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Morphometric and Allozymic Variation in the Southeastern Shrew (*Sorex longirostris*)

Wm. David Webster[1], Nancy D. Moncrief[2], Becky E. Gurshaw[1], Janet L. Loxterman[2,3], Robert K. Rose[4], John F. Pagels[5], and Sandra Y. Erdle[6]

ABSTRACT

Morphometric and allozymic variation was examined in specimens of *Sorex longirostris* to assess the status of *S. l. fisheri*, which is thought to be restricted to the Great Dismal Swamp region of southeastern Virginia and northeastern North Carolina. Significant geographic variation was detected in all cranial and external measurements and in body mass. Shrews from southeastern Virginia and throughout eastern North Carolina (*S. l. fisheri* Merriam 1895) are large overall but they have relatively narrow crania. Shrews from southern Georgia and Florida (*S. l. eionis* Davis 1957) also are large but they have relatively short tails. Shrews from elsewhere in the range of the species (*S. l. longirostris* Bachman 1837) are relatively small in all cranial and external dimensions and in body mass. Five of 25 genetic loci examined by starch-gel electrophoresis were variable, with one allele (MPI^C) occurring only in shrews from southeastern Virginia and several sites in eastern North Carolina. Allozymic evidence for intergradation was demonstrated through the presence of the MPI^C allele in specimens from central North Carolina that morphologically were assigned to *S. l. longirostris*. Shrews from the Lower Coastal Plain of eastern North Carolina were allozymically more similar to animals from the Great Dismal Swamp, the type locality of *S. l. fisheri*, than to shrews from western North Carolina and Virginia (*S. l. longirostris*). Thus, based on morphometric and allozymic information, we conclude that shrews referable to *S. l. fisheri* are distributed widely in the North Carolina Coastal Plain, well beyond the historic Great Dismal Swamp in southeastern Virginia.

INTRODUCTION

The southeastern shrew (*Sorex longirostris*) inhabits a mosaic of habitats in the southeastern United States (French, 1980). Three subspecies are currently recognized, based on external and cranial dimensions (Handley and Varn, 1994; Jones et al., 1991). *S. l. longirostris* Bachman 1837, which has a relatively small body and short tail, occupies most of the range of the species, from the Ohio and Mississippi River basins eastward to the Atlantic Ocean (Hall, 1981; Pagels et al., 1982). *S. l. eionis* Davis 1957, which has a relatively large body and short tail, is found throughout the northern two-thirds of peninsular Florida (Jones et al., 1991). Southeastern shrews that have the largest bodies and longest tails (*S. l. fisheri* Merriam 1895) are thought to be restricted to the Great Dismal Swamp region of southeastern Virginia and northeastern North Carolina (Handley, 1991; Jones et al., 1991; Rose and Padgett, 1991; Webster et al., 1985; Webster, 1987).

About 85% of the historic Dismal Swamp has been ditched and drained in the last two centuries, converting wetlands into habitats more likely to favor invasion of *S. l. longirostris*. Because of this, it was suggested that genetic swamping by *S. l. longirostris* might result in the extinction of the *S. l. fisheri* genotype (Handley, 1979; Handley and Varn, 1994; Padgett, 1991; Padgett et al., 1987; Rose and Jacobs, 1994).

The taxonomy and distributional ecology of *S. l. fisheri* in the Great Dismal Swamp region have been the focus of several studies (Erdle and Pagels, 1996; Everton, 1985; Padgett, 1991; Padgett et al., 1987; Rose

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1981, 1983; Rose and Padgett, 1991). These studies have shown that there is considerable variation in the size of southeastern shrews in the Dismal Swamp region, with the largest individuals being found in what remains of the original Dismal Swamp habitat and with progressively smaller individuals being found at greater distances away from the swamp (Padgett, 1991; Rose, 1983). The distributional limits of *S. l. fisheri* and *S. l. longirostris* in the Dismal Swamp region were not modified in the most recent revision of the species (Jones et al., 1991), although the distribution of *S. l. eionis* was enlarged to include much of peninsular Florida.

