). *Duplin Co.*: 4 km ENE Magnolia, Hwy 40 (4 UNCW); 2.5 km E Rose Hill (2 UNCW); 6 mi NE Wallace, SR 1947 (4 UNCW); 8 mi NE Wallace, Hwy 41 (2 UNCW); 10 km S Warsaw (1 UNCW); 4 km W Warsaw, Hwy 24 (4 UNCW). *Hoke Co.*: about 1.5 mi SW McCain, Hwy 211 (1 NCSM); 5 mi W Raeford, Hwy 211 (2 UNCW); 8 mi W Raeford (1 NCSM). *Jones Co.*: about 7 mi ESE Pollackville (3 NCSM). *New Hanover Co.*: Carolina Beach (1 NMNH [the holotype of *B. b. knoxjonesi*], 6 UNCW); 1.25 mi SW Carolina Beach, SR 1573 (1 NCSM); Castle Hayne (1 UNCW); Wilmington (11 UNCW); 6 mi N Wilmington (1 UNCW). *Pender Co.*: 8 km SSE Burgaw, Hwy 40 (4 UNCW); 6 km NNE Castle Hayne, Hwy 40 (2 UNCW); Holly Shelter Game Land (3 UNCW); Holly Shelter Game Land, 10 km E Burgaw (2 UNCW); Holly Shelter Game Land, 8 km NE Hampstead (1 UNCW); Scotts Hill, Hwy 17 (13 UNCW); 7 km SE Wallace, Hwy 40 (1 UNCW); 2 km E Watha, Hwy 40 (4 UNCW); 3 km E Willard, Hwy 40 (1 UNCW). *Pitt Co.*: Conetoe Creek, 3 mi W Bethel (1 NMNH). *Sampson Co.*: 3 mi W Roseboro (1 NMNH). *Richmond Co.*: 4.1 mi NNW Hoffman at Moore County line (2 NCSM). *Sampson Co.*: 5.9 mi NNW Delway, SR 1004 (1 NCSM); 2 km SW Newton Grove, SR 1648 (2 UNCW). *Scotland Co.*: 8 km SW Laurinburg, Hwy 15/401 (1 UNCW).

Blarina brevicauda talpoides (Gapper)

1830. *Sorex talpoides* Gapper, Zoological Journal, 5:202. Type locality: between York (Toronto) and Lake Simcoe, Ontario, Canada.
1837. *Sorex dekayi* Bachman, Journal of the Academy of Natural Sciences of Philadelphia, 7:377. Type locality: New Jersey (see Handley and Choate, 1970; Bangs, 1902:75; and Merriam, 1895:10).
1848. *G[alemys]. micrurus* Pomel, Archives des Sciences Physiques et Naturelles, Genève, 9:249 (= *S. talpoides* Gapper, see Handley and Choate, 1970).
1858. *Blarina angusticeps* Baird, Mammals, in Reports of explorations and surveys ... railroad routes, 8(1):34, 14 July. Type locality: Burlington, Chittenden County, Vermont. Holotype examined (NMNH 1318/2120; see *Acknowledgments* for institutional abbreviations).
1895. *Blarina telmalestes* Merriam, North American Fauna, 10:15, 31 December. Type locality: Lake Drummond, Dismal Swamp, City of Chesapeake (formerly Norfolk County), Virginia. Holotype examined (NMNH 71823).
1899. *Blarina simplicidens* Cope, Journal of the Academy of Natural Sciences, Philadelphia, 11:219. Holotype examined (ANSP 150), a left ramus bearing the molars and incisor from Port Kennedy Cave, Irvingtonian Mammal Age, Montgomery County, Pennsylvania, but not included in the Specimens Examined.
1908. *Blarina brevicauda ozarkensis* Brown, Memoirs of the American Museum of Natural History, 9:170, February. Holotype examined (AMNH 11794), anterior half of skull with molariform teeth from Conard Fissure, Irvingtonian Mammal Age, Newton County, Arkansas, but not included in the Specimens Examined.
1940. *Blarina brevicauda pallida* R. W. Smith, American Midland Naturalist, 24:223, 31 July. Type locality: Wolfville, Kings County, Nova Scotia. Holotype examined (MVZ 86682).
1942. *Blarina brevicauda kirtlandi* Bole and Moulthrop, Scientific Publications of the Cleveland Museum of Natural History, 5:99, 11 September. Type locality: Holden Arboretum, Kirtland Township, Lake County, and Chadron Township, Geauga County, Ohio. Holotype examined (UMMZ 121250, formerly CMNH 16895).
1942. *Blarina brevicauda churchi* Bole and Moulthrop, Scientific Publications of the Cleveland Museum of Natural History, 5:109, 11 September. Type locality: Roan Mountain, Mitchell County, North Carolina.

Holotype examined (UMMZ 121249, formerly CMNH 42158).

1942. *Blarina brevicauda hooperi* Bole and Moulthrop, Scientific Publications of the Cleveland Museum of Natural History, 5:110, 11 September. Type locality: Lyndon, Caledonia County, Vermont. Holotype examined (UMMZ 77380).

1943. *Blarina brevicauda angusta* Anderson, Annual Report of the Provancher Society of Natural History, Québec, p. 52, 7 September. Type locality: Kellys Camp, Berry Mountain Brook, near the head of Grand Caspédia River, Gaspé County, Québec, Canada, altitude about 1600 ft. Holotype not examined (CMN 11655).

Neotype: Young adult female, skin and skull, Royal Ontario Museum 21641, obtained on 12 September 1935 by S. C. Downing and prepared by G. H. Richardson, original number [GHR] 3. Skin in excellent condition; newly molted pelage except in the region of the hip glands. Total length, 108; length of tail, 28, length of hind foot, 15. Skull in excellent condition; left angular process broken to about half its normal length; mandibles separated at mandibular symphysis; teeth evincing scant wear. Occipito-premaxillary length, 22.1; P⁴-M³ length, 5.9; interorbital breadth, 5.6; cranial breadth, 12.6.

Type locality: Herein restricted to Pottageville (Kettleby Kabin), York County, Ontario.

Distribution: Southern Ontario, northeastern Minnesota, eastern Wisconsin, and eastern Illinois eastward across the Great Lakes and Ohio River regions to the Atlantic Coast (from Nova Scotia southward to northeastern North Carolina, save for the southern two-thirds of the Delmarva Peninsula), and southward along the Appalachian Mountains to western South Carolina, northern Georgia, and east-central Alabama, terminating in Lee and Elmore counties, Alabama, and Monroe and Jones counties, Georgia (14, 26-27, 29-59, 63-83, 86-103, 107-112; Fig. 5). A disjunct population occurs in Barbour County, Alabama, and Quitman and Stewart counties, Georgia, on opposite sides of the Chattahoochee River (French, 1981; Fig. 5).

Description: Uniform pelage coloration and intermediate characteristics including external and cranial measurements of size, development of the sagittal and lambdoidal crests, and dental pigmentation throughout the core of its geographic distribution. Larger and with a broader, more robust cranium in the southern Appalachian Mountains (64-65) and in eastern Wisconsin (27) and Illinois (29-31), where the sagittal and lambdoidal crests are more developed, the teeth are more darkly pigmented, and the pelage is darker in

coloration. Larger, but with a proportionately narrower cranium in the Northeast (70-82, 87-98), where the cranial crests are less developed and the teeth and pelage are less darkly pigmented. Smaller, especially in measurements reflecting cranial width, in the Great Dismal Swamp region of southeastern Virginia (110) and northeastern North Carolina (111).

Diagnosis: *B. b. talpoides* is highly variable throughout its geographic distribution, but specimens from most of its geographic range—southeastern Ontario (32-37), the Great Lakes region (38-55), Pennsylvania (93-97), New York (88-91), mainland New England (75-82, 87), and the Canadian Maritime Provinces (71-74)—are intermediate in most characters relative to other subspecies of *B. brevicauda*. In other words, *B. b. talpoides* is not as small as *B. b. aloga*, *B. b. cumberlandensis*, *B. b. delmarvensis*, or *B. b. knoxjonesi*, and it is not as large as *B. b. brevicauda*, despite the variability *B. b. talpoides* shows in cranial dimensions.

Comparisons: Specimens of *B. b. talpoides*, when compared to those of *B. b. brevicauda*, are smaller in external and cranial dimensions, especially in measurements of cranial width, their nasal and premaxillary bones are less inflated in the region of the external nares, their sagittal and lambdoidal crest are less well developed, their teeth are less darkly pigmented, and their pelage coloration is paler. However, individuals of *B. b. talpoides* become larger, with more robust crania, darker teeth, and darker pelages at higher elevations in the southern Appalachian Mountains (64-65) and along a zone of intergradation with *B. b. brevicauda* in eastern Wisconsin (27) and Illinois (29-31). Individuals from the Great Dismal Swamp of southeastern Virginia and northeastern North Carolina (110-111), which are in a zone of intergradation with *B. b. knoxjonesi*, however, are narrower in cranial dimensions, their cranial crests are less well developed, their teeth are less darkly pigmented, and they are paler in pelage coloration.

In terms of overall similarity, *B. b. talpoides* most closely resembles *B. b. jerrychoatei*, especially when comparing individuals of *B. b. talpoides* from Illinois (29-31) with individuals of *B. b. jerrychoatei* from northeastern Kansas (25). Specimens from these OTUs have moderately-sized skulls (Appendix 2) with long, narrow rostra, and the bones that form the external nares (nasals and premaxillaries) are not greatly inflated as in the massive individuals of *B. b. brevicauda* from the intervening region in southern Iowa (19-22) and northern Missouri (23-24). Average cranial measurements for *B. b. talpoides* from Illinois (29-31), *B. b. jerrychoatei* from northeastern Kansas (25), and samples of *B. b. brevicauda* from southern Iowa (19-22) and

northern Missouri (23-24), respectively, are: occipito-premaxillary length, 22.6, 22.4, 23.5, and 22.7; interorbital breadth, 5.8, 5.8, 6.1, and 6.0; cranial breadth, 12.6, 12.6, 13.2, and 12.8; and mandibular height, 7.1, 7.1, 7.6, and 7.4.

Remarks: Gapper (1830) described *Sorex talpoides* on the basis of specimens from southeastern Ontario, a region where he considered this shrew to be common in “marshy places.” According to Gapper (1830), a specimen of *Sorex talpoides* was presented to the Bristol Museum, ostensibly to serve as the holotype. However, the Bristol Museum suffered extensive damage “during the 2nd World War and much material was lost” (R. Rowson, pers. comm.). Because no type material of *B. b. talpoides* exists and because of the extensive geographic variation exhibited in *B. b. talpoides*, we designate as the neotype a specimen taken from near Gapper’s original type locality. The original type locality (“between York and Lake Simcoe”) encompasses a distance of approximately 45 km along the lone north-south route of Gapper’s day, what is known today as Yonge Street. The neotype was collected at Pottageville (Kettleby Kabin), which is midway between North York (Toronto) and Lake Simcoe and approximately 7.5 km west of Yonge Street. There are 12 additional specimens of *B. b. talpoides* from Pottageville and 3 more from Kettleby Kabin in the Royal Ontario Museum, although some of these have damaged skulls. These specimens likely came from the same locale, as Kettleby Kabin was the cottage used by biologists working the Pottageville area in the 1920s and 1930s (B. Millen, pers. comm.).

Specimens assignable to *B. b. talpoides* display a large amount of geographic variation relative to other subspecies. Much of the geographic variation within *B. b. talpoides* exists along the perimeter of this taxon’s distribution, as a result of intergradation with other subspecies that abut the margins of its geographic range. This is not unexpected in a widely distributed taxon. The geographic variation within *B. b. talpoides* exhibits no clear steps or patterns that would indicate breaks in gene flow. However, there are clear breaks where the geographic distribution of *B. b. talpoides* abuts those of the other subspecies. In other words, when specimens from the entire range of the species are compared simultaneously, specimens now assigned to *B. b. talpoides* are more similar to each other than they are to specimens that we assign to other subspecies.

The zone of intergradation between *B. b. talpoides* and *B. b. brevicauda* is located on the east side of the Mississippi River in Wisconsin and Illinois (26-27, 30). Shrews from west of the Mississippi River are clearly referable to *B. b. brevicauda* (1-13, 15-24) or *B. b.*

jerrychoatei (25), and those from Michigan (38-46) and Indiana (47-50) are clearly referable to *B. b. talpoides*. Moving west to east across the transition zone in Wisconsin and Illinois, specimens get smaller, especially in cranial and maxillary breadth, their sagittal and lambdoidal crests become less pronounced, and all more closely resemble *B. b. talpoides*, save for the population of *B. b. brevicauda* on the east side of the Mississippi River in southwestern Wisconsin (28). Specimens of *B. b. talpoides* from the zone of intergradation between *B. b. brevicauda* and *B. b. talpoides* in Wisconsin and Illinois (26-27, 30) average 22.5, 5.8, and 12.5, respectively, for occipito-premaxillary length, interorbital breadth, and cranial breadth, and specimens from Indiana (47-50), well east of the zone of intergradation, average 21.7, 5.7, and 12.2, for those 3 measurements, respectively. There is no direct gene flow between *B. b. talpoides* and *B. b. jerrychoatei* because these 2 subspecies are geographically isolated from each other by intervening populations of *B. b. brevicauda*. Additional comments comparing *B. b. talpoides* with *B. b. brevicauda* and *B. b. jerrychoatei* are provided in those accounts.

The zone of intergradation between *B. b. talpoides* and *B. b. cumberlandensis* (60-62) occurs in central Kentucky (56-59) and eastern Tennessee (63-65). Compared with specimens of *B. b. talpoides* from Indiana (47-50) and Ohio (51-55), specimens from central Kentucky (56-59) are slightly smaller overall, their sagittal and lambdoidal crests are less pronounced, and their teeth are less pigmented, but they are still more similar to *B. b. talpoides* than *B. b. cumberlandensis*. Differences are even more pronounced, and the transition even more abrupt, when comparing *B. b. talpoides* from the southern Appalachian Mountains (64-65) with *B. b. cumberlandensis* from the Cumberland Plateau of Tennessee (60-62). Comparative measurements for specimens from these OTUs are provided in the account of *B. b. cumberlandensis*.

The zone of intergradation between *B. b. talpoides* and *B. b. knoxjonesi* begins in southeastern Virginia (110) and northeastern North Carolina (111) and extends as far south as the Albemarle-Pamlico Peninsula (112). Shrews in this region are clearly assignable to *B. b. talpoides*—their skulls are relatively large, albeit narrow for the subspecies, their sagittal and lambdoidal crests are diminished in size, and their teeth are less pigmented. Farther to the south (113-114), specimens of *B. b. knoxjonesi* are noticeably smaller in all dimensions; they are smallest for the species in cranial and maxillary breadth, their cranial crests are modest when fully developed, and their teeth have scant pigmentation. Specimens from south of the Pamlico River are clearly

assignable to *B. b. knoxjonesi*, those from the Pamlico River northward to the Great Dismal Swamp (110-112) are intergrades more similar to *B. b. talpoides*, and those from north of the Great Dismal Swamp (102, 107) are clearly assignable to *B. b. talpoides*. Representative measurements for specimens from these OTUs are provided in the account of *B. b. knoxjonesi*.

A zone of intergradation exists between *B. b. talpoides* and *B. b. delmarvensis* where the Delmarva Peninsula connects to the mainland. To the north, in eastern Pennsylvania (97), southern New Jersey (99), northern Delaware (103), and the District of Columbia (102), specimens are typical of *B. b. talpoides* in all respects except that they are slightly smaller in all dimensions when compared to specimens from the remainder of Pennsylvania (93-96) and northern New Jersey (98). Specimens of *B. b. delmarvensis*, which occurs on the southern two-thirds of the Delmarva Peninsula (104-106), however, are much smaller in size, especially mandibular length and mandibular height. Comparative measurements of specimens from these OTUs are provided in the account of *B. b. delmarvensis*.

Another zone of intergradation exists between *B. b. talpoides* and *B. b. aloga* in the Cape Cod region. Specimens of *B. b. talpoides* from eastern Massachusetts (83) and eastern Connecticut (86) are smaller than specimens of *B. b. talpoides* from western and northern Massachusetts (81-82), western Connecticut (87), and the remainder of New England (75-80), but they are distinctly larger than specimens from Martha's Vineyard (84) and Nantucket Island (85), which are assigned to *B. b. aloga*. Additional comments about specimens from these OTUs are provided in the account of the latter.

Herein we place 2 fossil and 9 Recent taxa into synonymy with *B. b. talpoides*. The name *B. b. talpoides* as currently recognized includes 2 synonyms that were applied to fossils. The first fossil originally was named *Blarina simplicidens* by Cope (1899:219) but was reclassified as *B. b. simplicidens* by Hibbard (1957). Jones et al. (1984) demonstrated that this nominal taxon is indistinguishable from *B. b. talpoides*. The second fossil was named *Blarina brevicauda ozarkensis* by Brown (1908:170) and later elevated to the status of a separate species, *B. ozarkensis*, by Graham and Semken (1976). However, Jones et al. (1984) found no morphological differences that distinguish *B. ozarkensis* from Holocene *B. brevicauda*, and their morphometric analyses indicated that *B. ozarkensis* should be placed in synonymy with *B. brevicauda talpoides*. We have examined the type material for both

fossil taxa and support the taxonomic conclusions of Jones et al. (1984).

Bachman (1837:377) named and described *Sorex dekayi* from New Jersey, but Baird (1858), Bangs (1902), and Merriam (1895) considered *S. dekayi* to be synonymous with *B. b. talpoides*. Also, considering the location of capture we have no reason to doubt this conclusion. Pomel (1848:249) named and described *G[alemys]. micrurus*. Given the absence of type material we follow Handley and Choate (1970) in assigning *G[alemys]. micrurus* to *B. b. talpoides*. Finally, Baird (1858:34) named and described *B. angusticeps* from Burlington, Chittenden County, Vermont. We have examined the holotype, which is damaged, as well as another specimen captured from the same location at the same time, and conclude that both are indistinguishable from other specimens of *B. b. talpoides* from the New England region.

Merriam (1895:15) named and described *B. telmalestes* from the Great Dismal Swamp of southeastern Virginia (110), and characterized this short-tailed shrew as having a long, slender skull with sparsely pigmented teeth. Specimens sharing these characteristics are also found in northeastern North Carolina (111-112). However, our analyses indicate that northern short-tailed shrews from the Great Dismal Swamp region occupy a relatively narrow zone of intergradation between *B. b. talpoides* to the north and west in mainland Virginia (107-109), with its broad skull and richly pigmented teeth, and *B. b. knoxjonesi* (113-114), to the south and east in southeastern North Carolina, with its short, narrow skull and scantily pigmented teeth. However, northern short-tailed shrews from the Great Dismal Swamp region of southeastern Virginia (110) and northeastern North Carolina (111-112) are more similar to shrews from other mainland Virginia samples (107-109) than they are to shrews from southeastern North Carolina (113-114). We therefore conclude that specimens formerly assigned to *B. b. telmalestes* do not, in fact, represent a distinct subspecies. Rather, all specimens previously assigned to *B. b. telmalestes* should be included in the synonymy of *B. b. talpoides*.

Smith (1940:223) named and described *B. b. pallida* from Nova Scotia, and characterized it as being indistinguishable from *B. b. talpoides* in cranial characters but slightly paler in pelage coloration. The pelage coloration of specimens in our reference samples from New Brunswick (72-73) and Nova Scotia (74) is similar to that observed in specimens from the Great Lakes region (42-55), previously assigned to *B. b. kirtlandi*, and darker than that observed in specimens previously assigned to *B. b. angusta* from the Gaspé

Peninsula (71), but it is paler than that observed in specimens from southern Ontario (34-37) and the southern Appalachian Mountains (64-65), which in the past were assigned to *B. b. talpoides* and *B. b. churchi*, respectively. The crania of northern short-tailed shrews from New Brunswick (72-73) and Nova Scotia (74) are similar in size to those from the Upper Peninsula of Michigan (38-41) and southern Ontario (34-36), all of which are assigned to *B. b. talpoides*. Based on these results, we do not believe that *B. b. pallida* should be recognized as a valid subspecies.

Bole and Moulthrop (1942:99) named and described *B. b. kirtlandi* on the basis of a large series of specimens from the Holden Arboretum, which is located in Geauga and Lake counties, Ohio. These specimens were characterized as being medium-sized and dark, with strongly recurved maxillary projections and short, broad feet (Bole and Moulthrop, 1942). We examined the Bole and Moulthrop material from the type locality (52) and we examined specimens with similar characteristics from several other OTUs in eastern North America, including those earlier assigned to *B. b. kirtlandi* (48-51, 54, 100-103), *B. b. hooperi* (79), *B. b. pallida* (75-76), and *B. b. talpoides* (78, 83, 92). The material from the type locality of *B. b. kirtlandi* and other specimens previously assigned to *B. b. kirtlandi* fit well within the range variation of these OTUs. There are no steps or other evidence of differentiation from the surrounding populations. Based on this finding, we do not recognize *B. b. kirtlandi* as a separate subspecies.

Bole and Moulthrop (1942:109) named and described *B. b. churchi* from Roan Mountain, which straddles the border of eastern Tennessee and western North Carolina (65). *B. b. churchi* was characterized by its medium-to-large size, broad cranium, dark pelage, and deeply pigmented teeth (Bole and Moulthrop, 1942). Specimens from the Great Smoky Mountains (64) also are large in size and dark in pelage and dental pigmentation. However, we note that specimens of similar size and color (pelage and teeth) are found in other populations, such as northern Georgia (66-68), West Virginia (100-101), southwestern Pennsylvania (95), and western New York (89), including specimens that in the past have been referred to *B. b. churchi*, *B. b. kirtlandi*, and *B. b. talpoides*. Therefore, we see no valid reason to recognize *B. b. churchi* as a distinct subspecies as there are no clearly defined steps in variation to suggest that there is a reduction in gene flow in this large region.

Bole and Moulthrop (1942:110) also named and described *B. b. hooperi* on the basis of 13 specimens from Lyndon, Caledonia County, Vermont. These specimens

were characterized as being smaller than average compared with northern short-tailed shrews from other localities in New England, but with a disproportionately large head and feet and a long tail (Bole and Moulthrop, 1942). Specimens that we examined from Caledonia County, Vermont (79), including the type material, are similar in size to northern short-tailed shrews from other OTUs in eastern North America, particularly those from New England (75-78, 80-91) and the Maritime Provinces (71-74), which in the past have been assigned to either *B. b. angusta*, *B. b. pallida*, or *B. b. talpoides*; thus, we see no valid reasons to recognize *B. b. hooperi* as a distinct subspecies.

Anderson (1943:66) named and described *B. b. angusta* from the Gaspé Peninsula (71), and characterized this northern short-tailed shrew as being darker than *B. b. pallida* from Nova Scotia (74) but paler than *B. b. talpoides* from western Québec (70) and Ontario (34-37). In addition, its skull was characterized as being long and narrow in relation to the skull of *B. b. pallida*, but slightly smaller than that of *B. b. talpoides* (Anderson, 1943). Our reference sample from the Gaspé Peninsula (71) included specimens that were paler, on average, than those from New Brunswick (72-73) and Nova Scotia (74), which in the past have been assigned to *B. b. pallida*, and their skulls are slightly larger in both length and width dimensions when compared to skulls of the New Brunswick and Nova Scotia shrews. When compared to specimens of *B. b. talpoides* from near the type locality (35) and other locations in Ontario (34, 36-37) and western Québec (70), northern short-tailed shrews from the Gaspé Peninsula (71) are slightly paler in pelage coloration and their skulls are slightly longer but similar in measurements of cranial breadth. However, these differences do not rise to the level that we have recognized in other subspecies.

In our principal components analysis, OTUs for our reference samples from the vicinity of the type localities of *B. b. telmalestes* (110), *B. b. pallida* (74), *B. b. kirtlandi* (52), *B. b. churchi* (65), *B. b. hooperi* (79), and *B. b. angusta* (71) are thoroughly mixed with the remaining samples of *B. b. talpoides* from eastern North America, and all plot near OTU 35, which includes specimens from the vicinity of the type locality of *B. b. talpoides* (Figs. 3 and 4). Our analysis identified no clearly defined steps in the variation exhibited by *B. b. talpoides*, indicating that there has been no past or present reduction in gene flow within this large geographic area. We, therefore, propose that *B. b. telmalestes*, *B. b. pallida*, *B. b. kirtlandi*, *B. b. churchi*, *B. b. hooperi*, and *B. b. angusta* be placed in the synonymy of *B. b. talpoides*.

The molecular studies by Brant and Ortí (2002,

2003a) generally support our taxonomic arrangement. They found 2 well-defined monophyletic groups of *B. brevicauda*, separated by the Mississippi River, using the cytochrome-*b* and 16S rRNA mtDNA genes. Moreover, they found that the eastern clade consisted of 2 smaller subclades, 1 centered in the Ohio River and Great Lakes region and the other extending north to south along the Appalachian Mountains and East Coast (Brant and Ortí, 2003a). Their samples did not include individuals from any type localities, but the Ohio River and Great Lakes subclade included specimens within the geographic distributions of *B. b. kirtlandi* (eastern Wisconsin, west-central Indiana, and northeastern Ohio) and *B. b. cumberlandensis* (southwestern Kentucky). The Appalachian Mountains and East Coast subclade included specimens within the geographic distributions of *B. b. telmalestes* (southeastern Virginia), *B. b. kirtlandi* (northeastern Ohio, West Virginia, and Pennsylvania), *B. b. talpoides* (northwestern Vermont, central New Hampshire, northern New York, and eastern Massachusetts), *B. b. churchi* (southeastern Tennessee), and *B. b. hooperi* (northern Vermont). The molecular data did not reliably differentiate among samples within each Eastern subclade and, in fact, haplotypes of both subclades were found at 2 sites in Ohio (Brant and Ortí, 2003a).

In our opinion *B. b. telmalestes*, *B. b. pallida*, *B. b. kirtlandi*, *B. b. churchi*, *B. b. hooperi*, and *B. b. angusta* are not valid, and recognizing them would result in oversplitting of the subspecies *B. b. talpoides*, which would, in turn, obscure the more pronounced differences among *B. b. brevicauda*, *B. b. jerryrchoatei*, *B. b. talpoides*, *B. b. aloga*, *B. b. delmarvensis*, *B. b. knoxjonesi*, and *B. b. cumberlandensis*. Clearly, *B. b. talpoides* is variable, ranging in size from the relatively small specimens found in parts of Michigan (42-43, 45), southern Ohio (55), and in zones of intergradation with *B. b. aloga* (83, 86), *B. b. delmarvensis* (97, 99, 102-103), *B. b. knoxjonesi* (110-112), or *B. b. cumberlandensis* (56-59) to the relatively large specimens in the southern Appalachian Mountains (64-65), northeastern Minnesota (14), and the zone of intergradation with *B. b. brevicauda* (26-27, 30). Nonetheless, specimens identified as *B. b. talpoides* in this investigation are more similar to each other than they are to specimens identified as *B. b. brevicauda*, *B. b. jerryrchoatei*, *B. b. aloga*, *B. b. delmarvensis*, *B. b. knoxjonesi*, and *B. b. cumberlandensis*.

It seems appropriate at this time to compare *B. b. talpoides* with a congener, *B. carolinensis*, because the geographic distributions of these species abut in parts of Alabama, Georgia, South Carolina, western North Carolina, and south-central Virginia. Along this long

zone of parapatry, these taxa differ in size and karyotype. Hybridization has not been documented between *B. brevicauda* and *B. carolinensis* (French, 1981; Pagels and French, 1987; Tate et al., 1980). Selected cranial measurements for 12 *B. b. talpoides* from Alabama (69), 22 *B. b. talpoides* from Georgia (66-68), and 31 *B. b. talpoides* from western Virginia (108-109), followed by those of 22 *B. carolinensis* from southeastern North Carolina (Appendix 3), are: occipito-premaxillary length, 22.0, 21.8, 21.7, and 18.4; P⁴-M³ length, 6.1, 6.1, 6.0, and 5.0; interorbital breadth, 5.8, 5.8, 5.6, and 4.9; and cranial breadth, 11.9, 12.1, 12.1, and 9.9. In southeastern Virginia and eastern North Carolina, however, these species are sympatric but not syntopic. Specimens of *B. b. talpoides* occupy mesic to wet pocosins, river floodplains, and associated wetlands on poorly-drained organic soils; specimens of *B. carolinensis* are found in upland fields, oak-hickory forests, and hardwood-pine forests on well-drained sandy soils (Webster et al., 1985; Webster, 1996). Selected cranial measurements for 35 *B. b. talpoides* from southeastern Virginia and northeastern North Carolina (110-111), followed by those of 22 *B. carolinensis* from southeastern North Carolina (Appendix 3), are: occipito-premaxillary length, 22.0 and 18.4; P⁴-M³ length, 5.9 and 5.0; interorbital breadth, 5.6 and 4.9; and cranial breadth, 12.0 and 9.9. In addition, specimens of *B. carolinensis* have a karyotype of 2N = 46 and FN = 48 throughout most of the geographic range, with exceptions in Florida and western Tennessee (Beck et al., 1991; Elrod et al., 1996; Qumsiyeh et al., 1997, 1999; M. L. Kennedy, pers. comm.). The karyotype of *B. brevicauda* is 2N = 48-50 and FN = 48 (George et al., 1982; Thompson and Hoffman, 2009).

Blarina brevicauda talpoides

Specimens Examined (10,619) See *Acknowledgments* for institutional abbreviations.

NEW BRUNSWICK, CANADA (260). *Albert Co.*: Albert (4 ROM). *Charlotte Co.*: 6 mi N St Andrews (14 CMN); St Andrews (3 ROM); Scotch Lake (3 UMMZ). *Gloucester Co.*: Carron Pt, 3 mi N Bathurst (5 CMN); Bathurst (61 CMN); 15 mi along Miramichi Rd from Bathurst (17 CMN); Youghall (4 CMN). *Kent Co.*: Buctouche (2 CMN). *Kings Co.*: Bald Peak, 47°10'N, 67°06'W (11 CMN); Browns Flat (3 CMN); Eagle Rock, 45°26'N, 66°19'W (1 CMN); Hampton (5 NMNH); Lakeside (51 AMNH). *Madawaska Co.*: Baker Lake (4 CMN); 9 mi NE Edmundston (8 CMN); 12 mi NE Edmundston (4 CMN); 2 mi N Lac Baker, 47°22'N, 68°39'W (9 CMN); St Leonard (5 CMN); 5 mi N St Leonard (9 CMN); 6 mi

N St Leonard (1 CMN); 9 mi NE St Leonard (1 CMN). *Restigouche Co.*: 2 mi SW Jacquet River (1 ROM); Little Belledune Pt (2 CMN). *St. John Co.*: Balls Lake (1 CMN); Musquash, 45°11'N, 66°20'W (2 CMN); St John (2 CMN). *Sunbury Co.*: Rasigornis (1 CMN). *Victoria Co.*: Andover (1 AMNH); Gulquac Lake (2 AMNH); Long Lake (1 AMNH); Perth (3 CMN); 4 mi S Perth (2 CMN); Scotch Lake (2 AMNH); Tobique Pt (3 AMNH); forks of Tobique River (3 AMNH); Trousers Lake (2 AMNH). *York Co.*: Fredericton (1 CMN, 1 ROM); McAdam Jct (3 ROM); Scotch Lake (1 CMN, 1 ROM).

NOVA SCOTIA, CANADA (261). *Annapolis Co.*: Bear River (5 CMN); Kedgemakooge (3 NMNH, 14 UMMZ); Kedgemakooge Lake (10 NMNH); 2 mi S South Milford (1 AMNH). *Antigonish Co.*: James River (6 NMNH). *Cape Breton Co.*: Aberdeen (2 CMN); Kingston (2 ROM); North Sydney (1 ROM). *Colchester Co.*: 25 km N, 7.4 km E Truco (3 NMNH); Worwick Mtn, 45°36'N, 63°24'W (2 CMN). *Cumberland Co.*: 3 mi S Wentworth Centre, 45°38'N, 63°34'W (1 CMN). *Digby Co.*: Digby (4 NMNH). *Guysborough Co.*: East Roman Valley (15 CMN). *Halifax Co.*: Halifax (5 NMNH); 3 mi S Halifax (5 NMNH); Moser River (4 ROM); Sackville (3 ROM). *Hants Co.*: Newport (16 AMNH). *Inverness Co.*: Deepdale (1 CMN); Frizzleton, Cape Breton Island (3 CMN); 8 mi SE Frizzleton, Cape Breton Island (1 CMN); Margaree Harbour, Cape Breton (2 CMN); Upper Margaree River, Cape Breton (3 CMN); 7.5 km N, 2 km E Margaree Valley (1 NMNH); Nevada Valley (1 CMN). *Kings Co.*: Black River Lake (1 AMNH); Wolfville (4 AMNH, 1 MVZ [the holotype of *B. b. pallida*], 2 ROM, 4 UMMZ); 2 mi E Wolfville (4 ROM); 3 mi E Wolfville (1 ROM); no specific locality (19 CMN). *Queens Co.*: Tobeatic Sanctuary (2 CMN). *Richmond Co.*: Bucklaw (2 CMN); St Peters, Cape Breton Island (1 CMN). *Shelburne Co.*: Barrington Passage (61 CMN). *Victoria Co.*: Cape North, Cape Breton Island (9 CMN); Ingonish (1 ROM); Ingonish Centre, Cape Breton Island (7 CMN); West Middle Sable (1 CMN). *Yarmouth Co.*: Wedgeport (7 ROM). *County unknown*: Kejimikujik National Park, 44°30'N, 65°15'W (18 CMN); Admin Bldg, Kejimikujik National Park, 44°30'N, 65°15'W (1 CMN); Norway Island, Kejimikujik National Park, 44°30'N, 65°15'W (1 CMN).

ONTARIO, CANADA (849). *Algoma Dist.*: Amyot (1 ROM); Bruce Mines, Cloudslee RR (1 CMN); Garden River (1 ROM); Laird (4 ROM); Maclennan (4 ROM); Maskinonge Bay, Maclennan (1 ROM); Pancake Bay (21 CMN); Tarenturus Twp (8 CMN). *Bruce Co.*: Berford Lake (1 UWSP); Red Bay, Bruce Peninsula (1 ROM); Chesley (1 ROM); Lions Head (6 CMN); Port Elgin (1 ROM); Hwy 21, Southhampton (2 CMN); Tobermony (7 ROM); 2.5 mi N Walkerton (2 ROM). *Cochrane Dist.*: Fraserdale PO (6 ROM); Kapuskasing River (1 CM); O'Brien Twp, Kapuskasing (1 CM); Camp 15, Kapuskasing River, Kapuskasing (1 ROM); Camp 33, Saganash Lake,

Kapuskasing (6 CM, 1 ROM); Smoky Falls, Kapuskasing (1 ROM); Moosonee (3 ROM); Onakawana (43 ROM); Palmquist (1 ROM). *Dufferin Co.*: 1 mi W Glen Cross (3 ROM). *Dundas Co.*: Iroquois (1 ROM); Ghost River, Lake Abitibi (1 ROM); Lowbush, Lake Abitibi (1 ROM). *Durham Co.*: Clark Twp, Orono (4 ROM); Port Hope (2 ROM). *Elgin Co.*: Jaffa (3 ROM); Whites Pond, Malahide Twp (2 ROM); Port Burwell (1 ROM); St Thomas (1 CMN); 4 mi E St Thomas (1 ROM); 3 mi SW St Thomas (3 ROM); 4 mi S St Thomas (1 ROM); Yarmouth Twp (12 ROM). *Essex Co.*: 6 mi NE Amherstburg (2 ROM); Leamington (1 ROM); Pt Peele (4 CMN, 5 ROM). *Frontenac Co.*: Kennebec Twp, 0.5 mi N Arden (1 ROM); Arden (9 ROM); W shore Clear Lake, Arden (1 ROM); Kennebec Twp, 4 mi S Arden (2 ROM); Collins Lake, Inverary (1 CMN); Loughborough Lake, Inverary (1 CMN); Hartington (1 ROM); Kingston (2 ROM); 4.5 mi E Kingston (1 ROM); Mountain Grove (1 ROM); Plevna (1 ROM). *Grenville Co.*: Kemptville (2 CMN). *Grey Co.*: Durham (1 ROM); Meaford (7 ROM); Proton (1 CMN); Redwing (1 ROM). *Haldimand Co.*: Nanticoke (7 ROM). *Haliburton Co.*: Dysart Twp (7 ROM); Lake Boshkung (1 ROM); Minden Twp (2 ROM); about 160 mi NE Toronto, Moose Lake (1 CM); Mountain Lake (1 ROM). *Halton Co.*: Rattlesnake Pt, Milton, Nelson Twp (1 ROM); Norval (1 ROM); Oakville (2 ROM); Andersons Bush, Oakville (4 ROM); Trafalgar Twp (1 ROM). *Hastings Co.*: Sydney Field Station, 13 mi N Belleville (1 CMN). *Huron Co.*: Benmiller (2 ROM); Maitland, Goderich (1 ROM); Meneset, Goderich (3 ROM); Menesetung, Goderich (1 ROM); Pipers, Goderich (1 ROM); Sunset, Goderich (2 ROM). *Kenora Dist.*: near Ingolf, Kalmar (2 ROM); Kenora (1 ROM, 2 UWSP); Trans Canada Hwy, 20 mi E Kenora (1 CMN); Alexandria Isle, Lake of the Woods (2 ROM); Big Isle, Lake of the Woods (1 ROM); Malachi (2 ROM); Nester Falls Airport (1 UWSP); Perrault Falls (6 UWSP); Rat Portage (5 NMNH); Sioux Lookout (15 ROM); Frog Rapids, Sioux Lookout (1 ROM); Wartime Housing, Sioux Lookout (1 ROM); Trans Canada Hwy, Manitoba Ontario boundary (2 CMN); Wabigoon (3 ROM); Willard Lake (3 MMMN). *Kent Co.*: Chatham (6 CM); Mitchells Bay (2 ROM); Morpeth (3 ROM); Paincourt (1 ROM); Rondeau (1 CM); Pointe Aux Pins, Rondeau Provincial Park (4 ROM). *Lambton Co.*: Thedford (1 ROM). *Leeds Co.*: Gananoque (1 ROM); 44°30'N, 75°56'W, front of Escott Twp, Junestown (1 CMN); Lansdowne (1 AMNH); Seeleys Bay (1 CMN); Waterton (6 ROM); Yonge Mills (1 ROM). *Lanark Co.*: Clayton (2 CMN). *Lennox Addington Co.*: 3 mi S Bon Echo Provincial Park (1 ROM); Buckshot Lake (1 ROM); 7 mi N Cloyne (7 CM); Bon Echo Creek, 5.5 mi N Cloyne (4 CM); 5.5 mi S Denbigh (1 CM); 10 mi S Denbigh (3 CM); 1.25 mi SE Massanoga (2 CM). *Manitoulin Dist.*: 1 mi N Excelsior (1 ROM); Gore Bay (1 ROM); 8 mi W Gore Bay (2 ROM); Mindemoya (2 ROM). *Middlesex Co.*: near Bryanston (1

ROM); Byron (7 ROM); Caradoc Twp (3 AMNH); Coldstream (15 ROM); Hyde Park (1 ROM); Kerwod (1 ROM); Kilworth (1 ROM); Komoka (3 ROM, 1 NMNH); Komoka Swamp (1 ROM); Lambeth (2 ROM); London (6 ROM); 8 mi N London (5 ROM); Foster Ponds, 7 mi E London (1 ROM); Poplar Hill (2 ROM); Strathray (1 ROM); 0.5 mi S, 2 mi W Thamesford [*in* Oxford Co.] (2 KU). *Muskoka Dist.*: Otter Lake, Dorset (1 ROM); Ranger School, Dorset (1 ROM); Go Home (1 ROM); Honey Harbor (2 ROM); Huntsville (2 ROM); Camp Billie Bear, Huntsville (5 ROM); Lake Solitaire, Huntsville (2 ROM); Limberlost Lodge, Trail 7-4, Huntsville (1 ROM); Limberlost Lodge, Huntsville (12 ROM); Kahshe Lake (2 ROM); Lake of Bays (2 NMNH); Port Carling (4 ROM); Port Sydney (1 ROM); Ridout (5 CMN). *Nipissing Dist.*: Aileen Stream (1 ROM); Algonquin Park (2 CMN); Bigger Lake, Algonquin Park (1 ROM); Brule Lake, Algonquin Park (3 ROM); Cache Lake, Algonquin Park (7 ROM); Skymount Bay, Cache Lake, Algonquin Park (1 ROM); Canoe Lake, Algonquin Park (2 ROM); Clarke Lake, Algonquin Park (1 ROM); Joe Lake, Algonquin Park (3 ROM); Lake Sasajewan, Algonquin Park (5 ROM); Lister Twp, Algonquin Park (2 ROM); Little Island Lake, Algonquin Park (1 ROM); Red Rock Lake, Algonquin Park (1 ROM); Smoke Lake, Algonquin Park (4 ROM); Two Rivers Lake, Algonquin Park (6 CMN); Austen Bay (1 ROM); Balsam Creek, 25 mi NE North Bay (5 ROM); Source Lake, Canisbay Twp (1 ROM); Lake of Two Rivers (4 ROM); Temagami (5 ROM); Cross Bay, Temagami (1 ROM); Gull Lake Torrent, Temagami (6 ROM); island in SW arm of Temagami (1 ROM); Portage Bay, Temagami (1 ROM); Sandy Inlet, Temagami (4 ROM); Afton, 30 mi SW Temagami (1 ROM). *Norfolk Co.*: Long Point (2 ROM); Port Rowan (5 CMN). *Northumberland Co.*: Bewdley (1 ROM). *Ontario Co.*: Glen Major (6 ROM); Pickering (2 ROM). *Ottawa-Carleton Co.*: near Burritts Rapids (1 CMN); Ottawa (8 CMN, 1 ROM); Long Swamp, near Billings Bridge (6 CMN); Rideau River, near Billings Bridge, Ottawa (2 CMN); Rockcliffe Park, Ottawa (28 CMN); Dows Swamp, near Ottawa (15 CMN); Ottawa East (2 CMN). *Oxford Co.*: Thamesford, 43°04'N, 81°00'W (4 CMN). *Parry Sound Dist.*: Ardbeg (2 AMNH); Emsdale (1 AMNH); Franklin Island (1 ROM); French River (1 ROM); Gordon Bay (12 ROM); Katrine Station (3 ROM); Sundridge, Lake Bernard (4 ROM); Franks Bay, Lake Nipissing (9 ROM); Patterson Twp, Franks Bay, Lake Nipissing (1 ROM); Noganosh Lake (3 ROM); Parry Sound (1 ROM); Pickeral Lake (2 ROM). *Peel Co.*: Belfountain, Caledon Twp (4 ROM); Credit Forks, Caledon Twp (12 ROM); Credit (3 CMN); Erindale (1 ROM); Ferndale (2 ROM); Heart Lake (1 ROM); Lorne Park (1 AMNH, 1 CMN, 3 NMNH). *Peterboro Co.*: West Shore Eel Creek, 3 mi N Clarina PO (3 CM); Island 76, 0.25 mi NE Clarina PO (1 CM); Drummer Twp (8 ROM); 1 mi W Villiers (1 ROM). *Prince Edward Co.*: Hallowell (3 ROM); Wellers Bay (2 ROM); Wellington (3 ROM); Woodrout (1 ROM). *Rainy River Dist.*: N end Agnes Lake (2 ROM); Emo (1 ROM); Off Lake (1 ROM); Rainy River (4 ROM). *Renfrew Co.*: Bark Lake (1 ROM); Lake Dore (1 CMN). *Russell Co.*: Bourget (1 CMN). *Simcoe Co.*: Little Lake, Barrie (4 ROM); Big Cedar Pt (1 CMN); Holland River, Bradford (1 ROM); Craighurst (2 ROM); Minesing (1 ROM); Orillia Twp (2 ROM); Penetanguishene (1 ROM); Sturgeon Creek, Wasaga (1 ROM). *Sudbury Dist.*: Biscotasing (6 ROM); Chapleau (1 ROM); Bonniview, Lake Penage (3 ROM); Whitefish, Lake Penage (2 ROM). *Thunder Bay Dist.*: Grand Bay, Lake Nipogon (2 ROM); Macdiarmid, Lake Nipogon (16 ROM); Wabinosh Bay, Lake Nipogon (1 ROM); Fort William, Lake Superior (1 NMNH); Port Arthur (1 ROM); Rossport (1 ROM); Silver Islet, Perry Bay (1 CMN); Savanne (1 ROM); Schreiber (7 ROM); Big Duck Lake, 20 mi N Schreiber (3 ROM); N shore Lake Superior, Schreiber (3 CMN); Blue Jay, 5 mi E Schreiber (1 CMN); “mileage 113 E” Schreiber (1 ROM); Perry Bay, Silver Islet (1 CMN); near Nakina, Twin Lake (1 ROM). *Timiskaming Dist.*: Hough Lake (1 ROM); Kenogami (2 ROM); Lebel Twp, 1 mi W King Kirkland (3 ROM); Gauthier Twp, 7 mi E King Kirkland (3 ROM); Gauthier Twp, 9 mi E King Kirkland (1 ROM); Marter Twp, Wenidgo Lake (13 ROM). *Victoria Co.*: Bobcaygeon (18 ROM); Coboconk (5 ROM); Fenelon Falls (1 ROM); Woodville (1 ROM). *Waterloo Co.*: Bridgeport Dam (1 ROM); Galt (1 ROM); Preston (6 CMN, 1 ROM); 1.5 mi E St Jacobs (1 ROM); 3 mi NW Waterloo (3 ROM); Waterloo (2 ROM); Centreville, Waterloo Twp (8 ROM); Erbsville, Waterloo Twp (5 ROM); 1 mi S Mannheim, Wilmot Twp (1 ROM). *Welland Co.*: Niagara Glen (3 ROM); Point Abino (1 ROM, 2 KU); 14.5 mi W Port Colbourne (1 ROM). *Wellington Co.*: Guelph (1 CMN); Southcote (1 ROM); no specific locality (1 ROM). *Wentworth Co.*: Beverly Swamp, Beverly Twp (2 ROM); Valens, Beverly Twp (1 ROM); Hamilton-Wentworth Region Agreement (1 ROM). *York Co.*: Elgin Mills (1 ROM); King Twp (1 ROM); Kettleby Kabin, King Twp (4 ROM); Nancy Lake, King Twp (2 ROM); Pottageville, King Twp (6 ROM, including the neotype of *B. b. talpoides*); Lambton (2 ROM); Maple (1 ROM); Milliken (1 ROM); Oriole (1 CMN); Purpleville (1 ROM); Toronto (26 ROM); Armour Heights, Toronto (1 CM, 12 ROM, 1 UCONN); Blythwood Park, Toronto (4 ROM); Cedarvale, Toronto (2 ROM); Etobicoke River, Toronto (3 ROM); Heath Ravine, Toronto (1 ROM); High Park, Toronto (3 ROM); Humber River, Toronto (1 CM); east bank of Humber River, Toronto (5 ROM); Kew, Toronto (1 CMN); Mt Dennis, Toronto (1 UCONN, 3 ROM); Rosedale, Toronto (3 ROM); Strathgowan Park, Toronto (1 ROM); Strathgowan Woods, Toronto (1 ROM); Woodbine Ave, Toronto (1 ROM); North Toronto (1 ROM); Vandorf (2

ROM); Weston (1 ROM).

PRINCE EDWARD ISLAND, CANADA (2). *Queens Co.*: near Charlottetown (1 CMN); Mount Herbert (1 CMN).