In this study, we examined morphometric variation in specimens of *Sorex longirostris* from east-central and southeastern North Carolina (regions that were not the focus of the last revision, Jones et al., 1991), in relation to shrews from Charleston County, South Carolina (near the type locality of *S. l. longirostris*, see Jackson, 1928, and Handley and Varn, 1994), the Dismal Swamp (the type locality of *S. l. fisheri*), and Citrus County, Florida (the type locality of *S. l. eionis*), as well as from locations throughout the range of the species. Our allozymic analyses included samples collected in southern Virginia and throughout eastern North Carolina. The purpose of this investigation was to review the taxonomic and distributional status of *S. longirostris* in the southeastern United States using morphometric and biochemical techniques, with special emphasis directed towards resolving the status of shrews from southeastern Virginia and eastern North Carolina.

MATERIALS AND METHODS

Morphometric analysis.— Six-hundred and twenty-six specimens of *Sorex longirostris* from throughout the southeastern United States were used in the morphometric analysis (Appendix 1). Six cranial characters (greatest length of skull, condylobasal length, maxillary breadth, interorbital breadth, P4-M3 toothrow length, and cranial breadth) were measured to the nearest 0.1 mm with Mitutoyo dial calipers by one of us (WDW) as described by Jackson (1928) and Junge and Hoffmann (1981). We also measured palatal length (defined as the distance between the anteriormost point of the upper incisors and the antero-medialmost point on the hind edge of the bony palate) and calculated the length of braincase (the difference between the greatest length of skull and palatal length) for each specimen. Total length, tail length, and length of hind foot (in mm) and body mass (in g) were recorded from specimen tags if available, and head and body length (the difference between total length and tail length) was calculated.

Specimens were grouped into 28 Operational Taxonomic Units or OTUs (identified herein by bold letters) on the basis of geographic proximity, with due consideration to physiographic and previously recognized taxonomic boundaries, to increase sample sizes (Appendix 1). OTU "**A**" contained specimens from the Great Dismal Swamp, including the holotype of *S. l. fisheri*; "**Y**" contained shrews from near Charleston, South Carolina, including the holotype of *S. l. longirostris*; and "**a**" contained specimens from central Florida, including the holotype of *S. l. eionis*. Secondary sexual and age-class variations are slight and inconsistent in *Sorex* (Findley, 1955; Jackson, 1928; Van Zyll de Jong, 1980); we found similar patterns in *S. longirostris*, so specimens of both sexes and all age classes in each OTU were pooled to increase sample sizes for statistical analyses. A single-classification ANOVA was used to test for significant geographic variation ($P < 0.05$) in each cranial and external measurement, and a Duncan's multiple-range test was used to determine maximally nonsignificant OTUs. A principal component analysis was performed on the cranial measurements. A product-moment correlation matrix was derived from standardized character values, eigenvectors were extracted, and a two-dimensional plot of OTUs was generated. External measurements were excluded from the principal component analysis because the algorithm requires complete data, and external measurements were not available for many specimens.

Allozymic analysis.— One-hundred and three specimens of *S. longirostris* from 22 counties throughout North Carolina and three counties in southern Virginia were examined by horizontal starch-gel electrophoresis. Collection sites within a 15-km radius were grouped into the same OTU to increase sample sizes. This resulted in 25 OTUs, with each OTU (identified herein by bold numerals) typically comprised of specimens from a single county (Appendix 1). OTUs **3** and **4** included specimens from the Great Dismal Swamp, the type locality of *S. l. fisheri*. Vouchers of these specimens are deposited in the Vertebrate Collections at the University of North Carolina Wilmington or in the Virginia Museum of Natural History (Appendix 1).

The heart, kidneys, and liver from each animal were maintained at -70°C until analyzed. Tissues were

combined, pulverized, and homogenized according to Harris and Hopkinson (1976). Resulting homogenates were electrophoresed and stained using methods described by Harris and Hopkinson (1976) and Murphy et al. (1990). Thirty presumptive loci were examined in each individual, of which 25 were consistently scorable. Buffer systems, enzyme names, and enzyme commission numbers are listed in Appendix 2. Five loci (ACN2, ADA, G3PD, PEPD, and XDH2) were not consistently interpretable and were not included in the analysis. The most common allele was designated "A" for multi-allele loci. The most anodal locus was labeled "1" in enzymes with more than one locus.