QUEBEC, CANADA (306). *Argenteuil Co.*: Barkmere (1 CMN). *Bonaventure Co.*: 4.5 mi N, 0.5 mi E [Saint-] Elzéar de Bonaventure (3 CM); Fleurant (3 ROM); Grand Cascapedia (11 CMN); Kellys Camp, Grand Cascapedia (1 CMN); Maria (1 CMN); Middle Camp, Cascapedia River (1 AMNH); New Derreen, Cascapedia River (1 AMNH); Red Camp, Cascapedia River (3 AMNH); St Omer (2 CMN). *Brome Co.*: 1 mi W Glen Mtn (8 CMN); Glen Mtn (4 CMN); Glen Sutton (3 CMN); Knowlton (1 CMN); 4 mi N Mont Echo (1 CMN); 2 mi N Mont Echo (1 CMN); Mont Echo (5 CMN); Mt Pevee, north slope (1 CMN); Mt Pevee, south slope (1 CMN); 5 mi N South Bolton (1 CMN); South Bolton (31 CMN). *Champlain Co.*: Lake Edward (1 ROM). *Compton Co.*: New Hampshire-Canada border, Lakes Customs Station (8 AMNH); Lennoxville, 45°22'N, 71°51'W (1 CMN); Megantic Mtn (4 CMN). *Gaspé Co.*: 2 mi W Coin du Banc (1 NMNH); Gasperian National Park (3 AMNH); Gasperian National Park, base of Mt Alberta (1 AMNH); Gasperian Provincial Park (1 KU); 1.25 mi S Town Riviere au Renard (1 CMN); Ste Anne des Monts (7 AMNH); St Helier (1 CMN). *Gatineau Co.*: Blue Sea Lake (4 CMN); Big Island, Blue Sea Lake (2 CMN, 1 NMNH); near Messines, Blue Sea Lake (4 CMN); Sunset Point, Blue Sea Lake (1 CMN); Camp Fortune (2 CMN); St Charles Lake, Farrellton (4 CMN); Gracefield (1 CMN); Gatineau Park, Lac Philip (1 CMN); road W of Old Woman Creek, Tomasine-Jack Pine Flat (1 CMN); Wakefield (1 CMN). *Huntingdon Co.*: Dundee (13 CMN). *Iberville Co.*: St Sebastien (1 CMN). *Kamouraska Co.*: Ste Anne de la Pocatiere (1 CMN). *Labelle Co.*: Kiamika Lake (16 CMN); Trout Lake (19 CMN). *Lake St John Co.*: 20 mi W Roberval (2 AMNH); St Felicien (3 CMN); Val Jalbert (2 CMN); Lake St John Area, Val Jalbert (5 CMN). *Manicougan Co.*: Godbout (1 NMNH); Sasaginata Lake, Kipawa Reserve, Temiskaming (1 UCONN); Wolf Lake, Kipawa Reserve, Temiskaming (2 UCONN). *Matane Co.*: Grosses Roches (1 CMN); Lac Metapedia (1 CMN). *Misisquoi Co.*: White Gru Laboratory, Entomology Branch, Clarenceville (1 CMN). *Montréal Co.*: Macdonald College (1 CMN); Montréal (1 NMNH). *Pontiac Co.*: Norway Bay (3 CMN). *Rimouski Co.*: Bic (1 CMN); Cap a'L'original (18 CMN); 3 mi S Lac Pointer (1 CMN); Rouville, Mont St Hilaire (3 CMN); Mount Yamaska (1 CMN). *Stanstead Co.*: 2 mi SE Dixville (8 CMN); Hatley (12 CMN); Magog (1 CMN); Mont Orford (5 CMN); Stanstead (1 CMN). *Temiscouata Co.*: Trois Pistoles (14 CMN); 2 mi S Trois Pistoles (1 CMN). *Wright Co.*: Messines (1 CMN). *County unknown*: Berry Mtn Brook, Cascapedia River (1 AMNH); La Coste (14 CMN); Lake Noel (4 AMNH); Camp Dorval, Laverendrye Parc on Hwy 58 (1 CMN); Meach Lake (1

CMN); Mont Tremblant Park (2 NMNH); St Méthode [de Frontenac] (1 CMN); St Roch [de Mékinac] (1 NMNH); Ste Rose (4 NMNH); Ste Veronique (1 CMN).

ALABAMA, UNITED STATES (22). *Chambers Co.*: T21N, R26E, Sec 5 (2 AUM); about 4 mi SW Lafayette (1 AUM). *Elmore Co.*: 15 mi SE Clanton [in Chilton Co.] (3 AUM). *Lee Co.*: Auburn (10 AUM, 3 UMMZ); 0.5 mi E of Lee County Public Lake on Lee Co 12 (1 AUM); 4 mi E Opelika on Lee Co 77 (1 AU); 0.7 mi S jct Lee Co 12 and Alabama Hwy 169 (1 AUM).

CONNECTICUT, UNITED STATES (535). *Fairfield Co.*: Cos Cob (4 NMNH, 1 ROM); 1 mi NNW Cos Cob (1 UCONN); 0.75 mi NW Cos Cob (1 UCONN); Monroe (1 NMNH); Norwalk (1 UCONN); Trumbull (1 UCONN); Weston (1 UCONN); Westport (17 UCONN); Wilton (3 UCONN). *Hartford Co.*: Avon (1 UCONN); East Granby (2 UCONN); East Hartford (2 NMNH); 0.5 mi W Glastonbury, East Hartford (1 UCONN); Glastonbury (5 UCONN); Hartford (1 UCONN); New Britain (1 UCONN); 1.5 mi NE Newington (1 UCONN); Suffield (3 AMNH); West Hartford (2 AMNH); Wethersfield (1 NMNH); Pyquang Village, Wethersfield (1 UCONN); Windsor (18 AMNH); Windsor Locks (3 UCONN). *Litchfield Co.*: Barkhamstead [post office] (4 UCONN); Falls Village, Canaan (1 UCONN); Goshen (3 UCONN); Kent (1 AMNH); Morris Wildlife Sanctuary, Litchfield (1 UCONN); White Memorial Forest, Litchfield (1 UCONN); Bear Mountain, New Milford, Milford (6 AMNH); Pumpkin Hill, New Milford, Milford (2 UCONN); Norfolk (1 UCONN); Walcott Preserve, 1.5 mi S, 2 mi E Norfolk (1 UCONN); Plymouth (1 UCONN); Salisbury (2 UCONN); Bear Mountain, 1500 ft, Salisbury (6 AMNH, 1 UCONN); Lakeville, Salisbury (2 UCONN); Lime Rock, Salisbury (5 UCONN); Mt Riga, Salisbury (1 AMNH); Mt Riga, Bald Peak, 1950 ft, Salisbury (1 AMNH); Sharon (7 AMNH, 8 UCONN); Sharon Mountain, Sharon (6 UCONN). *Middlesex Co.*: Clinton (7 AMNH); near Burnham, East Haddam (1 UCONN); Middletown (1 UCONN); Westbrook (2 AMNH). *New Haven Co.*: Ansonia (2 UCONN); 2.7 mi NNW Cheshire, 160 ft (4 NMNH); Hamden (1 UCONN); Meriden (1 UCONN); Middlebury (5 UCONN); Naugatuck (3 UCONN); New Haven (1 UCONN); Oxford (1 UCONN); 1 mi E Wallingford (2 UCONN); Waterbury (7 UCONN); Bunker Hill, Waterbury (2 UCONN); West Haven (1 CM); Wolcott (2 UCONN); Chestnut Hill Reservoir, Wolcott (2 UCONN). *New London Co.*: Bozrah (2 UCONN); Colchester (2 UCONN); Niantic, East Lyme (3 AMNH, 2 UCONN); Franklin (1 UCONN); Hopeville, Griswold (1 UCONN); Pachaug State Forest, Griswold (14 UCONN); Lebanon (7 UCONN); 1 mi NE Lebanon, Lebanon (1 UCONN); Ledyard (4 UCONN); North Stonington (1 UCONN); Preston (3 UCONN); near Long Society, Preston (2 UCONN); Stonington (3 NMNH); Barn Island, Stonington (16 UCONN); Pachaug State Forest, Voluntown (6 UCONN); Waterford (6 AMNH, 1

UCONN); Manacoke Island, Waterford (7 UCONN). *Tolland Co.*: Andover (2 UCONN); Bolton (1 UCONN); Bolton Notch State Park, Bolton (1 UCONN); Coventry (10 UCONN); Nathan Hale State Forest, Coventry (7 UCONN); Ripley Hill Road, Coventry (1 UCONN); South Coventry, Coventry (1 UCONN); Gay City State Park, Hebron (2 UCONN); Mansfield (119 UCONN); Tolland (6 UCONN); Union (3 UCONN); Nipmuck State Forest, Union (46 UCONN); Bigelow Hollow State Park, Vernon (11 UCONN); Talcottville, Vernon (9 UCONN); Willington (10 UCONN). *Windham Co.*: Ashford (4 MHP, 13 UCONN); Brooklyn (6 UCONN); Eastford (1 UCONN); Natchaug State Forest, Eastford (3 UCONN); Phoenixville, Eastford (1 UCONN); Pomfret (1 KU): on Hampton town line, Pomfret (1 KU); Windham (5 UCONN); Woodstock (8 AMNH, 2 UCONN).

DELAWARE, UNITED STATES (9). *New Castle Co.*: Bellvue (6 DMNH); Lums Pond State Park (3 DMNH).

DISTRICT OF COLUMBIA, UNITED STATES (105). Berwyn (1 NMNH); near Bladensburg on Eastern Ave (1 NMNH); Broad Branch (1 NMNH); Brookland (1 NMNH); Chain Bridge (1 NMNH); Chevy Chase (4 NMNH); 6633 Barnby Rd, Chevy Chase (1 NMNH); Grant Rd (1 NMNH); Rock Creek (17 NMNH); Zoo Park, Rock Creek (16 NMNH); Takoma Park (1 NMNH); Twining City (2 NMNH); Washington (54 NMNH); Beaver Dam Creek, Washington (1 NMNH): National Zoological Park, Washington (3 NMNH).

GEORGIA, UNITED STATES (57). *Clarke Co.*: Athens (8 GMNH); 5 mi N Athens (1 GMNH); dump S of Athens (5 GMNH); 4 mi S Athens (1 GMNH); 2 mi W Athens (1 GMNH); Lake Kirota, Athens (4 GMNH); 6 mi E Athens, Hwy 78 (1 GMNH); Sandy Creek (2 GMNH). *DeKalb Co.*: Atlanta (1 GMNH). *Fulton Co.*: 0.25 mi E of Chattahoochee River, Browns Lake, Fairborn (1 GMNH); Long Island Creek at Chattahoochee River (1 GMNH); Andrews Dr and Pharr Rd (1 GMNH). *Gwinnett Co.*: Duluth (1 GMNH); 2 mi W Duluth (2 GMNH). *Jones Co.*: Round Oak (1 NMNH). *Madison Co.*: 4 mi S Colbert (1 GMNH). *Monroe Co.*: no specific locality (1 NMNH). *Pickens Co.*: Tate, 1400 ft (1 GMNH). *Quitman Co.*: 8.1 mi NE jct US hwy 82 and Georgia 27 (2 NMNH). *Rabun Co.*: Black Rock Mountain State Park (2 GMNH). *Towns Co.*: Beech Creek (2 GMNH); Brasstown Bald, 4700 ft (1 GMNH); Enota[h] Glade (1 GMNH); Young Harris (1 NMNH). *Union Co.*: [near] Brasstown Bald (2 GMNH); Cooper Creek Recreation Area (1 GMNH); summit of Hawk Mountain (1 GMNH); Toccoa Experimental Station, 2250 ft, Margret [in Fannin Co.] (6 GMNH); 1 mi N Woodys Gap High School, Hwy 60 (1 GMNH). *White Co.*: Tray Mountain, 3100 ft (1 GMNH); no specific locality (1 GMNH). *Wilkes Co.*: Little River at Hwy 78 (1 GMNH).

ILLINOIS, UNITED STATES (161). *Champaign Co.*: Champaign (82 UIMNH); Brownfield Woods,

Champaign (1 KU, 2 LACM, 3 UCONN); railroad tracks behind Memorial Station (1 LACM); 0.5 mi S Champaign (1 UCONN); 2 mi S Champaign (1 LACM); Urbana (1 UCONN); 1 mi N, 2 mi E Urbana (1 KU); 1.75 mi N, 3 mi E Urbana (1 KU); 2.5 mi NE Urbana (1 LACM); Trelese Woods, NE Urbana (1 UCONN); Mayview Prairie, 4 mi E Urbana (7 LACM); 2.5 mi S, 2.5 mi E Urbana (1 LACM). *Clark Co.*: Marshall (4 ISUVC). *Cook Co.*: Lemont (1 LACM); West Northfield (3 NMNH); no specific locality (9 UIMNH). *Dekalb Co.*: Dekalb (2 NMNH). *Du Page Co.*: Naperville (1 LACM). *Fulton Co.*: no specific locality (8 UIMNH). *Hancock Co.*: Warsaw (3 NMNH). *Kane Co.*: 2 mi W Sugar Grove (1 UMMZ). *Lake Co.*: Prairie View (1 LACM); Waukegan (1 NMNH). *Mason Co.*: Mason (3 UIMNH). *McLean Co.*: Bloomington (7 UMMZ). *Piatt Co.*: 2.5 mi S, 5 mi W Monticello (1 LACM); 1.25 mi NW White Heath (1 LACM). *Will Co.*: 4.1 mi W Joliet (3 KU); no specific locality (6 UIMNH). *Winnebago Co.*: Rockford (2 UWSP).

INDIANA, UNITED STATES (450). *Adams Co.*: 4 mi S Berne (2 NMNH). *Allen Co.*: Fort Wayne (1 NMNH); 7 mi SW Fort Wayne (1 NMNH). *Bartholemew Co.*: no specific locality (1 NMNH). *Benton Co.*: Foresman (4 NMNH). *Blackford Co.*: 4 mi NW Hartford City (4 NMNH); 4 mi WNW Hartford City (1 NMNH). *Boone Co.*: 5 mi N Lebanon (1 NMNH); 2.5 mi N Thorntown (1 NMNH). *Carroll Co.*: 10 mi S Delphi (2 NMNH). *Cass Co.*: 0.5 mi S Clymers (2 NMNH). *Clark Co.*: Clark State Forest (1 NMNH); Clark State Forest, 1 mi N Henryville (1 NMNH); Clark State Forest, Henryville (1 NMNH). *Clay Co.*: Brazil (11 NMNH); Terre Haute (104 ISUVC). *Clinton Co.*: Edna Mills (2 NMNH). *Crawford Co.*: Wyandotte (1 UMMZ); Wyandotte Cave (1 UMMZ). *Dearborn Co.*: Bright (1 ISUVC); Lawrenceburg (3 ISUVC); 4 mi N Lawrenceburg (1 KU); no specific locality (1 NMNH, 1 UMMZ). *Daviess Co.*: 4 mi E Odon (1 NMNH). *Decatur Co.*: 6 mi S, 2 mi E Greensburg (1 NMNH). *Dekalb Co.*: 1 mi W Waterloo (1 NMNH). *Delaware Co.*: 2 mi SE Albany (1 NMNH); 1 mi NE Royerton (1 NMNH). *Elkhart Co.*: 1 mi E Goshen (1 NMNH); 2 mi SE Goshen (2 NMNH); Osceola (1 ISUVC). *Fayette Co.*: 5 mi E Connorsville (1 NMNH); Mary Gray Bird Sanctuary (2 NMNH). *Fountain Co.*: 5 mi E Attica (2 NMNH); 1 mi E Hillsboro (1 NMNH); T18N, R6W, Sec 33 (1 NMNH). *Franklin Co.*: Brookville (1 NMNH); "Ind 252" (1 NMNH). *Fulton Co.*: Rochester (1 MMNH, 1 NMNH). *Gibson Co.*: 1 mi S Patoka (1 NMNH); 1 mi E Princeton (3 NMNH). *Grant Co.*: Fairmont (1 NMNH); 1 mi E Fairmont (3 NMNH); Bethal Cemetery, 3 mi E Jonesboro (2 NMNH). *Greene Co.*: Worthington (1 NMNH). *Hancock Co.*: 3 mi S Greenfield (1 NMNH). *Harrison Co.*: Corydon (1 NMNH); State Forest, 9 mi SW Corydon (1 NMNH). *Hendricks Co.*: 2 mi SW Danville (1 NMNH); Plainfield (1 NMNH). *Howard Co.*: 1.5 mi E Russiaville (1 NMNH). *Huntington Co.*: 1 mi SE Roanoke

(2 NMNH). *Jackson Co.*: Kurtz (2 NMNH). *Jasper Co.*: 3 mi S Demotte (2 MMNH); Jasper Pulaski Game Preserve (1 NMNH); Rensselaer (1 ISUVC). *Jay Co.*: 3 mi N, 9 mi E Portland (1 NMNH); 2 mi N, 4.7 mi E Portland (1 NMNH); 2 mi N, 9 mi E Portland (1 NMNH); 1.5 mi NE Portland (2 NMNH). *Jefferson Co.*: Blakewoods, 1 mi N, 8 mi W Hanover (2 NMNH); 1 mi N Hanover (1 NMNH). *Jennings Co.*: Crosley Fish and Game Area (1 NMNH). *Johnson Co.*: 4 mi N Franklin (1 NMNH); Franklin (1 NMNH). *Knox Co.*: Monroe (1 ISUVC). *Kosciusko Co.*: Tri County State Game Area (1 NMNH). *Lagrange Co.*: Curtis Creek Trout Rearing Station (1 NMNH); 3 mi W Mongo (1 NMNH); 2 mi W Mongo (1 NMNH); 0.5 mi E Ontario (6 NMNH); 1 mi E Ontario (2 NMNH); Pigeon River Fish and Game Area (1 NMNH); no specific locality (1 UMMZ). *Lake Co.*: Schererville (1 NMNH); 1.5 mi NW Schererville (6 NMNH); Schneider (1 UMMZ). *LaPorte Co.*: 7 mi E Hanna (3 NMNH); 1.5 mi S Union Center (1 NMNH). *Lawrence Co.*: 4 mi N Mitchell (1 NMNH). *Marion Co.*: Indianapolis (2 NMNH). *Marshall Co.*: Lake Maxinkuckee (2 NMNH); near Lake Maxinkuckee, Culver (1 NMNH). *Martin Co.*: Crane (3 NMNH). *Monroe Co.*: Bloomington (1 NMNH). *Montgomery Co.*: 5 mi SW Crawfordsville (1 NMNH); Shades State Park (1 NMNH). *Morgan Co.*: Paragon (1 NMNH). *Newton Co.*: 2.5 mi NW Enos (1 NMNH); Morocco (1 ISUVC, 1 NMNH); 4 mi NW Morocco (1 NMNH); Mount Ayr (3 NMNH); Kankakee, 6 mi W Roselawn (8 NMNH); Rt 10, Roselawn (2 MMNH); Willow Slough (9 ISUVC). *Noble Co.*: 0.25 mi E Ligonier (2 NMNH); 0.5 mi S Rome City (1 NMNH); 1 mi S, 0.5 mi E Rome City (1 NMNH); 1 mi S Wilmot on Rt 5 (4 NMNH); 1.5 mi S Wilmot on Rt 5 (1 NMNH). *Ohio Co.*: 0.25 mi S Aberdeen on Rt 56 (1 NMNH); 0.1 mi S Aberdeen (2 NMNH); Bascom [Corner] (2 NMNH). *Orange Co.*: 5 mi SW Huron [in Martin Co.] (1 NMNH). *Parke Co.*: Turkey Run (7 ISUVC); Turkey Run State Park (5 UMMZ, 1 NMNH). *Perry Co.*: Cannelton (1 NMNH). *Pike Co.*: Purdue Enos Study Area (1 NMNH); 2 mi NE Surgeon (2 NMNH); no specific locality (1 UMMZ). *Porter Co.*: Hebron (3 NMNH); no specific locality (24 NMNH). *Posey Co.*: Hovey Lake (2 ISUVC, 1 NMNH); New Harmony (4 UMMZ, 2 NMNH). *Pulaski Co.*: 3.5 mi N Medaryville (1 NMNH); Winamac Fish and Game Area (1 NMNH). *Putnam Co.*: 1 mi S, 1 mi W Reelsville (1 NMNH). *Randolph Co.*: 7 mi N Farmland (1 NMNH); Herbert Davis Forestry Farm, 6 mi N Farmland (5 NMNH). *Ripley Co.*: 0.25 mi E Rexville (1 KU, 1 NMNH); 0.5 mi E Rexville (1 NMNH); Versailles State Park (1 NMNH). *Rush Co.*: 0.5 mi S Carthage (1 NMNH); 2 mi NE Mays (1 NMNH). *St Joseph Co.*: 6 mi N, 1 mi E Lakeville (1 MSB); 5 mi W South Bend (3 KU); Jackson Rd, South Bend (1 NMNH). *Scott Co.*: jct. Hwy 56 and 3, 4 mi E Scottsburg (1 NMNH). *Shelby Co.*: 5 mi NW Morristown (1 NMNH); 1 mi NE Shelbyville (1 NMNH). *Spencer Co.*: 3 mi S

Hatfield (1 KU, 1 NMNH). *Starke Co.*: 2 mi SW Bass (5 NMNH); Knox (1 NMNH); 6 mi E Knox (1 NMNH); 6 mi S Knox (1 NMNH). *Steuben Co.*: Lake James, 7 mi N Angola (2 CMN); 2.7 mi E Orland (1 NMNH); 6.5 mi E Orland on Rt 120 (1 NMNH); 0.5 mi S Orland (5 NMNH); 2 mi S Orland (1 NMNH); Snow Lake Marsh (1 NMNH). *Sullivan Co.*: Paxton (1 NMNH). *Tippecanoe Co.*: 1 mi W LaFayette (3 NMNH); 10 mi W LaFayette (1 NMNH); Purdue Horticultural Farm (1 NMNH); West LaFayette (2 KU, 1 NMNH); 1 mi W West LaFayette (3 NMNH); 8 mi W West LaFayette (6 KU); 10 mi W West LaFayette (4 KU). *Tipton Co.*: 1 mi S, 1 mi E Russiaville (1 NMNH); 1 mi S, 2 mi E Russiaville (1 NMNH); 1 mi S Tipton (1 NMNH). *Union Co.*: 0.5 mi S Liberty (3 NMNH). *Vanderburgh Co.*: 4 mi N Evansville (2 NMNH). *Vigo Co.*: Terre Haute (19 ISUVC). *Wabash Co.*: 1 mi W Wabash (1 NMNH); no specific locality (1 ISUVC). *Warren Co.*: 7.5 mi E Pine Village (4 NMNH); 8 mi SE Pine Village (3 NMNH). *Warrick Co.*: 5 mi N Newbergh (2 NMNH). *Wayne Co.*: Centerville (1 CUI); 0.5 mi N, 0.5 mi E Centerville (1 KU); 0.5 mi N, 1 mi E Centerville (2 KU); Richmond (1 KU); 1 mi W Richmond (1 NMNH); near Clear Creek, Richmond (3 CUI). *White Co.*: 3 mi E Brookston (2 NMNH); Buffalo (1 ISUVC); Chalmers (2 NMNH). *Whitley Co.*: 1.5 mi S Wilmot (2 NMNH).

KENTUCKY, UNITED STATES (102). *Bell Co.*: 7 mi W Middlesboro (7 NMNH). *Breathitt Co.*: Camp Robinson (1 UKEN); Jackson (1 NMNH); Quicksand (2 UKEN); Robinson Forest, near Noble (2 UKEN). *Carroll Co.*: Ghent (1 NMNH). *Clark Co.*: 5.5 mi N Winchester (1 UKEN); 6 mi W Winchester (2 UKEN); Winchester Water Works (9 UKEN). *Fayette Co.*: 1 mi from Lexington (2 UKEN); 4 mi E Lexington (1 UKEN); Dry Branch, near Spears (2 UKEN); Shawneetown (1 UKEN); Blue Grass Oark (1 UKEN); 2 mi E Lexington (1 UKEN); UK Farm (1 UKEN); 6 mi S Lexington (1 UKEN). *Harlan Co.*: Black Mountain, 4000 ft, 4.5 mi SE Lynch (1 NMNH); Black Mountain (9 UKEN). *Jefferson Co.*: Anchorage (3 LSUMZ); Pleasure Ridge Park (1 UKEN); 1 mi S Okolana (2 UKEN). *Lewis Co.*: Kinniconwick Creek (1 CM). *Madison Co.*: 4 mi E Waco (2 UKEN); Big Hill (2 UKEN); 3 mi SE Waco (2 UKEN). *Mason Co.*: Charleston Bottoms, 2 mi W Maysville (1 CM); Charleston Bottoms, 2.5 mi W Maysville (8 CM); 0.5 mi W Maysville (11 CM); Orangeburg Rd, 2.5 mi SE Maysville (1 CM); 1.75 mi N Moransburg (1 CM). *Meade Co.*: 1.5 mi E Brandenburg (2 NMNH). *Pulaski Co.*: Eubank (3 NMNH). *Scott Co.*: Georgetown (6 UKEN); 3 mi E Georgetown (1 UKEN); 0.5 mi S Georgetown (1 UKEN); 4 mi NE Oxford (4 UKEN); 0.5 mi W White Sulfur (2 UKEN); Stamping Ground (2 UKEN);

MAINE, UNITED STATES (295). *Androscoggin Co.*: Auburn (3 UCONN); Lisbon Center, Lisbon (4 UCONN). *Aroostook Co.*: St Francis, Alagash (1 KU); Ashland

(2 UMMZ); 4 mi N Macwahoc (1 CMN); Masardis (1 UCONN); Presque Isle (3 NMNH); T11, R9 (13 UCONN); T11, R10 (11 UCONN); T11, R11 (11 UCONN); T12, R15 (2 UCONN); T12, R16 (7 UCONN); T16, R12 (11 UCONN). *Franklin Co.*: Dryden, Jay (11 AMNH, 1 KU); Weld (8 UCONN); Mt Blue, 11 mi N Dixfield, Weld (2 UCONN); 11 mi N Dixfield, Weld (7 UCONN); 4 mi N Dixfield, Weld (1 UCONN). *Hancock Co.*: Acadia National Park (1 UMMZ); Bar Harbor (1 NMNH); Brooklin (6 NMNH); Castine (3 AMNH); North Castine, Castine (1 AMNH); 6 mi S of Rt 9 on Rt 179, Mariaville Rest Stop (1 AMNH); Mt Desert (4 UCONN); Mt Desert Island, Mt Desert (2 UMMZ); Hospital Island, Penobscot Bay (1 AMNH); Walker Pond (7 NMNH). *Kennebec Co.*: Gardiner (1 UCONN); Oakland (3 NMNH). *Lincoln Co.*: Isle of Springs, Sheepscoot Bay (1 NMNH). *Oxford Co.*: Dixfield (19 UCONN); 2 mi N Dixfield (2 UCONN); Fryeburg (1 AMNH); South Waterford (4 AMNH); Upton (3 UCONN). *Penobscot Co.*: East Branch Penobscot River (18 NMNH); South Twin Lake, Indian Purchase 4 (1 AMNH); 20 mi E Mt Katahdin, Stacyville (3 NMNH); T6, R7 (1 UCONN). *Piscataquis Co.*: Baxter State Park (2 UMMZ); Frost Pond, T3, R11 (22 CMN, 8 UCONN); Greenville (1 UCONN); Mt Katahdin, 4250 ft (2 NMNH); Mt Katahdin, Basin Pond (1 NMNH); Mt Katahdin, South Basin, 3000 ft (1 NMNH); Mt Katahdin, South Basin Chimney Pond, 3000 ft (6 NMNH); T7, R9 (8 UCONN). *Sagadahoc Co.*: Ashdale (1 UMMZ); East Harpswell [*in Cumberland Co.*] (3 AMNH); Small Point (1 NMNH). *Somerset Co.*: Enchanted Pond, 1500 ft (3 AMNH); Enchanted Pond, 1700 ft (2 AMNH); Grace Pond, 2000 ft (2 AMNH); 0.5 mi N, 1 mi W Lakewood, Madison (4 UCONN); 1 mi W Lakewood, Madison (5 UCONN); Mercer (1 UCONN); Taunton and Raynham (1 UCONN); no specific locality (5 AMNH). *Waldo Co.*: Isleboro Island, Dark Harbor (3 NMNH). *Washington Co.*: Moosehorn, Baring (1 UCONN); Calais (8 UCONN); 3 mi SE Calais (1 UCONN); 6 mi SE Calais (2 UCONN); Moosehorn Wildlife Refuge, Edmonds Unit, Edmonds (1 UCONN); Grand Lake Stream Township (2 UCONN); T5ND (1 UCONN); T6ND (1 UCONN); Vanceboro (7 UCONN). *York Co.*: Kittery (1 ROM); Wells (4 NMNH).

MARYLAND, UNITED STATES (357). *Allegany Co.*: McCoole (4 CM); 3 mi E Oldtown (2 NMNH); 4 mi E Oldtown (2 NMNH); South end Townhill Mtn, 9 mi E Oldtown (3 NMNH). *Anne Arundel Co.*: 3 mi NW Annapolis (38 NMNH); 1 mi W Annapolis (2 NMNH); 4 mi W Annapolis (3 NMNH); Ivy Neck, Smithsonian Chesapeake Bay Center (1 NMNH); Java Farm, Smithsonian Chesapeake Bay Center (6 NMNH); Hwy 50 and South River (1 NMNH); 2 mi E jct Hwy 50 and Rt 301 (1 NMNH). *Baltimore Co.*: Arbutus (2 CMNH); Baltimore (3 AMNH, 9 CMNH, 1 NMNH); Catonsville (1 ROM); Glenartney (1 CMNH); Homeland (4 AMNH); Delaney Valley Rd, Loch Raven Reservoir (2 NMNH). *Calvert Co.*: cypress swamp

along Battle Creek (2 NMNH); Breezy Point (2 NMNH); Plum Point (1 NMNH); on Scientists Cliffs Rd, 1 mi E Rt 2 (2 NMNH); Solomons (2 NMNH); along Hungerford Creek, 3.5 mi N Solomons Island (3 NMNH); 0.75 mi N Solomons Island (10 NMNH). *Charles Co.*: Newport (7 NMNH); W side Patuxent River, Benedict (1 NMNH); 3 mi. SW Port Tobacco (1 NMNH). *Frederick Co.*: 1.5 mi N Wolfsville, 1300 ft (38 NMNH). *Garrett Co.*: Altamont (3 CM, 7 NMNH); Bittinger (5 NMNH); Camp Algawa, near Bittinger (4 CM); 6 mi N Frostburg, Finzel (14 NMNH); Negro Mtn, 2800 ft, Grantsville (1 NMNH); 3 mi E Grantsville (4 NMNH); Savage River State Forest, 2500 ft, 5 mi SE Grantsville (5 UMMZ); 7 mi W Frostburg, 2875 ft, Guntertown (3 UMMZ); Mountain Lake Park (2 NMNH); Swanton (5 NMNH). *Montgomery Co.*: near Arenal Rd, NW Branch Anacostia River (1 NMNH); USNCMN NMRI, Bethesda (2 CM); Army Map Service grounds, Brookmont (1 NMNH); Robert B Moorse Filter Plant, Burnt Mills (2 NMNH); Cabin John PO (1 NMNH); Chevy Chase (1 LACM); Cropley (1 NMNH); 2 mi NW Gaithersburg (1 KU); Seneca Creek State Park, Gaithersburg (1 NMNH); C and O Canal, near Great Falls (2 CM); Kensington (1 NMNH); 1 mi N Kensington (2 NMNH); Little Falls (1 NMNH); Plummers Island, Potomac River (13 NMNH); Poolesville (1 NMNH); Rockville (17 NMNH); 2.3 mi N Rockville (7 NMNH); 0.1 mi N Seneca (1 NMNH); 1.5 mi NW Seneca (1 NMNH); 3 mi W Seneca (1 NMNH); 1 mi N Silver Springs (3 NMNH); Takoma Park (1 NMNH). *Prince Georges Co.*: 1 mi S Branchville (2 CM); 3 mi N Camp Springs (1 NMNH); Greenbelt (3 NMNH); Barnaby Run, Hillcrest Heights (51 NMNH); Hyattsville (5 NMNH); Lanham (1 NMNH); Laurel (10 NMNH); Oxon Hill (12 NMNH); Patuxent Wildlife Research Center (1 NMNH); Riverdale (1 NMNH).

MASSACHUSETTS, UNITED STATES (342). *Barnstable Co.*: Barnstable (4 CM); Chatham, Monomoy Island, Morris Island (1 AMNH); Woods Hole, Falmouth (1 NMNH); Orleans (1 UCONN); East Sandwich, Sandwich (1 UCONN); Wellfleet (2 CM); Wellfleet Audubon Sanctuary, South Wellfleet, Wellfleet (1 UCONN). *Berkshire Co.*: Mt Greylock, Adams (1 UCONN); Mt Greylock, 3200 ft, Adams (6 UCONN); Mt Greylock, 2600-2900 ft, Adams (3 UCONN); Mt Greylock, 3000-3100 ft, Adams (2 UCONN); Hinsdale (11 UCONN); October Mountain State Park, Lee (1 NMNH); 2.5 mi SE Monterey (1 CUI); Mt Washington (5 AMNH, 11 UCONN); Saddle Ball Mtn, New Ashford (1 UCONN); Peru (15 UCONN); Ashley Falls, Sheffield (20 UCONN). *Bristol Co.*: Raynham (1 UCONN); Taunton (1 UMMZ). *Essex Co.*: Andover (5 CM, 1 NMNH); Danvers (1 CM); Essex (1 UMMZ); Gloucester (2 AMNH); Methuen, 200 ft (1 KU); Mandsleigh, Newburyport (8 NMNH). *Franklin Co.*: Ashfield (18 UCONN); 1 mi N, 2 mi W Old Deerfield, Deerfield (2 KU); Northfield (7 UCONN); Warwick (3

CONN); Whately (1 UCONN); 1 mi W Whately (4 UCONN); 3 mi W Whately (2 UCONN). *Hampden Co.*: Brimfield State Forest, Brimfield (16 UCONN); Chester (11 UCONN); Holland (3 UCONN); Montgomery (3 UCONN); Mt Tekoa, Montgomery (3 UCONN). *Hampshire Co.*: Belchertown (1 MMNH); Chesterfield (16 UCONN); Mt Tom, East Hampton (1 UCONN); Huntington (2 UCONN); West Chesterfield (2 AMNH). *Middlesex Co.*: Cambridge (15 NMNH); near Cambridge (1 KU); 1 mi W jct Rts 4 and 25 on Rt 2, Lexington (2 NMNH); Pepperell (1 NMNH); Wakefield (11 NMNH); 2 mi NW Wakefield (1 KU); Waban, Watertown (1 AMNH); Wilmington (37 NMNH). *Norfolk Co.*: Wellesley Street, near Middlesex Co. line, Wellesley (3 NMNH). *Plymouth Co.*: Hanson (2 UCONN); Lakeville (5 UCONN); near Snake Hill, South River, Marshfield (1 NMNH); Middleboro (14 NMNH); 1 mi S, 3.7 mi E Middleborough (5 MSB); 1.5 mi W Plympton (1 UCONN); Raynham (1 UMMZ); Wareham (1 UMMZ); Whitman (2 UCONN). *Worcester Co.*: Bolton (4 AMNH); 5 mi W Charlton (1 ROM); Harvard (3 NMNH); 2 mi N Gilbertville, New Braintree (1 KU); Harvard Forest, Petersham (5 UCONN); New England Primate Research Center, Southborough (3 NMNH); 0.4 mi N Purgatory, Sutton (2 KU); 3.5 mi S Uxbridge (3 KU); 3.5 mi S Uxbridge Center, Uxbridge (2 KU); Jamesville Pond, Worcester (2 KU); 4 mi W Worcester (8 KU).

MICHIGAN, UNITED STATES (660). *Alcona Co.*: Harrisville (1 UMMZ); 3 mi S Harrisville (1 UMMZ). *Alger Co.*: 14 mi SW Grand Marais (1 UMMZ); 7 mi NE Munising (2 UMMZ); no specific locality (5 UMMZ). *Allegan Co.*: Swan Creek Wildlife Experiment Station (1 UMMZ); jct Swan Creek and Kalamazoo River (3 UMMZ). *Antrim Co.*: N side Benway Lake (1 UMMZ). *Baraga Co.*: T48N, R32W, NE 1/4 Sec 10 (1 UMMZ). *Barry Co.*: S of Hastings, in Bingham Twp (2 AMNH). *Bay Co.*: Munger (1 MSU). *Benzie Co.*: 7 mi NW Honor (1 UMMZ). *Berrien Co.*: Warren Estate, Lakeside, Chikaming (1 MSU); Warren Dones State Park (1 MSU); Warren Woods (8 UMMZ); no specific locality (1 MSU). *Branch Co.*: Coldwater (4 AMNH). *Calhoun Co.*: E of Biology Preserve, Battle Creek (1 AMNH); Marshall (1 MSU). *Charlevoix Co.*: Boyne Falls (29 UMMZ). *Cheboygan Co.*: Burt Lake (1 NMNH, 1 ROM, 3 UMMZ); Douglas Lake (3 KU, 1 MMNH, 1 NMNH, 1 ROM, 5 UMMZ). *Chippewa Co.*: 0.5 mi NE Drummond PO, Drummond (1 UMMZ); 0.25 mi NE Spring Pond, Drummond Island (1 UMMZ); 0.25 mi E Drummond, Drummond Island (1 MSU); McNearney Lake, Maple Cutover (2 UMMZ); Sugar Island (1 UMMZ); Chase S. Osborn Reserve, Sugar Island (1 UMMZ); T46N, R2E, SW 1/4 Sec 25, Sugar Island (2 UMMZ). *Clare Co.*: Harrison (2 UMMZ). *Clinton Co.*: 3 mi E Bath (1 MSU); Park Lake, Bath (1 MSU); 1 mi E DeWitt (1 UMMZ); Rose Lake Wildlife Research Area, T5N, R1W, Sec 14 (3 MSU); Rose Lake Wildlife Research Area, T5N, R1W,

Sec 23 (17 MSU). *Crawford Co.*: 4 mi SW Graylins (2 UMMZ); no specific locality (1 MSU). *Delta Co.*: 2 mi NW Fairport (2 UMMZ); Garden (8 MSU); 7 mi N, 2mi E Garden (1 MSU). *Dickinson Co.*: Brown Lake (3 UMMZ); Iron Mountain (1 MSU); T44N, R28W, Sec 25 (2 UMMZ). *Emmot Co.*: 0.5 mi E Pellston (1 UMMZ). *Gladwin Co.*: 5 mi E Gladwin (1 UMMZ). *Gogebic Co.*: Fish Hawk Lake (6 UMMZ); Ironwood (3 UMMZ); 1 mi SE Little Girls Point (1 UMMZ); 2 mi SE Little Girls Point (1 UMMZ); 3 mi SE Little Girls Point (2 UMMZ); Mud Lake, 0.25 mi SE Thousand Island Lake (3 UMMZ). *Grand Traverse Co.*: Grawn (1 MSU); Marion Island (2 UMMZ); Monroe Center (1 MSU). *Gratiot Co.*: Alma (1 UMMZ); 1.75 mi N Alma (3 UMMZ); 1 mi NE Alma (1 UMMZ). *Hillsdale Co.*: 4 mi NE Jonesville (2 UMMZ). *Ingham Co.*: 3 mi E Bath (1 MSU); East Lansing (6 MSU); Fogles Farm (1 MSU); Lansing city limits (2 MSU); MSU campus (1 MSU); Riverside Farm, 2 mi E Okemos (3 MSU). *Iron Co.*: Crystal Falls (2 MSU); Hopes Creek (1 UMMZ); headwaters of Mallard Creek (2 UMMZ); T45N, R37W, N 1/4 Sec 26 (1 UMMZ); T46N, R35W, Sec 7 (2 UMMZ). *Jackson Co.*: Blackman Twp (7 UMMZ); Napoleon (1 UMMZ); Mud Lake, Norville Twp (1 KU); Round Lake, near Lenawee Co line (3 KU); Waterloo (1 UMMZ). *Kalamazoo Co.*: Kellogg Bird Sanctuary (2 MSU); Rose Twp (1 MMNH). *Kalkaska Co.*: T25N, R5W, Sec 32 (1 MSU). *Kent Co.*: Casnovia (1 MSU); Cedar Springs (1 MSU); East Grand Rapids, 0.5 mi SW Reeds Lake (1 MSU). *Keweenaw Co.*: Bete Gris (2 UMMZ); Copper Harbor (2 UMMZ); Clark Mine, 2.2 mi SE Copper Harbor (6 UMMZ); 5 mi E Eagle Harbor (1 UMMZ). *Lake Co.*: 1 mi NW Chase (2 UMMZ). *Leelanau Co.*: 1 mi N Leland (2 UMMZ); 0.5 mi N Leland (2 UMMZ); Leland (1 UMMZ); Duck Lake, 2 mi S Leland (2 UMMZ); Provemont (1 AMNH). *Livingston Co.*: George Reserve (1 KU, 1 NMNH, 21 UMMZ); S side George Reserve (1 NMNH). *Luce Co.*: 8 mi N Bass Lake (2 UMMZ); Two Hearted River, 18 mi N Newbury (7 UMMZ); 12 mi NW Newbury (2 UMMZ). *Mackinac Co.*: Egadine (1 UMMZ); 9 mi S Rudyard (8 KU, 5 MSB). *Marquette Co.*: Huron Mtn Club (32 UMMZ); Michigamme (4 NMNH). *Mason Co.*: 9 mi N Ludington (2 UMMZ). *Mecosta Co.*: Paris (2 UMMZ). *Menominee Co.*: 5 mi SW Banat (5 UMMZ); 8 mi SW Banat (5 UMMZ); 6 mi NW Banat (1 UMMZ); 0.5 mi SW Cedar River (1 UMMZ); 5 mi SW Cedar River (1 UMMZ); 5 mi E Daggett (6 UMMZ); 8 mi N Hermansville (7 UMMZ); 5 mi N Menominee (13 UMMZ); 7 mi E Stephenson (8 UMMZ); 13 mi WSW Stephenson (1 UMMZ). *Midland Co.*: Sanford (2 UMMZ). *Missaukee Co.*: T24N, R5W, Sec 4 (1 MSU). *Montmorency Co.*: Hunt Creek Experimental Station (1 UMMZ). *Muskegon Co.*: north of Muskegon State Park, Lake Michigan (3 UMMZ); 4 mi NW North Muskegon (1 UMMZ). *Oakland Co.*: Birmingham (1 UMMZ); Orange Lake, Bloomfield

(1 AMNH); Southfield (1 AMNH). *Ogemaw Co.*: N shore Sage Lake (2 UMMZ). *Ontonagon Co.*: Lake Gogebic (4 KU, 5 UMMZ); Porcupine Mtns (19 UMMZ). *Oscoda Co.*: Mio (1 UMMZ). *Otsego Co.*: 5 mi S Elmira (1 UMMZ); Pigeon River State Forest, 8 mi N Headquarters (2 UMMZ); Pigeon River State Forest, Headquarters (4 UMMZ); 3 mi E Vanderbilt (1 UMMZ). *Presque Isle Co.*: [Lower] Barnhart Lake (21 UMMZ); 1.5 mi SE Barnhart Lake (2 UMMZ); T35N, R4E, Sec 30 (1 MSU). *Roscommon Co.*: Higgins Lake (3 KU); 2 mi W Nellsville (2 MSU); 1 mi W Nellsville (1 MSU); Roscommon (2 NMNH); 8 mi SW Roscommon (2 UMMZ). *Sanilac Co.*: 3 mi N Lexington (2 UMMZ). *Schoolcraft Co.*: Floodwood (1 UMMZ); Manistique (1 MSU); Seney National Wildlife Refuge (4 MMNH, 80 NMNH). *Shiawassee Co.*: 2 mi N Bryon (4 UMMZ); 0.25 mi S Bryon (4 UMMZ); 0.5 mi NW Bryon (2 UMMZ); 3 mi NW Bryon (1 UMMZ). *Van Buren Co.*: Paw Paw (2 MSU); Van Auken Lake (2 UMMZ); Wolf Lake Fish Hatchery (6 UMMZ). *Washtenaw Co.*: Ann Arbor (18 MMNH, 9 NMNH, 23 UMMZ); 3 mi NE Ann Arbor (2 NMNH); 5.5 mi NE Ann Arbor (1 UMMZ); 5 mi NE Ann Arbor (2 NMNH); 1 mi E Ann Arbor (1 KU, 1 UMMZ); 2 mi E Ann Arbor (1 NMNH); 5 mi E Ann Arbor (2 UMMZ); S edge of Ann Arbor (1 UMMZ); 3 mi S Ann Arbor (1 UMMZ); 5 mi SW Ann Arbor (2 UMMZ); 4 mi W Ann Arbor (1 KU); W edge of Ann Arbor, Eber, White Woods (1 UMMZ); W edge of Ann Arbor, field SW White Woods (1 UMMZ); Steeres Swamp, near Ann Arbor (4 UMMZ); Ann Arbor Twp, Sec 5 (1 LACM); 1 mi N Dixboro (4 NMNH); 1 mi SE Dixboro, 800 ft (1 KU); Huron River Drive, East Madden (1 NMNH); Lodi Twp (2 NMNH); Portage Lake (1 UMMZ); Saline (1 UMMZ); Scio Twp (1 NMNH); T15, R5E, NE 1/4, NE 1/4, SW 1/4 Sec 1 (1 UMMZ); T15, R5E (2 UMMZ); T2S, R6E, NW 1/4 SE 1/4 Sec 12 (3 UMMZ); T2S, R6E, SE 1/4, NE 1/4 Sec 14 (3 UMMZ); Whitmore Lake (5 ROM). *Wayne Co.*: Plymouth (3 MSU). *Wexford Co.*: 3 mi SW Cadillac (2 UMMZ).