Allozyme data were analyzed using the BIOSYS-1 program (Swofford and Selander, 1981). The percentage of polymorphic loci (*P*) was estimated for each OTU using a 0.95 standard, where the frequency of the most common allele is <95%. Average heterozygosity (*H*) was calculated by direct count. Expected heterozygosity per OTU was computed (Nei, 1978) and a Chi-square test was used to compare observed and expected heterozygosities. BIOSYS-1 was used to compute Rogers' (1972) modified genetic distance between all pairs of OTUs using all loci combined. UPGMA (unweighted pair group method with arithmetic averaging; Sneath and Sokal, 1973) cluster analysis was used to construct a phenogram based on the matrix of Rogers' (1972) modified genetic distance (Wright, 1978). We then focused our allozymic comparisons on OTUs with sample sizes of >4 individuals, which we selected arbitrarily post priori based on the total number of individuals from each OTU for which tissues were available, in order to eliminate some of the vagaries that might be associated with small sample size.

RESULTS

Morphometric analysis.— There was significant geographic variation ($P < 0.0001$) in all cranial measurements examined, with OTUs from southeastern Virginia (**A-C**, **L**), eastern North Carolina (**D-K**), and southern Georgia and Florida (**a-b**) being much larger than OTUs from elsewhere in the range (**M-Z**) of the species (Table 1). There also was significant geographic variation ($P < 0.0001$) in external measurements and weight, which typically followed the same pattern (Table 1).

All cranial characters loaded positively on Principal Component I, explaining 85.6% of the total phenetic variation in the data, whereas on Principal Component II three characters (maxillary breadth, interorbital breadth, cranial breadth) loaded positively and four (greatest length of skull, condylobasal length, palatal length, length of braincase) loaded negatively, explaining 7.7% of the variation (Table 2). A two-dimensional plot of OTUs (Fig. 1) produced three groups of OTUs. One group (labeled "I" in Fig. 1) included shrews from southern Georgia and Florida (**a-b**) that had long and wide crania. Shrews from southeastern Virginia (**A-C**, **L**) and eastern North Carolina (**D-K**) formed the second group ("II" in Fig. 1); they had long but relatively narrow crania. The third group ("III" in Fig. 1) included shrews from elsewhere in the range of the species (**M-Z**), which were smaller in all cranial measurements. This two-dimensional plot explained 93.2% of the total morphometric variation exhibited in *S. longirostris* crania (Table 2).

Size variation in this species, as shown in Table 1 and Fig. 1, can be summarized as follows: the largest specimens were from the Dismal Swamp (**A**), and the smallest specimens were from Indiana (**V**), south-central Virginia (**T**), and eastern Tennessee and northern Georgia (**W**). Specimens from immediately east (**C**) and west (**L**) of the present Great Dismal Swamp were smaller than shrews from the Great Dismal Swamp (**A**) in cranial and external measurements. Specimens from the Piedmont and Mountain physiographic regions of Virginia and North Carolina (**M-U**, **X**) were only slightly smaller than those from coastal South Carolina (**Y**). Shrews from southern Georgia and the Florida panhandle (**b**) were very similar to specimens collected in central Florida (**a**).

Allozymic analysis.— Twenty of 25 loci examined in 25 OTUs of *S. longirostris* were monomorphic for the same allele: ACN2, CK1, CK2, GOT1, GOT2, G6PD, IDH1, IDH2, LDH1, LDH2, MDH1, MDH2, ME, NP, PEPS, PGI, PGM2, PGM3, SDH, and XDH1. Three loci (PEPA, PEPB, and 6PGD) were variable in only one or two OTUs, as follows: Isle of Wight, **1** ($PEPA^A$ 0.96, $PEPA^B$ 0.04; $PEPB^A$ 0.98, $PEPB^B$ 0.02); Chesapeake, **3** ($6PGD^A$ 0.92, $6PGD^B$ 0.08); Camden, **4** ($6PGD^A$ 0.83, $6PGD^B$ 0.17); Perquimans and Chowan, **5** ($PEPB^A$ 0.94, $PEPB^B$ 0.06). Two loci (ACN1, MPI) were polymorphic in many OTUs (Table 3). The percentage of polymorphic loci ranged from 0.0 to 12.0 and averaged 4.16% (Table 3) for all OTUs. The percentage of polymorphic loci among OTUs containing >4 individuals ranged from

Table 1. Geographic variation in cranial and external measurements and body mass (mean ± 2 standard deviation, range, and sample size) among 28 OTUS of *Sorex longirostris*. See Fig. 3a and Appendix 1 for location of samples.