MINNESOTA, UNITED STATES (188). *Aitkin Co.*: T48N, R22W, NE 1/4 Sec 1 (1 MMNH); T51N, R24W, SW 1/4 Sec 36 (3 MMNH); T52N, R23W, SW 1/4 Sec 5 (1 MMNH). *Beltrami Co.*: T147N, R33W, NW 1/4 Sec 4 (1 MHP); T147N, R35W, NE 1/4 Sec 5 (1 MMNH); T150N, R35N, SW 1/4 Sec 32 (2 MMNH); T153N, R35W, SW 1/4 Sec 6 (1 MMNH); T158N, R37W, SW 1/4 Sec 29 (2 MMNH). *Cass Co.*: Cherneys Resort, 4.5 mi SE Bena (1 CUI); T133N, R29W, SE 1/4 Sec 20 (1 MMNH); T141N, R29W, NW 1/4 Sec 8 (8 MMNH); T141N, R31W, SW 1/4 Sec 18 (1 MMNH); T143N, R25W, SE 1/4 Sec 9 (7 MMNH). *Cook Co.*: Caribou River (1 MMNH); Cascade Lake (2 MMNH); mouth of Cascade River (1 MMNH); Cross River (2 MMNH); W Devils Track Lake (4 MMNH); Devils Track River (5 MMNH); Four Mile Lake (1 MMNH); 1.5 mi N, 10 mi W Grand Marais,

T61N, R2W, SW 1/4 Sec 15 (1 MMNH); 2 mi N, 7.5 mi E Grand Marais, T61N, R2W, SW 1/4 Sec 15 (1 MMNH); 6 mi N, 9 mi E Grand Marais, T62N, R2E, NW 1/4 Sec 25 (2 MMNH); 13.5 mi N, 4.5 mi W Grand Marais, T63N, R1W, SW 1/4 Sec 10 (1 MMNH); 15.5 mi N, 6 mi E Grand Marais, T63N, R2E, NW 1/4 Sec 4 (1 MMNH); 1.5 mi S, 7.5 mi W Grand Marais, T61N, R1W, SW 1/4 Sec 30 (1 MMNH); Grand Portage (3 MMNH); 1.5 mi S, 2 mi W Grand Portage, T63N, R6E, SE 1/4 Sec 7 (1 MMNH); Poplar River, Hagbergs (4 MMNH); 3 mi N, 1 mi E Hovland, T62N, R3E, SE 1/4 Sec 1 (1 MMNH); 3 mi N Hovland, T62N, R4E, SE 1/4 Sec 6 (1 MMNH); 3.5 mi N, 1 mi W Hovland, T63N, R3E, SE 1/4 Sec 36 (2 MMNH); 4.5 mi N, 1 mi E Hovland, T63N, R4E, SE 1/4 Sec 29 (1 MMNH); Otter Lake, 10 mi N, 1.5 mi W Hovland, T64N, R3E, NW 1/4 Sec 36 (2 MMNH); 10 mi N, 3 mi E Hovland, T64N, R4E, NE 1/4 Sec 34 (1 MMNH); 4 mi NE Hovland (1 MMNH); islands in Lake Saganaga (1 MMNH); Lower Brule River (1 MMNH); Pigeon River, T64N, R6E, SW 1/4 Sec 20 (1 MMNH); Popular Lake (1 MMNH); 1 mi N, 1.5 mi E Schroeder, T59N, R4W, SW 1/4 Sec 29 (1 MMNH); 2 mi N Schroeder (2 MMNH); 38.5 mi N, 4.5 mi E Schroeder, T65N, R4W, SW 1/4 Sec 22 (1 MMNH); 4 mi W Schroeder, T58N, R4W, NW 1/4 Sec 4 (1 MMNH); 2 mi S, 2 mi W Taconite Harbor (1 MMNH); mouth of Temperence River (1 MMNH); Toffe (1 MMNH); T62N, R3E, SE 1/4 Sec 8 (1 MMNH); T62N, R3E, NE 1/4 Sec 25 (2 MMNH); T62N, R3E, NE 1/4 Sec 33 (3 MMNH); T62N, R4W, SW 1/4 Sec 7 (4 MMNH); T62N, R5W, SW 1/4 Sec 1 (1 MMNH); T64N, R1W, NW 1/4 Sec 8 (1 MMNH); T65N, R2W, NW 1/4 Sec 31 (1 MMNH). *Crow Wing Co.*: 3 mi W Wigwam Bay, Camp Lake, 690 ft (1 MMNH); 7 mi N Merrifield (2 MMNH); 1 mi N Nisswa (2 MSB); T44N, R29W, Sec 8 (4 MMNH); T44N, R30W, SE 1/4 Sec 2 (2 MMNH); T46N, R28W, NE 1/4 Sec 3 (3 MMNH); T46N, R28W, NE 1/4 Sec 18 (4 MMNH). *Ithasca Co.*: Nashwaluk (1 MMNH); T53N, R24W, NW 1/4 Sec 36 (1 MMNH); T149N, R29W, NE 1/4 Sec 4 (4 MMNH). *Koochiching Co.*: Ericsburg (8 MMNH); T67N, R23W, NW 1/4 Sec 20 (3 MMNH); T154N, R29W, SW 1/4 Sec 32 (3 MMNH); T158N, R29W, NW 1/4 Sec 33 (2 MMNH). *Lake Co.*: Back Bay, Basswood Lake (1 MMNH); Two Harbors (2 MMNH); T63N, R7W, NW 1/4 Sec 15 (1 MMNH). *Lake of the Woods Co.*: Currys Island (1 MMNH); Magnuson Island (8 MMNH); Norris Camp (1 MMNH); 12 mi S, 4 mi W Roosevelt (1 MHP); Williams (6 MMNH); T158N, R33W, SW 1/4 Sec 28 (3 MMNH). *Pine Co.*: St Croix Park (1 MMNH); T38N, R20W, NE 1/4 Sec 15 (1 MMNH). *St. Louis Co.*: 7 mi NW Chisholm (1 MMNH); near Cramer (1 MMNH); Crane Lake (4 MMNH); Haines Gulch, Duluth (1 MMNH); 18 mi NW Ely (1 MMNH); Hibbing, T58N, R20W, NW 1/4 Sec 32 (1 MMNH); Ash Trail Lodge, Lake Kabetogama, T68N, R19W, SW 1/4 Sec 5 (1 MMNH); Pelican Lake, Orr (1 MMNH); T50N, R15W, SW 1/4 Sec

5 (2 MMNH); T50N, R17W, NW 1/4 Sec 2 (1 MMNH); T51N, R17W, NE 1/4 Sec 32 (1 MMNH); T57N, R15W, NE 1/4 Sec 32 (3 MMNH); T57N, R21W, SW 1/4 Sec 30 (1 MMNH); T59N, R17W, SW 1/4 Sec 20 (4 MMNH); T59N, R21W, SE 1/4 Sec 19 (1 MMNH); T60N, R21W, N 1/2 Sec 21 (1 MMNH); T61N, R21W, NE 1/4 Sec 29 (1 MMNH); T67N, R17W, NW 1/4 Sec 15 (1 MMNH).

NEW HAMPSHIRE, UNITED STATES (732). *Belknap Co.*: Alton (2 UCONN); Birch Island, Lake Winnepesaukee, Gilford (2 UCONN); 2.25 mi E Gilford (3 CM); 0.5 mi S, 5 mi E Gilford (1 CM). *Carroll Co.*: Bartlett (15 UCONN); Bartlett Experimental Forest, Bartlett (11 UCONN); Intervale, Conway (3 UMMZ); Snowville, Eaton (1 AMNH); Harts Location (21 UCONN); Washburn, Harts Location (1 UCONN); Washburn Sale, Harts Location (13 UCONN); Jackson (21 UCONN); Marshbrook Timber Sale, Jackson (3 UCONN); East Branch, West Timber Sale, Jackson (6 UCONN); Ossipee (15 NMNH); Center Ossipee, Ossipee (13 KU, 73 NMNH); Center Ossipee, 500 ft, Ossipee (2 KU); 2 mi S Center Ossipee, Ossipee (29 KU). *Coos Co.*: Bretton Woods (1 NMNH); Crawford Notch, Carroll (6 NMNH); Crawford Notch, Nancy Cascades, Carroll (2 NMNH); Crawford Notch, Notchland, Carroll (54 NMNH); Twin Mountain, Carroll (8 UCONN); Coleman State Park, 3.5 mi N, 9.5 mi E Colebrook (19 CM); 9 mi NNE Errol (6 AMNH); Moose Brook State Park, 1.25 mi N, 2.25 mi W Gorham (1 CM); 3 mi S, 10.5 mi W Gorham (2 CM); 4.5 mi S, 9.5 mi W Gorham (4 CM); 5 mi S, 9.3 mi W Gorham (8 CM); Jefferson Notch, 2050 ft (1 NMNH); Pinkham Notch, Pinkham Grant (2 AMNH, 3 KU); White Mountains, Pinkham Notch, Pinkham Grant (4 KU); First Conn Lake, Mettallak Pt, 1700 ft, Pittsburg (6 ROM); 6.25 mi N, 10.25 mi E Pittsburg (1 CM); 1.25 mi N, 11.5 mi E Pittsburg (1 CM); Lake Francis State Park, 0.5 mi N, 4.5 mi E Pittsburg (3 CM); Pittsburg (3 UMMZ); 1.25 mi S, 2.25 mi E Pittsburg (6 CM); Mizpah Spring, 3800 ft, Presidential Range (3 UMMZ); Mt Washington, 3 mi W of base station, Sargents Purchase (3 KU); Mt Washington, 3750 ft, Sargents Purchase (12 AMNH); halfway house, Mt Washington, Sargents Purchase (1 UCONN); Hermit Lake, 3600 ft, Mt Washington, Sargents Purchase (5 NMNH); summit of Mt Washington, Sargents Purchase (1 NMNH); Tuckerman Ravine, Sargents Purchase (8 AMNH); Tuckerman Ravine, about 4200 ft, Sargents Purchase (3 UMMZ). *Grafton Co.*: Camp Pasquaney, Bristol (25 NMNH); 1 mi S Franconia on Rt 116 (2 CM); 1 mi SE Franconia on Rt 18 (3 CM); Franconia Notch State Park, 3.25 mi S, 2.75 mi E Franconia (2 CM); Franconia Notch State Park, 4.75 mi S, 3.5 mi E Franconia (3 CM); Franconia Notch State Park, 5.75 mi S, 3 mi E Franconia (4 CM); Franconia Notch State Park, 8.75 mi S, 2 mi E Franconia (5 CM); Profile Lake, Franconia Notch, Franconia (5 UMMZ); West Lebanon, Lebanon (2 UMMZ); 3 mi S West Lebanon, Lebanon (3 UMMZ); Littleton (3 ROM); Livermore (6 UCONN); Mt

Tremont Sale, Livermore (1 UCONN); Mt Moosilauke (13 AMNH, 1 UMMZ); North Greeley Pond (7 NMNH); 0.5 mi S Warren (1 UMMZ). *Hillsborough Co.*: Brookline (4 UCONN); Hancock Creek (1 CM); Hancock Outflow (1 CM); Hancock P Garland Pasture (3 CM); Sargent Camp, Hancock (94 CM); Mont Vernon (1 UCONN); Peterborough (48 CM); Mayr Farm, Wilton (7 NMNH). *Merrimack Co.*: Pembroke (16 UCONN). *Rockingham Co.*: Greenland (2 UMMZ); 3 mi N, 1.5 mi E Hampton (3 CM); 3 mi N, 3 mi E Hampton (9 CM); 0.5 mi S, 2.5 mi W Hampton (2 CM); 1 mi S, 0.7 mi E Hampton (11 CM); 1 mi S, 0.75 mi E Hampton (8 CM); Northwood (3 UCONN); Pawtuckaway State Park, 4 mi W Nottingham (2 CM); 2.75 mi S, 3.5 mi W Nottingham (3 CM); Rye Beach, Rye (1 UCONN). *Strafford Co.*: 1 mi E Durham (8 UMMZ); New Durham (1 UCONN); 2.5 mi N Sunapee (2 UMMZ); Sunapee Harbor (4 NMNH).

NEW JERSEY, UNITED STATES (129). *Atlantic Co.*: Mays Landing (2 CMNH, 2 UMMZ, 6 NMNH); Brigantine National Wildlife Refuge, 0.7 mi ESE Oceanville (3 NMNH); head of Lily Lake, 0.2 mi WSW Oceanville (2 NMNH); Pleasantville (2 ROM). *Bergen Co.*: Demarest (10 AMNH); Englewood Cliffs (2 AMNH); Mahwah (1 AMNH); Northvale (1 AMNH); Ramsey (1 AMNH). *Cape May Co.*: Cape May (1 ISUVC, 2 NMNH). *Essex Co.*: Millburn (2 AMNH); Montclair (1 AMNH); [Florham] Park (6 AMNH); South Orange Reservoir (6 AMNH); Upper Montclair (6 AMNH); no specific locality (1 AMNH). *Hudson Co.*: Hackensack Meadows (9 AMNH). *Hunterdon Co.*: Fairmont (13 AMNH). *Mercer Co.*: East Windsor Twp (1 UMF); 1 mi W Highstown (1 UMF); 1.8 mi SW Highstown (1 UMF); Princeton (1 UMMZ); Dutch Neck, 12 mi NE Trenton (1 UMF). *Monmouth Co.*: Allaire (2 UMMZ). *Morris Co.*: Boonton (3 AMNH); Rockaway Valley, Boonton (1 AMNH); Chatham (1 NMNH); Hibernia Mine Region, Hibernia (1 AMNH); Mendham (2 AMNH); 7 mi NW Morristown (6 LTU). *Ocean Co.*: Lakehurst (4 AMNH); 0.25 mi S, 0.25 mi W Laurelton, Brick (1 KU); West Montoloking, Brick (2 AMNH); Tuckerton (7 NMNH). *Sussex Co.*: Lake Iliff, Andover Twp (1 AMNH); Berans (2 AMNH); 1.5 mi E Berans (3 AMNH); Lake Wawayanda, Xeron (1 NMNH). *Union Co.*: Elizabeth River, Salem Dam, Hillside (1 NMNH); Plainfield (1 AMNH); Union Twp (1 NMNH); 0.75 mi S, 0.25 mi W Westfield (3 KU). *County unknown*: Nurdhoff (2 AMNH).

NEW YORK, UNITED STATES (1,144). *Albany Co.*: Rensselaerville, Edmund Niles Huyk Preserve (7 NMNH); no specific locality (2 AMNH). *Bronx Co.*: Pelham Bay Park (1 NMNH). *Broome Co.*: Oquaga Lake (1 NMNH). *Cayuga Co.*: Victory (1 NYSM). *Chautauqua Co.*: Ottaway Park, 1 mi E Barcelona, Westfield (8 NMNH). *Clinton Co.*: Plattsburgh (1 UCONN); 1 mi N, 2 mi W Plattsburgh, 800 ft (1 UCONN); 2.5 mi N, 1.5 mi E Plattsburgh, 100 ft (2

UCONN); W Plattsburgh, Plattsburgh (1 UCONN); NW Plattsburgh, Plattsburgh (1 UCONN); 1 mi N, 2.5 mi W Schuyler Falls, 860 ft (2 UCONN). *Columbia Co.*: no specific locality (1 AMNH). *Delaware Co.*: Stamford (4 AMNH); Walton (1 AMNH). *Dutchess Co.*: Pine Plains (2 UCONN); 2 mi NW Pine Plains, Pine Plains (6 UCONN). *Erie Co.*: Allegany Park, Buffalo (7 NYISM). *Essex Co.*: Chapel Pond, 1100 ft, Adirondacks (1 AMNH); Clear Lake, Adirondacks Lodge, Adirondacks (2 NYISM); Cobble Hill, 1000 ft, Adirondacks (1 AMNH); Deer Brook, 1100 ft, Adirondacks (3 AMNH); Keene Valley, Adirondacks (1 AMNH); Beede Brook (1 NYISM); Elk Lake, 2000 ft (4 AMNH); North Wood (6 AMNH, 2 KU); Wilmington (1 UCONN); Whiteface Mtn, 4300 ft, 3 mi W Wilmington (1 UCONN); Marble Mtn, 1900 ft, 2 mi W Wilmington (1 UCONN); Whiteface Mtn, 4250 ft, 0.5 mi S, 3 mi W Wilmington (1 UCONN); Whiteface Mtn, 4350 ft, 1 mi S, 3 mi W Wilmington (1 UCONN); Whiteface Mtn, 4200 ft, 1 mi S, 3 mi W Wilmington (2 UCONN); Whiteface Mtn, 4240 ft, 1 mi S, 2.8 mi W Wilmington (1 UCONN); Little Whiteface Mtn, 3500 ft, 2 mi S, 3.75 mi W Wilmington (1 UCONN). *Franklin Co.*: Mountain View, Bellmont (1 NMNH); Spectacle Pond, Brighton Twp (8 AMNH); Moose Pond, Saranac Lake (3 AMNH); Mt Pisgah, Saranac Lake (3 AMNH); 1.5 mi E of south end of Tupper Lake (1 CM). *Greene Co.*: Catskill Mtns (24 NMNH); Catskill Game Farm (6 AMNH); Kiskatom, Catskill (1 AMNH); Hunter (1 NMNH); SW Edgewood, Hunter (4 NYISM); Lanesville, Hunter (1 AMNH); Notch Lake, 2000 ft, SSE Hunter (10 NYISM); Stony Clove, 2 mi S Hunter (4 UMF). *Hamilton Co.*: Piseco, Arietta (1 NMNH); Indian Lake, Indian Lake (2 NYISM); Speculator, Lake Pleasant (4 AMNH); Lake Eaton, Long Lake (6 KU, 4 MSB). *Herkimer Co.*: Big Burnt Lake (1 NYISM); Big Moose Lake, Webb (2 NMNH); Lake Charlotte (7 AMNH). *Jefferson Co.*: Alexandria Bay, Alexandria (1 CM); Harbor Island (1 LACM); Red Lake, Theresa (3 MMNH). *Lewis Co.*: Locust Grove, Leyden (30 NMNH); Lyons Falls (1 NMNH); Petries Corners (1 CM). *Madison Co.*: Hamilton (21 AMNH); Lebanon Reservoir, Lebanon (2 AMNH); Peterboro (34 NMNH). *Nassau Co.*: Jericho (3 KU); no specific locality (1 AMNH). *New York Co.*: Manhattan Borough, American Museum, New York City (1 AMNH). *Oneida Co.*: Alder Creek (4 AMNH, 2 NMNH). *Onandago Co.*: Syracuse (2 NMNH). *Orange Co.*: Cornwall (1 NYISM); Highland Falls, Highlands (7 NMNH); Canarda Swamp, Highland Falls, Highlands (1 NMNH); Cansook Island, Highland Falls, Highlands (1 NMNH); West Point, Highlands (1 AMNH, 13 NMNH); Tamarack Swamp (1 NMNH). *Oswego Co.*: Mexico (1 NMNH); West Monroe (2 AMNH). *Otsego Co.*: Burlington Twp (1 NYISM); Gilbert Lake State Park (7 NYISM); Hinman Hollow, Milford Twp (2 NYISM); Cooperstown, Ostego Twp (3 NYISM); Springfield Center (5 NYISM). *Queens Co.*: Fort Totten (2 NMNH); Elmhurst, Long Island (1 AMNH); Jamaica, Long Island (6 AMNH); Flushing, Long Island (3 AMNH); North Hills, Long Island [*in Nassau Co.*] (2 AMNH). *Rensselaer Co.*: Babcock Lake (1 NYISM); Berlin (20 AMNH); Best (1 NYISM); Capital District Game Refuge (2 NYISM); Dutch Church (2 NYISM); Hoag Corners (1 NYISM); Poetenskill (7 NYISM); Barberville, Poetenskill (2 NYISM); Rensselaer (5 NYISM); Taborton, Sand Lake (2 NYISM); Stephentown Center (6 NYISM); Troy (1 NMNH). *Richmond Co.*: Annadale, Staten Island (1 AMNH); Boylsted Swamp, Staten Island (1 AMNH); Giffords, Staten Island (1 AMNH); Huguenot, Staten Island (2 AMNH); Lakes Island, Staten Island (4 AMNH); Oakwood, Staten Island (5 AMNH). *Rockland Co.*: Germonds, Clarkstown (1 AMNH); Nyack (6 AMNH); Piermont (1 AMNH); South Nyack (1 AMNH); Queensboro Brook, Bear Mtn, Stony Point (2 AMNH); Trailside Museum, Bear Mtn, Stony Point (2 AMNH). *Saratoga Co.*: Burnt Hills, Balston (4 UCONN). *Schenectady Co.*: Glenville (25 UCONN). *Schoharie Co.*: North Blenheim, 1050 ft, Blenheim (1 NYISM); Petersburg Mtn, Cobleskill (8 NYISM); Lawyersville, Cobleskill and Seward (3 AMNH); Breakabeen, Fulton (2 NYISM); Gilboa, 1300 ft (2 NYISM); Richmondville, 1100 ft (4 NYISM); Summit, 2200 ft (2 NYISM). *Schuyler Co.*: Arnot Forest, 18 mi SW Ithaca (7 UMF). *Suffolk Co.*: Manorville, Brookhaven (4 AMNH); 2 mi S Mastic, Brookhaven (2 AMNH); Mt Sinai, Brookhaven (1 AMNH); Montauk Point, East Hampton (20 NMNH); 66 Sunset Dr, Huntington (1 AMNH); Kalbfleisch Field Research Station, Huntington (12 AMNH); Cedarhurst, Long Island [*in Nassau Co.*] (4 AMNH); Garden City, Long Island [*in Nassau Co.*] (2 AMNH); Greenport, Long Island (1 AMNH); Syosset, Long Island [*in Nassau Co.*] (1 AMNH); Shelter Island (2 AMNH, 2 KU); Wading River (1 AMNH). *Sullivan Co.*: Monticello (2 AMNH). *Tioga Co.*: Owego (9 NMNH). *Tompkins Co.*: Brooktondale, 1000 ft (1 AMNH); Danby Woods, Danby (1 MMNH); Ithaca (9 AMNH, 4 CMN, 2 KU, 1 NYISM, 95 UMF); 1406 Oak Ave, Ithaca (1 MSB); Beebe Lake, Ithaca (1 MMNH); head of Beebe Lake, Ithaca (1 AMNH); Cascade Creek, Ithaca (2 AMNH); Cascadilla Creek, Ithaca (6 UMF); Monkey Run Area, Ithaca (8 UMF); south side of Six Mile Creek, Ithaca (5 UMF); Turkey Hill, Ithaca (2 AMNH); near Ithaca (104 UMF); 4 mi N Ithaca (2 UMF); 3.5 mi NE Ithaca (3 UMF); 4 mi NE Ithaca (1 UMF); 4.2 mi E Ithaca (3 UMF); 4.8 mi E Ithaca (169 UMF); 4.9 mi E Ithaca (33 UMF); 6.8 mi E Ithaca (9 UMF); 3.6 mi SSE Ithaca (1 UMF); 2 mi S Ithaca (2 UMF); 6 mi SW Ithaca (7 UMF); Mclean Preserve (1 NYISM); Ringwood (4 MMNH). *Ulster Co.*: Highland (1 AMNH). *Warren Co.*: Lake George (39 NMNH); North Warrensburg (2 NYISM). *Washington Co.*: Indian Cave, 0.5 mi W Carvers Falls (10 CM); Easton (2 UCONN); Greenwich (27 UCONN). *Westchester Co.*: Bedford (1 AMNH); Hastings on Hudson, Greenburgh (8 AMNH);

Harrison (1 AMNH); Cross River, Lewisboro (1 AMNH); Mt Vernon (1 CM); New Rochelle (1 AMNH); Croton Falls, North Salem (1 AMNH); Ossining (5 AMNH); Pleasantville, Mount Pleasant (1 AMNH); Sleepy Hollow Rd, Pleasantville, Mount Pleasant (1 AMNH); Sing Sing (5 NMNH); Yorktown Heights, Yorktown (16 AMNH); no specific locality (4 AMNH).

NORTH CAROLINA, UNITED STATES (1,019). *Alexander Co.*: 6 km NW Ellendale, State Rd 1303, 1400 ft (2 UNCW). *Alleghany Co.*: Air Bellows Gap, 3472-3500 ft (2 UNCW); Beech Mountain, 3 mi N Traphill, State Rd 1100 (2 UNCW); 2 mi SW Glade Valley, State Rd 1123 (1 UNCW); 1 mi N, 1 mi W Roaring Gap, 3000 ft (1 KU). *Ashe Co.*: near Deep Gap (1 ASUVC); 10 mi NW Jefferson, Cherokee National Forest (1 UNCW); Todd (2 ASUVC); no specific locality (1 ASUVC). *Avery Co.*: Banner Elk (1 ASUVC); Grandfather Mtn (2 ASUVC, 3 NCSM, 2 NMNH); Grandfather Mtn, 2.7 mi from Caldwell Co line on Hwy 221 (1 MMNH); Idlewild Rd, 2 mi from Hwy 63 (1 ASUVC); Linville (2 UNCW); about 4.25 mi NE Linville, Grandfather Mountain (6 NCSM); Pineola (1 ASUVC); Rattlesnake Cliffs, 12.5 mi E Blue Ridge Pkwy (1 ASUVC); 0.5 mi up Shanty Springs Trail (1 ASUVC). *Bertie Co.*: 4 mi N Windsor (1 LSUMZ). *Buncombe Co.*: Asheville (2 UMMZ); 25 mi SW Asheville (1 UNCW); Bent Creek, Pisgah National Forest, Asheville (1 NMNH); Bent Creek Experimental Station, Pisgah National Forest (13 NMNH); Craggy Gardens at Forest Service Rd 63, 4700 ft (1 UNCW); Stony Fork, Hominy Creek, Dunsmore (2 CMNH); Sulphur Springs, Lower Hominy (1 CMNH); Weaverville (9 AMNH); West Asheville (5 CMNH). *Burke Co.*: Linville Fall Wilderness Area (1 NCSM). *Caldwell Co.*: Hwy 226 at GMC [NW corner of county] (3 ASUVC); Lenoir (3 ASUVC, 1 NCSM, 1 UMMZ). *Camden Co.*: Dismal Swamp State Natural Area (1 UNCW); 2.5 mi NE Horseshoe (1 NCSM); 6 mi W Moyock, State Rd 1218 (2 UNCW). *Cherokee Co.*: 9 mi SW Murphy (1 NMNH); Nancy Gap, 1.85 mi W end of Forest Service Rd 148 (6 GMNH). *Chowan Co.*: 3 km NNE Edenton, Hwy 32 (2 UNCW); 5 mi W Edenton, Hwy 17 at Chowan River (3 UNCW); 5 mi SW Gliden, Hwy 32 (1 ISUVC). *Clay Co.*: near Bristol Cabin (1 UM); Buck Creek, 0.7 mi S Hwy 64, Forest Service Rd 71 (9 GMNH); Buck Creek, 0.5 mi N Hwy 64, Forest Service Rd 6269 (9 GMNH); Fires Creek, near Bristol Cabin (3 UM); Fires Creek, 2 mi W Bristol Cabin (1 UM); Fires Creek (1 ISUVC); Fires Creek Rd (2 ISUVC); Fires Creek Recreation Area, 1.1 mi E jct Forest Service rds 340 and 340A (3 GMNH); 0.7 mi E entrance Fires Creek Recreation Area, Forest Service Rd 340 (1 GMNH); Fires Creek, 5 mi N Hayesville (3 ISUVC, 2 UNCW); Hayesville (1 NCSM); Martin Creek, 1600 ft (1 UMMZ); Naval Branch (1 ISUVC); Ramsey Bend, 1600 ft (3 UMMZ). *Currituck Co.*: Coinjock, State Rd 143 (1 NCSM); Currituck (1 ANSP); Maxine Bricketts farm (1

CM); 3 mi W Moyock, State Rd 1218 (2 NCSM); 5 mi W Moyock, State Rd 1218 (3 UNCW). *Dare Co.*: 1 km N Buffalo City (4 UNCW); off Hwy 64 (2 NCSM); Hwy 264, 1 mi S Navy Shell Rd (1 NCSM); 10 mi SW Stumpy Point (1 NMNH); 7 km WNW Stumpy Point (3 UNCW); 17 km WNW Stumpy Point (1 UNCW); specific locality unknown (1 NCSM). *Forsyth Co.*: Old Richmond (2 NMNH); Walkertown (1 MVZ); Winston-Salem (1 MVZ, 2 NCSM, 6 WFUVC). *Gates Co.*: 2.5 mi E Roduco, Hwy 158 (5 UNCW); 4 mi E Roduco, Hwy 158 (1 UNCW); 0.5 mi N Storys, State Rd 1200 (1 UNCW); 2 mi E Sunbury (1 UNCW); 5 mi E Sunbury (1 UNCW); 5.7 mi E Sunbury, Hwy 158 (6 UNCW); 7 mi E Sunbury (1 NCSM); 1 mi W Sunbury, Hwy 158 (5 UNCW); 9.5 mi W Sunbury, Hwy 158 (1 UNCW). *Graham Co.*: 10 mi W Robbinsville, 4250 ft (1 UNCW); 15 mi NW Robbinsville, Joyce Kilmer Memorial Forest (1 GMNH); 1 mi E Stratton Gap, Unicoi Mountains, 4200 ft (1 LSUMZ). *Guilford Co.*: Greensboro (1 ASUVC); Lake Higgin (5 UNCW). *Haywood Co.*: Black Camp Gap, 5 mi N Soco Gap at Hwy 19, 5000 ft (5 UNCW); Crawfords Creek, near Cruso (1 CHM); 8 mi S Cruso, Hwy 276 at Blue Ridge Pkwy (1 UNCW); Shining Rock, 5700-6120 ft (2 NCSM, 2 GMNH, 10 UNCW); Springdale, near Cruso (2 CHM); Sunburst (1 NCSM); 3 mi S Waterville, 2000 ft (1 UNCW); Waynesville (1 NMNH); 7.5 mi S Waynesville, Blue Ridge Pkwy, 5000 ft (1 CM); 2 mi N Wagon Road Gap at Blue Ridge Pkwy, Pisgah National Forest (2 UNCW); no specific locality (2 UNCW). *Henderson Co.*: Bat Cave, 1400 ft (3 NCSM); 2 mi NW Bat Cave, 1800 ft (1 UNCW); 3 mi WNW Bat Cave, Little Bearwallow Mountain, 3450-3580 ft (3 NCSM); Big Creek, Pisgah National Forest, 2300 ft (1 CMNH); Clear Creek (1 UMMZ); 1.5 mi SSE Hendersonville, 2200 ft (7 KU); 10 mi E Hendersonville (1 ASUVC); 1.5 mi N, 22 mi W Mills River (1 FMNH). *Hertford Co.*: 2 mi NW Ahoskie (2 UNCW); 3.5 mi N Ahoskie, Hwy 13 (1 NMNH); 3 mi S Winton, Hwy 13 (1 NMNH). *Hyde Co.*: 1 mi N Engelhard (2 NMNH); 10 km NE Engelhard, Hwy 264 (4 UNCW); 9 km NW Engelhard (1 UNCW); 12 km NNW Engelhard (2 UNCW); 1 mi W Lake Landing (7 NMNH); 3 mi W Lake Landing (2 NMNH); Lake Mattamuskeet National Wildlife Refuge (2 UNCW); 1 mi E New Holland (1 UNCW); 9 km SSE New Holland (2 UNCW); Swan Quarter (1 NMNH); 8 mi E Swan Quarter, Mattamuskeet National Wildlife Refuge (2 UNCW). *Jackson Co.*: Blue Valley (M. C. Howell Tract), 5.8 mi E Hwy 64 and 28, 3840 ft (1 GMNH); 3.5 mi S Cashiers, Hwy 107 (6 GMNH); Cove Gap, 3 mi ENE Hwy 64 and 28, Forest Service Rd 1107, 2900 ft (2 GMNH); 3 mi N Cullowhee (1 NCSM); Ellicott, 6.4 mi ESE Hwy 64 and 28, Forest Service Rd 1100, 2600 ft (5 GMNH); Ellicott Rock Forest, SE Highlands (1 WFUVC); Glade, 5.4 mi SE Hwy 64 and 28, Forest Service Rd 1100 (2 GMNH); Glen Falls, 2.7 mi WSW Hwy 64 and 28, 3500 ft (1 GMNH);

Licklog, 7 mi ESE Hwy 64 and 28, Forest Service Rd 1100, 3000 ft (5 GMNH); Polly Mountain, 1.8 mi W Hwy 107, SR 1100 (4 GMNH); Polly Mountain, 5.7 mi ESE Hwy 64 and 28, Forest Service Rd 1100, 2800 ft (1 GMNH); Sapphire, Rainy Knob Mountain (1 CHM); Scotsman, 5.4 mi ESE Hwy 64 and 28, 2800 ft (1 GMNH); Waterrock Knob, 5800 ft (2 UNCW); Whiteside Mountain, 4.0-4.4 mi ENE Hwy 64 and 28, 2840-4880 ft (13 GMNH); Wildcat, 2 mi E Hwy 64 and 28, Bowery Rd, 4000 ft (4 GMNH); no specific locality (3 GMNH). *Macon Co.*: Big Creek, 3.9 mi SSE Hwy 64 and 28, 2560 ft (5 GMNH); Brown Gap, 3.8 mi SW Hwy 64 and 28, 2800 ft (2 GMNH); Bull Pen Rd, 1.6 mi W Hwy 107, 2800 ft (1 GMNH); Burningtown Creek (1 NCSM); Cane Creek, 3.4 mi ESE Hwy 64 and 28, 2880 ft (4 GMNH); Cliffside Lake Campground (1 NCSM); Coweeta Hydrological Laboratory (57 GMNH); Coweeta Hydrological Laboratory, Albert Brook, 3250 ft (9 GMNH); Coweeta Hydrological Laboratory, Albert Mountain, 5000 ft (13 GMNH); Coweeta Hydrological Laboratory, Ball Creek Cove, 4300 ft (2 GMNH); Coweeta Hydrological Laboratory, Ball Flats, 2350 ft (3 GMNH); Coweeta Hydrological Laboratory, Bear Pen Gap, 4750 ft (9 GMNH); Coweeta Hydrological Laboratory, Big Butt, 4750 ft (5 GMNH); Coweeta Hydrological Laboratory, Cold Spring Cove, 4100 ft (6 GMNH); Coweeta Hydrological Laboratory, Commissioners Gap, 3550-3600 ft (5 GMNH); Coweeta Hydrological Laboratory, Drymans Fork Cove, 2900 ft (40 GMNH); Coweeta Hydrological Laboratory, Lick Branch, 2800 ft (2 GMNH); Coweeta Hydrological Laboratory, Reynolds Branch, 2900 ft (17 GMNH); Coweeta Hydrological Laboratory, Reynolds Gap, 3600-3700 ft (17 GMNH); Coweeta Hydrological Laboratory, Shope Fork, 2600-2700 ft (2 GMNH); Ed Henry, 2.6 mi SSW Hwy 64 and 28, 2600 ft (4 GMNH); Highlands (2 NCSM); near Highlands (3 CM, 14 GMNH); 4.8 km S Highlands, Hwy 28 (4 CM); Highlands Biological Station (3 NCSM, 8 GMNH, 2 NMNH, 2 UMMZ); Highlands Plateau (1 MSU); Horse Cove, 1 mi E Hwy 64 and 28, 3600 ft (1 GMNH); Horse Cove Clearcut, E Highlands (1 WFUVC); Judd, 2 mi SW Hwy 64 and 28, 3200 ft (3 GMNH); Ostin Knob, 3.5 mi SW Hwy 64 and 28, 2600 ft (6 GMNH); Slick Rock, 3.5 mi SE Hwy 64 and 28, 3240 ft (5 GMNH); Turtle Pond Rd, NW Hwy 64 and 106, 3520 ft (14 GMNH); 0.5 mi E Winding Stair Gap on Hwy 64 (4 GMNH); Wine Springs Bald, 5300 ft (1 KU, 3 GMNH, 1 LSUMZ); Wine Springs Basin, Nantahala National Forest (115 GMNH); Wine Springs Watershed, Nantahala National Forest (3 GMNH). *Madison Co.*: 3 mi W Hot Springs (2 UNCW); Marshall (2 CMNH). *McDowell Co.*: about 0.5 mi SE Marion, Hwy 226 (6 ASUVC); 2 mi W Marion, 1200 ft (1 CM); 3 km N Old Fort, Forest Service Rd 482, 1650 ft (3 UNCW). *Mitchell Co.*: Bald Mountain, 5826 ft (1 NCSM); Roan Mtn, 6.5 mi N, 2 mi E Bakersville, 6000 ft (1 CM); Roan Mtn, 6 mi N, 3.25 mi E Bakersville (9 CM); Roan Mtn (3 AMNH, 2 CMNH [including the holotype of *B. b. churchi*], 1 GMNH, 2 LSUMZ, 6 NCSM, 6 NMNH, 2 UINMH, 13 UMMZ, 7 UNCW); Roan Mtn, 6000 ft (4 NMNH); Roan Mtn, 6300 ft (6 NMNH); Cloudland, Roan Mtn, 6000 ft (3 AMNH, 2 CMNH); base of Roan Mtn, Magnetic City (5 NMNH). *Pasquotank Co.*: near Elizabeth City (1 NCSM); 9 km WNW Morgans Corner (2 UNCW); 7.5 mi W South Mills (1 NMNH). *Perquimans Co.*: Chapanoke (2 ANSP); Hertford (1 MVZ); 5 km SSW Hertford, Hwy 17/37 (1 UNCW); 6.5 km SSW Hertford, Hwy 17/37 (2 UNCW); 1.3 mi S Hickory Crossroads, State Rd 1202 at Perquimans River (1 UNCW). *Polk Co.*: 1 km NE Saluda, State Rd 1142, 2000 ft (3 UNCW); 3 km ENE Saluda, State Rd 1142 (1 UNCW); about 4.4 mi NE Saluda, Green River Game Land (1 NCSM); 6 km NE Saluda, State Rd 1151, 1100 ft (4 UNCW); 8 km NE Saluda, State Rd 1151, 1100 ft (8 UNCW); 10 km NE Saluda, State Rd 1151, 1000 ft (1 UNCW). *Rockingham Co.*: Rockhouse Creek, 8 mi NW Reidsville (1 NMNH). *Rutherford Co.*: Chimney Rock (2 NCSM); Lake Lure (1 NCSM); 1.2 mi SW Lake Lure, 2120-2307 ft (3 NCSM); Rumbling Bald (3 NCSM). *Stokes Co.*: King (2 UNCW). *Swain Co.*: Clingmans Dome, 6100-6642 ft (1 NMNH, 5 UNCW); 1 km WSW Newfound Gap, 5000 ft (3 NMNH); Old Indian Gap Rd, 5200 ft (1 UNCW); Silers Bald, 5600 ft (2 UIMNH); Smokemont, 2000 ft (1 UNCW); Straight Fork Creek, 3000 ft (1 UNCW). *Transylvania Co.*: Big Bald, Pisgah Ridge, 5300 ft (2 CMNH); Blantyre (1 NCSM); 7 mi S Blue Ridge Pkwy on Hwy 276 (1 UNCW); 9 mi SW Brevard (1 UNCW); Pisgah National Forest, Hwy 280 (3 NCSM); Thompson Ridge (1 UNCW). *Watauga Co.*: Bairds Creek Rd (7 ASUVC); Blowing Rock (1 ASUVC, 2 NCSM); 1.4 mi N Blowing Rock (1 ASUVC); 5 mi NW Blowing Rock (1 UMMZ); Blue Ridge Township (3 ASUVC); Boone (20 ASUVC); Boone, Howards Knob (4 ASUVC); Brookhollow (3 NCSM); Castle Ford Rd, near New River (1 ASUVC); Elk Creek Rd (7 ASUVC); Elk Knob, 7.5 mi N Boone, 5300 ft (1 NMNH); Hwy 105 at Watauga River (1 ASUVC); Hwy 194 (1 ASUVC); Howards Creek Rd (1 ASUVC); Meat Camp Rd (2 ASUVC); Mercury Rock Mountain, 3800 ft (1 NCSM); Price Lake, Blue Ridge Pkwy (1 ASUVC); Rainbow Mountain Rd (1 ASUVC); Rainbow Trail Rd (1 ASUVC); Rich Mountain, about 10 mi NE Boone (1 ASUVC); Russell Beach Rd (1 ASUVC); Shulls Mill Dam, Hwy 105, Watauga River (2 ASUVC); Silverstone Rd (3 ASUVC); Stony Fork (1 ASUVC); Zionville (1 ASUVC); no specific locality (1 ASUVC). *Wilkes Co.*: Air Bellows Gap (4 UNCW); Pores Knob, 7 km SSE Moravian Falls, 2000 ft (4 UNCW); 4.75 mi WNW Traphill (1 NCSM); Wilkesboro (1 ASUVC). *Yancey Co.*: Bald Knob, 3.5 mi N Mt Mitchell (9 UMMZ); Balsam Gap (1 UNCW); 4 mi N Busick, Toe River at Hwy 80 (10 UNCW); 2.6 mi NW Busick (3 UNCW); 1-5 mi SW Busick, Forest Service Rd 472, 3000-3900 ft (21 UNCW); about 4.5 mi W Busick (1 NCSM); Camp Alice, Mt Mitchell, 5800 ft (1 NMNH); Mt

Mitchell (4 NCSM); 1.8 mi S Mt Mitchell (1 NCSM); approx 2 mi SSW Mt Mitchell (1 MMNH). *County unknown*: Great Smoky Mtns (1 NMNH); Rocky Knob, 3900 ft (1 NMNH).

OHIO, UNITED STATES (823). *Adams Co.*: Rome (5 CMNH). *Ashtabula Co.*: Andover (1 CMNH); Mechanicsville, Austinburg (1 CMNH, 11 KU, 6 MSB); Farnham (5 CMNH); 4.9 mi N Geneva (7 CM); 5 mi N Geneva (7 CM); 5 mi NW Geneva (1 CM); 1 mi NW Geneva-on-the-Lake (2 CM). *Athens Co.*: Athens (3 NMNH); 7 mi W Athens (4 NMNH). *Belmont Co.*: Cats Run, Pawhatin Point (22 CMNH); St Clairsville (1 CM). *Brown Co.*: Ripley (5 CMNH). *Clark Co.*: Springfield (2 AMNH). *Clermont Co.*: 4 mi NW Batavia (2 LACM); Chilo (2 CMNH); Glen Este, Union Twp (2 LACM); no specific locality (1 CMNH). *Clinton Co.*: Wilmington (1 LACM). *Columbiana Co.*: Lisbon (32 CMNH). *Cuyahoga Co.*: Bedford (21 CMNH); Chagrin Falls (48 CMNH); Cleveland (1 CMNH); Cleveland Heights (6 CMNH, 1 KU); Cedar Rd and Gates Mills Blvd (3 KU); Cedar and Green Rds (1 KU); Gates Mills (4 CMNH, 2 KU); Hunting Valley (12 CMNH); Lyndhurst (43 CMNH); Mayfield Golf Course (11 KU); Mayfield Heights (5 KU); North Chagrin, Metropolitan Park (99 CMNH, 1 LACM); Moreland Hills (20 CMNH); Rocky River Valley (6 CMNH); Shaker Heights (4 KU, 1 MSB); University Heights (18 CMNH). *Erie Co.*: Sandusky (1 NMNH). *Fairfield Co.*: Sec 5, Bern Twp (7 NMNH); North Bern (1 NMNH); no specific locality (3 NMNH). *Geauga Co.*: Burton (2 CMNH); Carvers Pond (9 CMNH); Chesterland Caves (45 CMNH, 10 KU, 2 MSB); Grand River (6 CMNH); Hansens property between Rts 422 and 322 on Rt 306 (1 CMNH); Holden Arboretum (3 KU, 1 MSB); Little Mountain (124 CMNH, 1 LACM); Russell Center (5 CMNH); Stebbens Gulch (1 CMNH); no specific locality (1 AMNH). *Hamilton Co.*: California, Cincinnati (1 CM, 6 LACM, 1 UCONN); no specific locality (3 CMNH). *Lake Co.*: Holden Arboretum (1 CMNH (the holotype of *B. b. kirtlandi*), 5 KU); Little Mountain (12 CMNH); Mentor (15 CMNH). *Mahoning Co.*: Youngstown (1 AMNH). *Meigs Co.*: Carpenter (1 NMNH). *Ottawa Co.*: Williston (1 AMNH). *Portage Co.*: Garrettsville (10 NMNH); Ravenna (4 AMNH). *Seneca Co.*: Bettsville (1 AMNH, 82 CMNH); Maple Grove (25 CMNH). *Williams Co.*: 2.5 mi S Kunkle (1 AMNH).

PENNSYLVANIA, UNITED STATES (162). *Adams Co.*: Gettysburg (1 NMNH). *Allegheny Co.*: 1 mi N Aspinwall (2 CM); Clinton (1 NMNH); 0.1 mi N, 0.1 mi E Clinton (1 NMNH); 0.1 mi S, 1.75 mi W Clinton (1 NMNH); 1 mi S Dorseyville (3 CM); Oakmont (1 CM); Round Hill Regional Park (1 CM); Pittsburgh (11 CM); Upper St Clair (1 CM); W D Boyce Park (1 CM); no specific locality (1 NMNH). *Beaver Co.*: jct of Hwy 30 and Raccoon Creek (1 NMNH). *Berks Co.*: Rattling Run, Albany Twp (2 ROM); 0.75 mi S, 0.3 mi W Ecksville (1 CM); 1.75 mi S, 0.2 mi W Ecksville (1 CM); Schofers Mill,

350 ft, 3 mi NW Kutztown (1 NMNH); Furnace Creek, Pricetown (1 ROM); Museum Park, Reading (1 ROM); 2 mi W Strausstown, 560 ft (4 NMNH). *Bucks Co.*: 2 mi NW Doylestown (1 CM); Neshamony Creek, NE of Jamison (1 AMNH); near Point Pleasant (2 CM); 1.5 mi SW Point Pleasant (1 CM). *Centre Co.*: 2.5 mi E Snow Shoe (1 CM). *Clinton Co.*: Drury Run (3 NMNH); Tamarack, 9 mi NNW Renovo (4 CM); Tamarack Swamp (1 CM). *Crawford Co.*: Beaver Center (9 KU); 4 mi NE Beaver Center (1 KU); Hartstown (3 KU); 2 mi SSE Hartstown (4 KU, 1 MSB); Dumars Farm, South Shenago Twp (1 KU); Huckleberry Swamp, South Shenago Twp (4 KU). *Cumberland Co.*: Carlisle (1 NMNH). *Delaware Co.*: Tinicum Island, 0.5 mi W Philadelphia Internatl Airport (2 CM). *Erie Co.*: East Springfield (1 CM); Erie (1 AMNH); 2 mi N North East (4 CM); 4 mi SW North East (1 CM); 4.5 mi SW North East (10 CM); Presque Isle (3 CM); 3 mi N West Springfield (1 CM). *Greenbriar Co.*: White Sulphur Springs (2 NMNH). *Huntingdon Co.*: 1 mi SE Orbisonia (1 CM); 1 mi NE Spruce Creek (4 CM). *Lackawanna Co.*: Wyalusing Rocks, Carbondale (1 AMNH). *McKean Co.*: no specific locality (5 NMNH). *Mifflin Co.*: 1 mi SW Milroy (2 CM); Tea Creek, 3.5 mi WSW Milroy (1 CM); 1 mi NNW Reedsville (4 CM). *Monroe Co.*: Buck Hill Falls (1 CM); 1 mi ENE Kresgeville (1 CM); Swiftwater, 1150 ft (1 NMNH); 1.5 mi SSE Tannersville (1 CM). *Montgomery Co.*: Baederwood Park, Abington Twp (1 CM); Fox Chase Manor, Abington Twp (2 CM). *Northampton Co.*: 1 mi N Danielsville (1 CM); Nazereth (1 NMNH); 1 mi E Northampton (1 CM). *Perry Co.*: 4 mi SE Shermans Dale, 800 ft (1 NMNH). *Philadelphia Co.*: Pennypack Park (7 CM). *Pike Co.*: 2 mi NE Bushkill (1 CM); 5 mi E Greentown (3 CM); Promised Land Lake, 6 mi E Greentown (1 CM); 5 mi SE Greentown (5 CM). *Somerset Co.*: 4 mi SW Somerset (4 NMNH); no specific locality (1 NMNH). *Susquehanna Co.*: Laurel Lake, 9 mi NNW Montrose (2 CM). *Union Co.*: Glen Iron (2 CM); Penn Creek Mt, 0.5 mi S Glen Iron (1 CM). *Warren Co.*: Bensons Swamp, 5 mi E Columbus (1 NMNH). *Wayne Co.*: Lake Como (2 CM); 2 mi NE Orson (2 CM); Balls Creek, 5.5 mi NE Starucca (1 CM).

RHODE ISLAND, UNITED STATES (60). *Newport Co.*: Newport (2 AMNH, 15 NMNH); Fort Adams, Newport (21 NMNH); Peat Pond, Newport (2 NMNH). *Providence Co.*: Chepachet (5 NMNH). *Washington Co.*: Westerly (1 UCONN); no specific locality (14 UCONN).

SOUTH CAROLINA, UNITED STATES (3). *Greenville Co.*: Standing Stone Mountain, 3000 ft, 5 mi NE Caesars Head (1 NMNH); Caesars Head Mountain, 3000 ft, 9 mi E Caesars Head (1 NMNH). *Oconee Co.*: Chattooga Ridge, 1900 ft, 11 mi NW Walhalla (1 NMNH).

TENNESSEE, UNITED STATES (90). *Carter Co.*: Milligan College (1 ISUVC); Roan Mtn (5 UMMZ); Roan Mtn, 4100 ft (1 NMNH); Roan Mtn, 4800 ft (7 NMNH); Roan Mtn, 5000 ft (3 NMNH); Carvers Gap, Roan Mtn, 5400 ft (3 KU); Roan Mtn State Park (1 UM); 4.75 mi

S, 1.5 mi W Roan Mtn (7 CM); 5 mi S, 1.25 mi W Roan Mtn (4 CM); 5.5 mi S, 0.75 mi W Roan Mtn (2 CM); 6 mi S, 0.75 mi W Roan Mtn (1 CM); 6.5 mi S, 2 mi W Roan Mtn (3 CM, 1 MHP). *Cocke Co.*: Smoky Mtns, 4.5 mi SE Cosby, 3300 ft (1 NMNH); Smoky Mtns, 4.5 mi SE Cosby, 3400 ft (1 NMNH); Mt Guyot, Smoky Mtns, 6300 ft (1 NMNH); Snake Den Mtn, Smoky Mtns, 3800 ft (1 NMNH). *Johnson Co.*: Holston Mtn, 3800 ft, 4 mi NE Shady Valley (5 NMNH); Holston Mtn, 3000 ft, 3 mi NE Shady Valley (1 NMNH); Shady Valley, 2900 ft (2 NMNH). *Monroe Co.*: Beaver Dam Bald, 3950 ft, Cherokee National Forest (1 UM); Falls Branch Scenic Area, ca 3700 ft, Cherokee National Forest (3 UM); Haw Knob, 5407 ft, Cherokee National Forest (1 UM); Haw Knob, 5472 ft, Cherokee National Forest (1 UM); jct Laurel Branch and Roaring Branch, North River Rd, about 2200 ft, Cherokee National Forest (1 UM); Round Mtn Branch, North River Rd, about 2400 ft, Cherokee National Forest (2 UM); Round Mtn Branch, North River Rd, about 2900 ft, Cherokee National Forest (1 UM); NE slope Stratton Meadows, North River Rd, about 3800 ft, Cherokee National Forest (5 UM); Stratton Meadow, about 4350 ft, Cherokee National Forest (3 UM); Whig Meadow, about 4950 ft, Cherokee National Forest (2 UM). *Polk Co.*: Lost Creek Campground, Cherokee National Forest (1 UM); about 5 mi E Reliance, Cherokee National Forest (1 UM). *Sevier Co.*: Great Smoky Mtns National Park, 3200 ft (1 UCONN); above Hwy 44, Great Smoky Mtns National Park, 3100 ft (4 NMNH); Bullshead Trail to Mt LeConte, Great Smoky Mtns National Park, 3000 ft (1 UCONN); Chimney Tops, Great Smoky Mtns National Park (2 OU); Gatlinburg, Great Smoky Mtns National Park (5 OU); 0.9 mi W Rocky Springs Gap, 5900 ft, Great Smoky Mtns National Park (2 UCONN). *Sullivan Co.*: 17 mi SE Bristol (2 NMNH).

VERMONT, UNITED STATES (449). *Addison Co.*: Snake Mtn, 2 mi S, 1 mi E Addison, 1200 ft (4 CM); DAR State Park, 2.5 mi S, 5.5 mi W Addison, 160 ft (2 CM). *Bennington Co.*: Woodford State Park, 1 mi N, 8 mi E Bennington, 2320 ft (1 CM); 1.25 mi S, 1 mi E Bennington, 880 ft (2 CM); Dorset (6 NMNH); Green Mtn National Forest, Peru (1 UCONN); Freezing Hole Hollow, Readsboro (1 AMNH); 1 1/3 mi N, 8 1/4 mi W Wilmington, 2160 ft (1 CM). *Caledonia Co.*: Groton State Forest, Groton (2 CM); 4 mi NE Hardwick (1 UCONN); 3.3 mi NE Hardwick (9 UCONN); 1.4 mi NE Hardwick (7 UCONN); 1.3 mi NE Hardwick (2 UCONN); 0.5 mi W Hardwick (2 UCONN); Hardwick (16 UCONN); Lyndon (6 UCONN, 12 UMMZ [including the holotype of *B. b. hooperi*]); 1 mi S Lyndon, 750 ft (3 UCONN); Lyndon Center, Lyndon (3 UCONN); Lyndon Center, Lyndon, 760 ft (1 UCONN); 0.75 mi SW Lyndon Center, Lyndon, 980 ft (1 UCONN); 0.75 mi SW Lyndon, Lyndon, 1080 ft (1 UCONN); 0.8 mi SW Lyndon Center, Lyndon, 1100 ft (1 UCONN); 2 mi N Lyndonville, Lyndon (1 UCONN). *Chittenden Co.*: Burlington (2 NMNH, including the holotype of *B. angusticeps*). *Essex*

Co.: 2.5 mi N, 1.25 mi W Island Pond, Brighton (2 CM); 4 mi E Island Pond, Brighton (1 CM); 0.5 mi S, 2.25 mi W Island Pond, Brighton (2 CM); Brighton State Park, 1.25 mi S, 1.5 mi E Island Pond, Brighton (4 CM); 2 mi NE Victory, Concord (1 UCONN); 2 mi NE Victory, Concord, 1200 ft (1 UCONN). *Franklin Co.*: Swanton (1 UCONN). *Grand Isle Co.*: 0.75 mi S, 1.5 mi E Alburg (2 CM); Grand Isle (1 UCONN); North Hero State Park, 7 mi N, 2.5 mi E North Hero (4 CM); 1.25 mi S, 0.5 mi W North Hero (5 CM); 1 mi S, 0.75 mi W South Hero (2 CM). *Lamoille Co.*: Elmore State Park, 0.5 mi W Lake Elmore (18 CM); 2.5 mi S, 1 mi W Morrisville, Morristown (9 CM); 2 mi N, 3 mi E Underhill Center [in Chittenden Co.] (6 CM). *Orange Co.*: North Thetford, Thetford (5 UCONN); Williamstown (6 UCONN). *Orleans Co.*: 3 mi N, 1 mi W Island Pond (7 CM); 3.5 mi S, 4 mi W Island Pond (3 CM); 1.75 mi N, 2.25 mi W Lowell, 1250 ft (2 CM); 3 mi N, 3.5 mi W Lowell, 1700 ft (1 CM). *Rutland Co.*: 2.1 mi SSW Castleton, bearing 202° (2 CM); 2.2 mi SSW Castleton, bearing 196° (10 CM); 3.1 mi SE Castleton, bearing 131° (8 CM); 0.3 mi E Blissville, Castleton (2 CM); 0.7 mi E Blissville, Castleton (5 CM); Chittendon (3 AMNH); Fair Haven (6 CM); south side Fair Haven (7 CM); 1 mi S Fair Haven (1 CM); Poultney River, 1.3 mi W Fair Haven (4 CM); 2.7 mi NW Fair Haven (10 CM); 3 mi NW Fair Haven (9 CM); Mendon (1 UCONN); Mendon, 800 ft (1 UCONN); Mendon, 900 ft (18 AMNH, 2 CM, 4 UCONN); Mendon, 1100 ft (1 CM); Mendon, 1300 ft (2 CM); Rutland, Mendon (14 UCONN); Rutland, Mendon, 600 ft (3 UCONN); Rutland, Mendon, 700 ft (3 AMNH, 7 UCONN); 0.5 mi SE Rutland, Mendon, 900 ft (1 UCONN); 3 mi SE Rutland, Mendon, 900 ft (6 UCONN); 3.5 mi SE Rutland, Mendon, 900 ft (2 UCONN); 3.5 mi SE Rutland, Mendon, 950 ft (1 UCONN); 4 mi SE Rutland, Mendon, 1200 ft (3 UCONN); Bald Mtn, 4 mi SE Rutland, Mendon (1 UCONN); 4 mi ESE North Clarendon, 1400 ft (3 CM); Cold River Canyon, 4 mi ESE North Clarendon (8 CM); Mt Killington, 4000 ft, Sherburne (1 NMNH); Herrick Mtn, 3.1-3.4 mi NW Ira, West Rutland (6 CM). *Washington Co.*: Plainfield (9 UCONN); Goddard College, Plainfield (2 KU, 1 MSB); 1.9 mi SW Hardwick, Woodbury (2 UCONN). *Windham Co.*: Londonderry (1 UCONN); South Londonderry, Londonderry (5 UCONN); 1 mi N Saxtons River, Rockingham, 500 ft (2 UCONN); Saxtons River, Rockingham (14 UCONN); Saxtons River, Rockingham, 500 ft (1 CM); Saxtons River, Rockingham, 600 ft (1 UCONN); Whitingham, 1700 ft (3 AMNH); 0.25 mi N, 2.75 mi W Wilmington (1 CM); 0.75 mi E, 0.25 mi S Wilmington (5 CM); Molly Stark State Park, 1 mi S, 3 mi E Wilmington (4 CM). *Windsor Co.*: 0.25 mi N, 2.25 mi W Barnard (18 CM); 1 mi S, 1 mi E Barnard (6 CM); 1.5 mi W Bridgewater Center (6 CM); Hartland (2 AMNH); 4 mi SE Ludlow, Ludlow, 1500 ft (1 UCONN); Pomfret (3 AMNH, 2 UMMZ); Greendale Area, Green Mtn National Forest, Weston (2 UCONN); Ascutney State Park, 2.75 mi S, 2.25 mi W Windsor, 1740 ft (4 CM); Ascutney State Park, 3 mi

S, 0.5 mi W Windsor, 560 ft (11 CM). *County unknown*: Mt Mansfield (8 NMNH); Mt Mansfield, 3850 ft (7 NMNH); Smugglers Notch, Mt Mansfield, 1500 ft (2 NMNH).

VIRGINIA, UNITED STATES (486). *Alleghany Co.*: Clifton Forge, 1200 ft (1 NMNH); 0.5 mi N Clifton Forge (1 NMNH). *Arlington Co.*: Arlington (2 NMNH); Fort Myer (4 NMNH); Rosslyn (2 NMNH); no specific locality (1 NMNH). *Augusta Co.*: Elliot Knob (1 NMNH); 7 mi S Staunton (2 NMNH). *Bath Co.*: Hot Springs (1 UMMZ). *Bedford Co.*: Peaks of Otter, 4001 ft (5 NMNH). *Campbell Co.*: Lynchburg, 700 ft (8 NMNH). *Caroline Co.*: near Rappahannock River, 4 mi SE Port Royal (2 NMNH). *Chesapeake City* [formerly *Norfolk Co.*]: Deep Creek (1 ISUVC); Lake Drummond, [Great] Dismal Swamp (1 NMNH, the holotype of *B. telmalestes*); Wallaceton, [Great] Dismal Swamp (7 NMNH); 2 mi N Wallaceton (2 NMNH); 5 mi N Wallaceton (1 NMNH). *Culpepper Co.*: just W of Rappahannock River (2 NMNH). *Cumberland Co.*: 4 mi N Cumberland (1 NMNH). *Essex Co.*: 3.5 mi SW Center Cross (8 NMNH); 4.6 mi NW Tappahannock (1 NMNH). *Fairfax Co.*: Arlington (2 UCONN); 3.3 mi NW Fairfax, 440 ft (1 NMNH); Falls Church (6 NMNH); 3 mi SW Falls Church (6 NMNH); Fort Belvoir (4 NMNH); Four Mile Run (2 NMNH); 3.6 mi SE Great Falls (3 NMNH); Masons Neck Wildlife Refuge (1 NMNH); McLean (2 NMNH); 201 Highland Rd, Pine Ridge, Merrifield (1 NMNH); 303 Highland Rd, Pine Ridge, Merrifield (1 NMNH); 1.1 mi SSW Merrifield (4 NMNH); Mt Vernon (1 NMNH); opposite Plummers Island, Maryland (3 NMNH); Turkeycock Run, 4.6 mi from Glebe Rd, Pinecrest, 4 mi from Annandale (1 NMNH); Rt 193 and Scot Run (2 NMNH); Rt 193 and Swinks Mill Rd (4 NMNH); Spring Hill (1 NMNH); Vienna (2 KU, 1 NMNH). *Fauquier Co.*: 4.3 mi W Rectortown (1 NMNH); 2.5 mi W Thorofare [Gap] (2 NMNH); 6 mi N Warrenton (7 NMNH). *Fredrick Co.*: 0.8 mi SW Winchester, 770 ft (1 NMNH); 0.9 mi SW Winchester (2 NMNH); 1.2 mi WSW Winchester, 770 ft (8 NMNH). *Giles Co.*: 0.7 mi N Mtn Lake (1 LACM); 1 mi N Mtn Lake (1 LACM); 1.7 mi NNE Mtn Lake (1 LACM); 1.35 mi NE Mtn Lake (1 NMNH); 0.9 mi NNE Mtn Lake (1 LACM); 4.2 mi NNE Mtn Lake, 4100 ft (1 KU); Bald Mtn, Mtn Lake (5 AMNH); 6 mi N jct Hwys 601 and 42 on Hwy 42 (1 ASUMZ). *Gloucester Co.*: near Allmonds Wharf (1 NMNH); 1 mi SSE Bena (1 NMNH). *Grayson Co.*: Whitetop Mtn (2 UMMZ); Whitetop Mtn, 5400 ft (2 NMNH). *Hampton City*: Hampton City (1 NMNH). *Hanover Co.*: Ashland (1 NMNH). *Henrico Co.*: 3 mi ESE Highland Springs (1 NMNH). *Henry Co.*: 4.5 mi NNW Martinsville PO, 860 ft (1 NMNH); 1.5 mi S, 1.25 mi W Martinsville City Hall, DuPont Property (20 VMNH). *Highland Co.*: head of Newman Run, Allegheny Mtn, 3650 ft (2 NMNH); Laurel Fork, 3800 ft, 2.9 mi WNW Hightown (1 NMNH); Hightown (2 AMNH); Bear Wallow Run, 3200 ft, 9.5 mi NNW Monterey (2 NMNH); Laurel Fork, 3100 ft, 9 mi NNW Monterey (2 NMNH);

Laurel Fork, 8.5 mi NNW Monterey (1 NMNH). *James City Co.*: opposite Jamestown Island on mainland (4 NMNH); Mariners Museum, Newport News (1 NMNH); Williamsburg (5 NMNH); William and Mary Biological Experimental Station, Williamsburg (9 NMNH). *King and Queen Co.*: 3 mi SW Mascot (1 NMNH). *King George Co.*: Port Conway (1 NMNH). *King William Co.*: 4.5 mi NW West Point (1 NMNH). *Lee Co.*: 2 mi WSW Ewing (9 NMNH). *Madison Co.*: head of Brokenback Run, S face Thorofare Mtn, Shenendoah National Park (1 NMNH); head of Dark Hollow Trail, Big Meadows, Shenendoah National Park, 3300 ft (3 NMNH); Limberlost, Shenendoah National Park, 3500 ft (1 NMNH). *Mathews Co.*: Gwynn (1 NMNH); Rts 3 and 14 (1 NMNH). *Middlesex Co.*: Jamaica (4 NMNH). *Montgomery Co.*: Blacksburg (5 CM); Blacksburg, 2100 ft (14 NMNH); 0.5 mi W Blacksburg (1 NMNH). *New Kent Co.*: Shackleford Farms, Lanexa (2 CM); Shackleford Farms, 1 mi E Lanexa (1 CM); 2 mi E Lanexa (1 CM); 9 mi S Providence Forge (1 NMNH). *Page Co.*: Pinnacles Ranger Station, Shenendoah National Park, 3200 ft (6 NMNH). *Patrick Co.*: 5 mi SW Stuart (1 NMNH). *Powhatan Co.*: 5 mi WNW Powhatan CH (1 NMNH); Huguenot Academy, 300 ft, 2 mi NE Powhatan PD (6 NMNH). *Prince William Co.*: Buckland (2 NMNH); Catharpin (1 NMNH). *Pulaski Co.*: 1 mi N Pulaski (6 UCONN); 2 mi NE Pulaski (4 UCONN). *Rappahannock Co.*: near Amissville (1 NMNH); Thornton River, Shenendoah National Park, 1000 ft (4 NMNH). *Richmond Co.*: 1.4 mi SW Newland (2 NMNH). *Roanoke Co.*: Salem (1 NMNH). *Rockbridge Co.*: 2 mi NE Glasgon (2 NMNH); 3 mi S Goshen Pass (1 NMNH). *Rockingham Co.*: 1 mi W Broadway (2 NMNH). *Russell Co.*: Mudders Gap, Clinch Mtn (3 NMNH); Laurel Bed, Clinch Mtn, 3600 ft, 6 mi NNW Saltville (44 NMNH). *Shenendoah Co.*: 2.4 mi SE Strasburg, 950 ft (1 NMNH); Blue Hole Fort Valley, 4.3 mi S Strasburg, 680 ft (1 NMNH). *Smythe Co.*: Whitetop Mtn (1 NMNH, 6 UMMZ); Whitetop Mtn, 5300 ft (2 NMNH). *Southampton Co.*: Union Camp Land, Hwy 603, 0.5 mi E Blackwater River (1 CM); 2 mi SE Wakefield (1 NMNH); 9 mi NW Windsor on Hwy 635 (5 CM). *Suffolk City* [formerly *Nansemond Co.*]: Jerico Ditch, Lake Drummond, Dismal Swamp (1 NMNH); Suffolk (17 ISUVC); Dismal Swamp National Wildlife Refuge, Suffolk (3 NMNH); Dismal Swamp, Suffolk (2 CM); Interior Ditch at Lake Drummond, Dismal Swamp National Wildlife Refuge, Suffolk (4 CM); 200 m S Interior ditch near Lake Drummond, Suffolk (1 CM). *Surry Co.*: Blackwater River, 4.5 mi N Wakefield (1 NMNH). *Tazewell Co.*: Burkes Garden (55 NMNH). *Warren Co.*: near Cedarville (1 NMNH); Front Royal (1 NMNH); Smithsonian Conservation and Research Center, 2 mi S Front Royal (5 NMNH). *Washington Co.*: Kannarock (1 UMMZ). *Westmoreland Co.*: on Rappahannock River, Leedstown (1 NMNH); 3 mi NW Lyells (1 NMNH). *Wise Co.*: Hurricane (3 NMNH); 5 mi N Wise (2 NMNH); 4 mi NE Wise (1 NMNH). *Wythe Co.*: 2 mi NE Wytheville (4

NMNH). *York Co.*: near Yorktown, 1 mi S York River (2 NMNH). *County unknown*: Dismal Swamp (3 NMNH); Lake Drummond, Dismal Swamp (26 NMNH); Lake Drummond (1 AMNH); Potomac River (1 NMNH); CPS Camp 45, Shenendoah National Park, 3100 ft (1 NMNH); Pass Mtn Bog, Shenendoah National Park, 2600 ft (1 NMNH).

WEST VIRGINIA, UNITED STATES (289). *Brooke Co.*: Bethany (10 CM). *Cabell Co.*: 4 mi E Huntington (4 NMNH); 5 mi E Huntington (4 NMNH). *Grant Co.*: near Mt Storm (2 CM). *Greenbriar Co.*: White Sulphur (7 NMNH); 2 mi E White Sulphur Springs (2 NMNH). *Hampshire Co.*: 5 mi S Paw Paw (5 NMNH); near Wapocoma, 4.2 mi N Romney (2 NMNH); Mill Creek Mtn, near Wapocoma, 4.2 mi N Romney, 650 ft (3 NMNH); Mill Creek Mtn, near Wapocoma, 4.2 mi N Romney, 1250 ft (1 NMNH); Romney (14 NMNH); 3 mi NW Yellow Springs (1 NMNH). *Hardy Co.*: Lost River State Park (1 CM); 22 mi S Moorefield, 38°47'N, 79°06'W (3 NMNH); 5 mi W Wardensville (2 NMNH). *Kanawha Co.*: Charleston (4 AMNH, 1 NMNH). *Lincoln Co.*: Fourteen, 37 mi SE Huntington (2 NMNH). *Logan Co.*: Logan (1 CM). *Marion Co.*: Grant Town (1 CM). *Mason Co.*: Mercers Bottom (10 NMNH). *Mercer Co.*: Flat Top Mtn, Flat Top, 3500 ft (4 NMNH). *Mineral Co.*: Gerstell (1 CM); 4 mi NE Keyser, Gerstell (1 CM); on Allegheny Plateau, 6 mi SW Keyser (3 NMNH). *Monongalia Co.*: 1.5 mi NNE Dellslow, 1300 ft (1 KU); 0.5 mi E Dellslow (1 ROM); 0.5 mi SE Dellslow, 1200 ft (1 KU); 1 mi. SE Greer, 1500 ft (1 KU); Cheat Lake, 6.5 mi NE Morgantown (1 CM); Connors Camp, Cheat Lake, 6.25 mi NE Morgantown (6 CM); Pierpont Hill, 4 mi NE Morgantown (2 CM); Morgantown (3 CM, 3 KU, 3 ROM); Morgantown, 1000 ft (1 KU); 2 mi N Morgantown (1 AMNH); 3.5 mi SW Morgantown, 1000 ft (2 KU); behind University High School, Morgantown (3 CM); Cheat Lake, Morgantown (2 ROM); Cheat Lake, near Ices Ferry, Morgantown (3 AMNH); Falling Run, Morgantown (2 ROM); Suncrest, Morgantown (3 ROM). *Nicholas Co.*: Collison Creek Rd (1 CM); CCC Camp Woodbine (2 CM). *Ohio Co.*: Bethany Pike, Avalon (13 CM); Chicken Neck Hill, Wheeling (1 CM). *Pendleton Co.*: Franklin (1 NMNH); Spruce Knob (1 NMNH). *Pocahontas Co.*: Cranberry Glades (1 CM, 7 NMNH); Cranberry Glades, 3200 ft (1 NMNH); Cranberry Glades, 3300 ft (18 NMNH); Kennison Mtn, 1.5 mi SW Cranberry Glades, 4000 ft (5 NMNH); at Fairgrounds, 1 mi NE Marlinton (4 CM). *Preston Co.*: Cranesville Swamp, 2900 ft (1 CM); Cheat River, 3 mi NE Kingwood, 1200 ft (2 CM); Terra Alta (7 CM); 6 mi N Terra Alta (1 CM); Lake Terra Alta, Terra Alta (3 CM); 1 mi E Terra Alta (28 CM). *Raleigh Co.*: Flat Top Mtn, Ghent, 2900 ft (5 NMNH); Flat Top Mtn, Odd, 2900 ft (9 NMNH); Winding Gulf, Southwest of Pemberton (4 NMNH). *Randolph Co.*: Cheat Mtn, 3800 ft, 3 mi W Cheat Bridge (2 NMNH); Cheat Bridge, 3900 ft (7 NMNH); Blister Pine Run, 1 mi SE Cheat Bride PO,

3675 ft (5 CM); Middle Mtn, Durbin (8 NMNH); Blister Swamp, Shaver Mtn (1 KU); Red Run at Shavers Fork (2 MMNH); Travellers Repose (6 NMNH). *Tucker Co.*: Beaver Creek, Davis, 3100 ft (1 CM); 1.5 mi SE Davis, 3400 ft (1 KU). *Webster Co.*: 1.5 mi S Cambden, Gauley, 2100 ft (1 KU). *Wyoming Co.*: White Oak Run, 9.5 mi NE Pineville (2 CM). *County unknown*: Monongahela National Forest, boundary line (1 NMNH); Williams River, 3300 ft (9 NMNH).

WISCONSIN, UNITED STATES (262). *Ashland Co.*: Madeline Island, Apostle Islands (2 NMNH); La Pointe, Apostle Islands (2 NMNH). *Barron Co.*: 4.5 mi S, 0.5 mi E Rice Lake (1 KU). *Bayfield Co.*: Drummond (4 UWSP); Herbster (9 NMNH); Namakagon Lake (1 NMNH); Orienta (8 NMNH); Port Wing (2 NMNH). *Chippewa Co.*: Holcombe (2 NMNH). *Clark Co.*: Hewett Township (1 AMNH); Thorp Township (1 AMNH, 1 KU); Wither [Withee] (5 NMNH); Worden Township (4 AMNH, 5 NMNH). *Columbia Co.*: Duck Creek (1 UWSP); Poynette (1 UWSP). *Dane Co.*: Oregon (1 UWSP); Sun Prairie (1 UWSP); no specific locality (1 NMNH). *Dodge Co.*: Ashippun (1 HMNH). *Door Co.*: Clarke Lake (3 NMNH); Ellison Bay (4 NMNH); Fish Creek (3 NMNH); Sturgeon Bay (1 UWSP). *Douglas Co.*: Solon Springs (1 NMNH). *Dunn Co.*: Meridean (2 NMNH). *Florence Co.*: Florence (1 NMNH). *Fond du Lac Co.*: no specific locality (1 UWSP). *Forest Co.*: Alvin (2 UWSP); Armstrong Creek (1 UWSP); Pickerel Lake (1 UWSP); Popple River (2 UWSP); Roberts Lake (1 UWSP). *Green Lake Co.*: Green Lake (5 NMNH). *Iowa Co.*: Hollandale (1 UWSP). *Iron Co.*: 2 mi N Mercer (1 NMNH); Mercer (2 NMNH). *Jackson Co.*: 10 mi W of City Point (1 MMNH). *Juneau Co.*: Camp Douglas (4 NMNH); Fountain Twp (1 UWSP); Mather (2 NMNH). *Kenosha Co.*: Kenosha (1 UWSP). *Langlade Co.*: Camp Susan (3 UWSP); Kempster (1 UWSP). *Lincoln Co.*: Merrill (2 UWSP). *Manitowoc Co.*: Manitowac (6 UWSP). *Marathon Co.*: Abbots Ford (2 UWSP); Knowlton (2 UWSP); Lake du Bay (1 UWSP); Milladore [in Wood Co.] (1 UWSP); Rib Hill (2 NMNH). *Oconto Co.*: Kelley Lake (3 NMNH); Lakewood (3 NMNH). *Oneida Co.*: Crescent Lake (1 NMNH); Rhinelander (1 NMNH, 3 UWSP). *Outagamie Co.*: Nichols (2 UWSP). *Pierce Co.*: Prescott (1 NMNH). *Polk Co.*: Balsam Lake (1 MMNH); St Croix Falls (2 NMNH). *Portage Co.*: Coddington (1 UWSP); Custer (1 UWSP); Meadow Creek (1 UWSP); Nelsonville (1 UWSP); Plover (1 UWSP); Spring Lake (1 UWSP); Stevens Point (1 NMNH, 47 UWSP); N Reserve St, Stevens Point (1 PSUMC); Jordon Pond, Stevens Point (16 UWSP); 5 mi E Stevens Point (1 PSUMC). *Price Co.*: Ogema (1 NMNH). *Racine Co.*: Racine (2 NMNH); Root River, Racine (1 NMNH); Wind Lake (2 UWSP). *Rock Co.*: Milton (1 NMNH); 10 mi SSE Potosi, 2 mi N Illinois line (1 NMNH). *Sauk Co.*: Devils Lake (1 NMNH); Kilbourn (2 NMNH). *Sawyer Co.*: Connors Lake, 18 mi WNW

Phillips (1 NMNH). *Sheboygan Co.*: Sheboygan Swamp, Elkhart Lake (2 NMNH). *Taylor Co.*: Medford (2 UWSP); Westboro (1 UWSP). *Vilas Co.*: Eagle River (1 UWSP); Mamie Lake (3 NMNH). *Walworth Co.*: Delavan (2 NMNH); La Grange (1 AMNH); Turtle Lake (2 NMNH).

Washburn Co.: Long Lake (4 NMNH). *Washington Co.*: Myra (1 UWSP). *Waukesha Co.*: Nashotah (7 NMNH). *Waupaca Co.*: King (2 UWSP). *Waushara Co.*: Richford (1 UWSP); Wild Rose (11 NMNH). *Wood Co.*: Arpin (5 UWSP); Stevens Point [*in Portage Co.*] (1 UWSP).



Fig. 5. Geographic distribution of subspecies of *Blarina brevicauda*: **A**(○) = *B. b. brevicauda*; **B**(▲) = *B. b. jerrychoatei*; **C**(●) = *B. b. talpoides*; **D**(◻) = *B. b. aloga*; **E**(■) = *B. b. delmarvensis*; **F**(△) = *B. b. cumberlandensis*; **G**(+) = *B. b. knoxjonesi*. Shading indicates distribution of 4 peripheral subspecies. *B. b. aloga* (not shaded) occurs on Martha's Vineyard and Nantucket Island, Massachusetts. Inset shows numbers associated with operational taxonomic units (OTUs) used in this study. See Appendix 1 for additional information about OTU localities and subspecies assignments; see Fig. 4 for size relationships of subspecies and specimens in each OTU.

DISCUSSION

Because 12 subspecies of *B. brevicauda* were recognized at the beginning of our study, there was reason to suspect that this species would be extremely variable in morphology across its geographic distribution. However, there had been no comprehensive review of geographic variation within the species since the revision by Bole and Moulthrop (1942), a period of more than 65 years. Some subspecies recognized in Hall (1981) were described on the basis of morphological variation in a small series of specimens from isolated locations—*B. b. aloga*, *B. b. compacta*, and *B. b. hooperi*—as compared to that seen in specimens from nearby regions. Other subspecies recognized in Hall (1981) were described on the basis of larger series of specimens from the periphery of the geographic range of the species—*B. b. angusta*, *B. b. churchi*, *B. b. manitobensis*, *B. b. telmalestes*, and *B. b. pallida*—but did not take into account the total scope of morphological variation across the entire geographic range of the species. The final subspecies recognized by Hall (1981)—*B. b. kirtlandi*—was described on the basis of a large series of specimens from throughout the Great Lake and Allegheny Mountain regions.

Our analysis demonstrates that *B. brevicauda* consists of 7 well-defined subspecies (Figs. 4 and 5). Two subspecies, *B. b. brevicauda* and *B. b. talpoides*, occupy almost the entire geographic range of the species, with restricted gene flow between these 2 subspecies where their geographic distributions abut in the vicinity of the Mississippi River and its valley (Brant and Ortí, 2002, 2003a). Both of these widely distributed subspecies are geographically variable, but the differences within each of them are subtle with no clear breaks, steps, or patterns in the variation. Conversely, the differences between the 2 subspecies are substantial. In this regard, our morphological data from Recent material are congruent with the Pleistocene (Jones et al., 1984) and molecular (Brant and Ortí, 2002, 2003a) data. Moreover, the fossil and molecular data indicate a substantial division between *B. b. brevicauda* and *B. b. talpoides*, and these taxa have been called semispecies by Jones et al. (1984) and Brant and Ortí (2002, 2003a). The molecular data indicate that *B. b. brevicauda* and *B. b. talpoides* have been separated since approximately 1.2 mya (Brant and Ortí, 2002), and the fossil data indicate that both phenons have occurred in the same region in the past, although not at the same time (Jones et al., 1984).

The other 5 subspecies occupy small-to-modest geographic ranges at the periphery of the range of the species (Fig. 5). These subspecies occur in isolated

geographic areas—*B. b. aloga* on islands, *B. b. delmarvensis* at the end of a peninsula, *B. b. knoxjonesi* along the North Carolina coast isolated by habitat and a population of *B. carolinensis*, *B. b. cumberlandensis* surrounded on 3 sides by the Tennessee River and *B. carolinensis*, and *B. b. jerryrchoatei* disjunct in the Kaw River Valley and surrounded by *B. hylophaga*. In each of these geographic areas, gene flow has been stopped or greatly restricted. Specimens from these peripheral populations average smaller than the populations of *B. b. talpoides* with which their geographic ranges abut. The exception is *B. b. jerryrchoatei*, the range of which abuts with *B. hylophaga* and may approach the geographic range of *B. b. brevicauda*. Analysis of mtDNA indicates that specimens of *B. b. talpoides* from Indiana, Massachusetts, New Hampshire, New York, Pennsylvania, Ohio, Tennessee, Vermont, Virginia, and Wisconsin and *B. b. cumberlandensis* from western Kentucky form a monophyletic clade that is distinct from a monophyletic clade that includes specimens of *B. b. brevicauda* from Iowa, Nebraska, and Manitoba (Brant and Ortí, 2002, 2003a). We interpret the morphological, distributional, and mtDNA data to mean that *B. b. aloga*, *B. b. cumberlandensis*, *B. b. delmarvensis*, and *B. b. knoxjonesi* are derived from *B. b. talpoides*.

The disjunct population of shrews from northeastern Kansas, *B. b. jerryrchoatei*, represents an anomaly; it is geographically closer to *B. b. brevicauda*, but its cranial morphology exhibits characteristics that are more similar to *B. b. talpoides*. If *B. b. jerryrchoatei* were in geographic contact with *B. b. talpoides*, we probably would not recognize it as a distinct subspecies. However, populations of these 2 subspecies are separated by 400 kilometers and the intervening populations of *B. b. brevicauda* and *B. hylophaga*. It is possible that *B. b. jerryrchoatei* represents another offshoot of *B. b. talpoides*, which was widely distributed west of the Mississippi River in the Pleistocene (Jones et al., 1984). Unfortunately, the mtDNA of this subspecies has not been examined, so we offer this as a testable hypothesis for future work.

We have chosen to recognize these 7 subspecies because we believe that each has begun to follow its own evolutionary path. These taxa are arranged in a geographic configuration that fits the pattern termed centrifugal speciation. Brown (1957) first described this pattern of speciation, which is characterized by the development of small, isolated peripheral populations. As the parent species undergoes normal population expansion and contraction cycles, some population(s) become isolated in refugial area(s) (Briggs, 2000). Brown (1957) believed that the peripheral populations

would adapt to the local environmental conditions, but that the primary evolutionary changes would occur in the central population.

We hypothesize that Pleistocene glacial advances and retreats (and resultant cycles of population expansion and contraction) led to the formation of the current peripheral populations of *B. brevicauda*. We maintain that the central population, consisting of *B. b. brevicauda* and *B. b. talpoides*, presently is at, or near, its maximum geographic range following the retreat of the Wisconsinan ice sheet. The fact that the peripheral populations (which we recognize as *B. b. aloga*, *B. b. cumberlandensis*, *B. b. delmarvensis*, *B. b. jerryrchoatei*, and *B. b. knoxjonesi*) have not been genetically swamped indicates to us that they are adapting to their local conditions and are able to maintain their genetic identities (Gavrilets et al., 2000).

Shrews from southwestern Wisconsin (28) are unusual in that they are the only population of *B. b. brevicauda* that currently exists east of the Mississippi River (Figs. 4 and 5). These specimens are from a region known as the driftless area, a relatively large expanse on either side of the Upper Mississippi River (southeastern Minnesota and northeastern Iowa on the west side and southwestern Wisconsin and northwestern Illinois on the east side) that was not glaciated during the Wisconsinan Glacial Period. Much of the northern Great Plains was under ice and much of central Canada became the huge Lake Agassiz in the Wisconsinan. *B. b. brevicauda* might have found a refugium in this driftless area of southwestern Wisconsin. In the Post-Valders Phase and Hypsithermal Interval, approximately 2,500-10,000 BP, *B. b. brevicauda* likely reinvaded the northern Great Plains, and its current distribution there is relatively recent. Populations of *B. b. talpoides* replaced *B. b. brevicauda* east of the Mississippi River, except in the driftless area of southwestern Wisconsin.

Individuals of 4 subspecies (*B. b. aloga*, *B. b. cumberlandensis*, *B. b. delmarvensis*, and *B. b. knoxjonesi*) share the characteristic of being smaller in size than individuals of the taxon (*B. b. talpoides*) whose range they abut. The term “island rule” or “island effect” has been used to refer to insular populations that exhibit significant differences in size from their mainland counterparts, with large-bodied species typically becoming much smaller on islands and small-bodied species becoming much larger (Foster, 1964; Lomolino, 1985). The intensity of the island effect is thought to be positively influenced by the distance from the mainland population (Foster, 1964) and inversely

proportional to island size (Heaney, 1978). We believe that this phenomenon is related to the reason these subspecies consist of smaller individuals, but the exact mechanisms by which it operates in the case of these shrews is unclear.

In conclusion, our morphological analyses identified an overall east-west grouping of samples that is roughly coincident with the Mississippi River. This is in agreement with Brant and Orti’s (2002, 2003a) molecular phylogeny of *B. brevicauda* and can be explained by past fragmentation and divergence during allopatry, followed by range expansion, contact, and genetic intergradation. There are a few pockets of size discontinuities—smaller individuals that may represent populations that underwent divergence during periods of past (*B. b. knoxjonesi*, *B. b. cumberlandensis*, and *B. b. delmarvensis*) or current (*B. b. aloga* and *B. b. jerryrchoatei*) segregation from the remainder of the species. Molecular studies of specimens from those regions are necessary to quantify more precisely the extent to which these populations have diverged genetically.

Our revision based on morphology has identified several questions that remain unresolved. With respect to *B. b. jerryrchoatei*, additional information about the extent of its geographic distribution needs to be ascertained, and its phylogenetic relationships with *B. b. brevicauda* and *B. b. talpoides* need to be determined. The effect of climate-induced change in body size on peripheral taxa is a fertile area for future research. The fact that the geographic relationship between *B. b. brevicauda* and *B. b. talpoides*—that is, a parapatric relationship that has moved in response to climatic changes throughout the Pleistocene and Holocene (Jones et al., 1984)—has been in existence for such a long period of time lends credence to the suggestion that these intergrading subspecies are acting as semispecies. This hypothesis is ripe for further investigation inasmuch as the genetic mechanisms that maintain this relationship and the evolutionary consequences of it are unknown. Finally, given the long zones of parapatry between *B. brevicauda* and *B. hylophaga* in the mid-western United States and between *B. brevicauda* and *B. carolinensis* in the eastern United States, studies of the contact zones between pairs of *Blarina* species (e.g., Benedict, 1999a, 1999b) should provide critical information necessary to elucidate the phylogenetic relationships of short-tailed shrews. Such studies should also shed light on speciation events that result from evolutionary processes associated with chromosomal rearrangements.

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APPENDIX 1

Operational taxonomic unit (OTU) number, general collecting localities, sample size for morphometric analysis, and subspecies assignments for 114 samples of *Blarina brevicauda*.

OTU Number	State(s) or Province	County(ies) or place name(s)	Number of specimens used in morphometric analysis	Subspecies
1	Manitoba	Turtle Mountains	6	<i>B. b. brevicauda</i>
2	Manitoba	Dauphin, Dauphin Lake, Lake Winnipegosis, Riding Mountain National Park, Swan River City, Wasagaming	27	<i>B. b. brevicauda</i>
3	Manitoba	Brandon, Glenboro, Holland, Margret, Oak Lake	11	<i>B. b. brevicauda</i>
4	Manitoba	Winnipeg, Portage la Prairie	6	<i>B. b. brevicauda</i>
5	Manitoba	Middlebro, Pine Falls, Rennie, Sandilands Forest Preserve, Telford, Whitshell Park	27	<i>B. b. brevicauda</i>
6	North Dakota	Richland, Traill	14	<i>B. b. brevicauda</i>
7	South Dakota	Grant, Marshall	6	<i>B. b. brevicauda</i>
8	South Dakota	Bon Homme, Union	8	<i>B. b. brevicauda</i>
9	Nebraska	Cherry, Rock	8	<i>B. b. brevicauda</i>
10	Nebraska	Cedar, Knox, Wayne	17	<i>B. b. brevicauda</i>
11	Nebraska	Washington	11	<i>B. b. brevicauda</i>
12	Nebraska	Cass, Lancaster, Saunders	19	<i>B. b. brevicauda</i>
13	Minnesota	Ottertail	11	<i>B. b. brevicauda</i>
14	Minnesota	St. Louis	17	<i>B. b. talpoides</i>
15	Minnesota	Hennepin, Sherburne	25	<i>B. b. brevicauda</i>
16	Iowa	Chickasaw, Howard, Winneshiek	27	<i>B. b. brevicauda</i>
17	Iowa	Hamilton, Hardin, Story	20	<i>B. b. brevicauda</i>

Appendix 1. *continued.*

OTU Number	State(s) or Province	County(ies) or place name(s)	Number of specimens used in morphometric analysis	Subspecies
18	Iowa	Black Hawk, Butler, Tama	24	<i>B. b. brevicauda</i>
19	Iowa	Fremont, Guthrie, Mills, Montgomery, Page, Pottawattamie	30	<i>B. b. brevicauda</i>
20	Iowa	Adams, Decatur, Ringgold, Taylor, Union	56	<i>B. b. brevicauda</i>
21	Iowa	Keokuk, Lucas, Mahaska, Marion, Monroe, Poweshiek	62	<i>B. b. brevicauda</i>
22	Iowa	Clinton	8	<i>B. b. brevicauda</i>
23	Missouri	Grundy, Mercer	20	<i>B. b. brevicauda</i>
24	Missouri	Adair, Clark, Lewis	10	<i>B. b. brevicauda</i>
25	Kansas	Douglas	5	<i>B. b. jerrychoatei</i>
26	Wisconsin	Bayfield, Washburn	11	<i>B. b. talpoides</i>
27	Wisconsin	Portage	43	<i>B. b. talpoides</i>
28	Wisconsin	Grant	8	<i>B. b. brevicauda</i>
29	Illinois	Cook, Will	16	<i>B. b. talpoides</i>
30	Illinois	Fulton, Mason	11	<i>B. b. talpoides</i>
31	Illinois	Champaign	87	<i>B. b. talpoides</i>
32	Ontario	Kenora District	11	<i>B. b. talpoides</i>
33	Ontario	Thunder Bay District	5	<i>B. b. talpoides</i>
34	Ontario	Kent, Middlesex	5	<i>B. b. talpoides</i>
35	Ontario	York	17	<i>B. b. talpoides</i>
36	Ontario	Peterboro, Parry Sound District, Durham, Victoria	15	<i>B. b. talpoides</i>
37	Ontario	Frontenac, Prince Edward	5	<i>B. b. talpoides</i>

Appendix 1. *continued.*

OTU Number	State(s) or Province	County(ies) or place name(s)	Number of specimens used in morphometric analysis	Subspecies
38	Michigan	Ontonagon	11	<i>B. b. talpoides</i>
39	Michigan	Marquette	28	<i>B. b. talpoides</i>
40	Michigan	Menominee	36	<i>B. b. talpoides</i>
41	Michigan	Chippewa, Luce, Mackinac	18	<i>B. b. talpoides</i>
42	Michigan	Charlevoix, Cheboygan, Montmorency, Otsego, Presque Isle	24	<i>B. b. talpoides</i>
43	Michigan	Alcona, Benzie, Clare, Crawford, Grand Traverse, Kalkaska, Lake, Leelanau, Mason, Missaukee, Ogemaw, Roscommon, Wexford	22	<i>B. b. talpoides</i>
44	Michigan	Clinton	21	<i>B. b. talpoides</i>
45	Michigan	Allegan, Berrien, Kalamazoo, Van Buren	25	<i>B. b. talpoides</i>
46	Michigan	Washtenaw	26	<i>B. b. talpoides</i>
47	Indiana	Lake, Porter	23	<i>B. b. talpoides</i>
48	Indiana	Lagrange, Noble, Steuben, Whitley	15	<i>B. b. talpoides</i>
49	Indiana	Clay, Tippecanoe, Vigo	65	<i>B. b. talpoides</i>
50	Indiana	Blackford, Fayette, Jay, Randolph, Union, Wayne	19	<i>B. b. talpoides</i>
51	Ohio	Seneca	40	<i>B. b. talpoides</i>
52	Ohio	Lake, Geauga	106	<i>B. b. talpoides</i>
53	Ohio	Ashtabula	20	<i>B. b. talpoides</i>
54	Ohio West Virginia	Belmont, Columbiana Brooke, Ohio	29	<i>B. b. talpoides</i>
55	Ohio	Adams, Brown	5	<i>B. b. talpoides</i>
56	Kentucky	Jefferson	6	<i>B. b. talpoides</i>

Appendix 1. *continued.*

OTU Number	State(s) or Province	County(ies) or place name(s)	Number of specimens used in morphometric analysis	Subspecies
57	Kentucky	Scott	14	<i>B. b. talpoides</i>
58	Kentucky	Clark, Fayette, Madison	25	<i>B. b. talpoides</i>
59	Kentucky	Breathitt, Harlan	13	<i>B. b. talpoides</i>
60	Tennessee	Dickson, Humphreys, Stewart	14	<i>B. b. cumberlandensis</i>
61	Tennessee	Davidson, Rutherford, Williamson	7	<i>B. b. cumberlandensis</i>
62	Tennessee	Campbell	21	<i>B. b. cumberlandensis</i>
63	Tennessee	Monroe, Polk	7	<i>B. b. talpoides</i>
64	Tennessee	Cocke, Sevier	9	<i>B. b. talpoides</i>
65	North Carolina Tennessee	Mitchell Carter	42	<i>B. b. talpoides</i>
66	Georgia	Rabun, Union	7	<i>B. b. talpoides</i>
67	Georgia	Fulton, Gwinnett	5	<i>B. b. talpoides</i>
68	Georgia	Clarke	10	<i>B. b. talpoides</i>
69	Alabama	Chambers, Elmore, Lee	12	<i>B. b. talpoides</i>
70	Québec	St. Roch, Ste. Rose, Wright	5	<i>B. b. talpoides</i>
71	Québec	Gaspé	16	<i>B. b. talpoides</i>
72	New Brunswick	Victoria	7	<i>B. b. talpoides</i>
73	New Brunswick	Kings	27	<i>B. b. talpoides</i>
74	Nova Scotia	Annapolis, Antigonish, Colchester, Digby, Kings, Halifax, Hants, Inverness, Yarmouth	36	<i>B. b. talpoides</i>
75	Maine	Aroostook	33	<i>B. b. talpoides</i>
76	Maine	Penobscot, Piscataquis	24	<i>B. b. talpoides</i>

Appendix 1. *continued.*

OTU Number	State(s) or Province	County(ies) or place name(s)	Number of specimens used in morphometric analysis	Subspecies
77	Maine	Franklin, Oxford	23	<i>B. b. talpoides</i>
78	New Hampshire	Carroll, Coos, Grafton	173	<i>B. b. talpoides</i>
79	Vermont	Caledonia	36	<i>B. b. talpoides</i>
80	Vermont	Bennington, Rutland, Windham, Windsor	88	<i>B. b. talpoides</i>
81	Massachusetts	Berkshire	37	<i>B. b. talpoides</i>
82	Massachusetts	Middlesex	34	<i>B. b. talpoides</i>
83	Massachusetts	Barnstable, Bristol, Plymouth	13	<i>B. b. talpoides</i>
84	Massachusetts	Dukes	17	<i>B. b. aloga</i>
85	Massachusetts	Nantucket	9	<i>B. b. aloga</i>
86	Connecticut	New London, Windham	36	<i>B. b. talpoides</i>
87	Connecticut	Fairfield, Litchfield	25	<i>B. b. talpoides</i>
88	New York	Essex, Franklin, Clinton	14	<i>B. b. talpoides</i>
89	New York	Tompkins	137	<i>B. b. talpoides</i>
90	New York	Madison, Otsego, Schoharie	30	<i>B. b. talpoides</i>
91	New York	Greene, Rensselaer, Schenectady	53	<i>B. b. talpoides</i>
92	New York	Nassau, Suffolk	15	<i>B. b. talpoides</i>
93	Pennsylvania	Crawford, Erie	23	<i>B. b. talpoides</i>
94	Pennsylvania	Monroe, Pike, Susquehanna, Wayne	19	<i>B. b. talpoides</i>
95	Pennsylvania	Allegheny	19	<i>B. b. talpoides</i>
96	Pennsylvania	Centre, Clinton, Huntingdon, Mifflin, Union	20	<i>B. b. talpoides</i>

Appendix 1. *continued.*

OTU Number	State(s) or Province	County(ies) or place name(s)	Number of specimens used in morphometric analysis	Subspecies
97	Pennsylvania	Berks, Bucks, Delaware, Montgomery, Northampton, Philadelphia	19	<i>B. b. talpoides</i>
98	New Jersey	Bergen, Morris, Sussex	18	<i>B. b. talpoides</i>
99	New Jersey	Atlantic, Cape May, Monmouth, Ocean	7	<i>B. b. talpoides</i>
100	West Virginia	Monongalia, Preston	39	<i>B. b. talpoides</i>
101	Maryland West Virginia	Allegany, Garrett Mineral, Randolph, Tucker	20	<i>B. b. talpoides</i>
102	District of Columbia		53	<i>B. b. talpoides</i>
103	Delaware	New Castle	9	<i>B. b. talpoides</i>
104	Delaware	Sussex	10	<i>B. b. delmarvensis</i>
105	Maryland	Dorchester	18	<i>B. b. delmarvensis</i>
106	Virginia	Northampton	19	<i>B. b. delmarvensis</i>
107	Virginia	Essex, Gloucester, James City, King and Queen, King George, King William, Middlesex	22	<i>B. b. talpoides</i>
108	Virginia	Giles, Montgomery, Pulaski	12	<i>B. b. talpoides</i>
109	Virginia	Henry	19	<i>B. b. talpoides</i>
110	Virginia	Chesapeake, Suffolk	23	<i>B. b. talpoides</i>
111	North Carolina	Gates, Pasquotank	12	<i>B. b. talpoides</i>
112	North Carolina	Hyde	11	<i>B. b. talpoides</i>
113	North Carolina	Beaufort	10	<i>B. b. knoxjonesi</i>
114	North Carolina	New Hanover	12	<i>B. b. knoxjonesi</i>

APPENDIX 3*Blarina carolinensis carolinensis*

Specimens Examined (22) See *Acknowledgments* for institutional abbreviations.

NORTH CAROLINA, UNITED STATES (22). *Brunswick Co.*: 0.5 km N Rabontown (2 UNCW); 1 km N Rabontown (4 UNCW); 1 km NW Rabontown (2 UNCW); 2 km NW Rabontown (3 UNCW); near Rabontown (7 UNCW); 5.3 mi W Wilmington, Hwy 17 (2 UNCW); 3 mi NW Winnabow (2 UNCW).



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