OTU	Greatest skull length	Condylobasal length	Palatal length	Maxillary breadth	Interorbital breadth	P4-M3 length	Length of braincase	Cranial breadth	Total length	Head and body length	Tail length	Length of hind foot	Body mass
A	16.44 ± 0.58	15.57 ± 0.70	6.84 ± 0.4	4.45 ± 0.26	3.14 ± 0.16	3.80 ± 0.24	9.59 ± 0.43	7.77 ± 0.33	94.07 ± 9.34	59.18 ± 8.46	34.85 ± 5.49	11.57 ± 1.67	3.80 ± 1.13
	(16.0-17.1)28	(15.0-16.5)28	(6.5-7.3)29	(4.1-4.7)29	(3.0-3.3)29	(3.6-4.1)29	(9.3-10.0)28	(7.5-8.1)28	(83-105)45	(51-71)45	(29-40)48	(9-13)50	(2.9-4.8)12
B	16.03 ± 0.59	15.17 ± 0.59	6.68 + 0.34	4.36 ± 0.23	3.07 ± 0.22	3.74 ± 0.21	9.35 ± 0.40	7.63 ± 0.34	92.24 ± 10.68	59.23 ± 11.10	33.15 ± 4.56	11.37 ± 1.46	3.87 ± 1.97
	(15.4-16.8)50	(14.5-15.7)51	(6.3-7.0)50	(4.0-4.7)51	(2.8-3.3)51	(3.4-3.9)51	(8.8-9.9)50	(7.2-8.1)51	(80-102)33	(48.5-69)34	(30-39)33	(10-13)34	(2.5-6.6)25
C	15.60 ± 0.90	14.87 ± 1.72	6.54 ± 0.32	4.25 ± 0.31	3.01 ± 0.22	3.65 ± 0.27	9.06 ± 0.64	7.54 ± 0.41	91.50 ± 9.44	59.67 ± 6.65	31.83 ± 6.86	11.33 ± 2.07	3.93 ± 1.18
	(15.2-16.9)14	(14.2-16.1)15	(6.4-6.9)14	(4.0-4.5)15	(2.9-3.2)15	(3.4-3.9)15	(8.8-10.0)14	(7.3-8.0)15	(85-97)6	(56-65)6	(29-38)6	(10.0-13.0)	(3.3-4.7)4
D	15.79 ± 0.55	15.03 ± 0.54	6.62 ± 0.31	4.42 ± 0.18	3.06 ± 0.21	3.70 ± 0.21	9.19 ± 0.41	7.59 ± 0.29	91.55 ± 9.30	59.15 ± 7.95	32.62 ± 6.94	11.09 ± 1.40	4.08 ± 1.04
	(15.1-16.3)17	(14.3-15.5)16	(6.4-6.9)16	(4.2-4.6)16	(2.9-3.3)17	(3.5-3.8)16	(8.7-9.5)16	(7.2-7.9)16	(81-100)20	(51-65)20	(28-40)21	(10-13)22	(2.7-4.95)15
E	15.83 ± 0.46	15.00 ± 0.33	6.59 ± 0.29	4.41 ± 0.21	3.07 ± 0.19	3.74 ± 0.11	9.24 ± 0.45	7.59 ± 0.29	94.92 ± 9.55	62.67 ± 6.51	32.25 ± 6.16	11.73 ± 2.38	4.50 ± 3.64
	(15.5-16.2)7	(14.7-15.2)7	(6.5-6.8)7	(4.2-4.5)7	(3.0-3.2)7	(3.7-3.8)7	(8.9-9.5)7	(7.4-7.8)7	(88-105)12	(56-68)12	(27-37)12	(11-15)11	(2.8-7.4)5
F	15.78 ± 0.22	14.86 ± 0.73	6.60 ± 0.35	4.37 ± 0.34	3.09 ± 0.18	3.70 ± 0.22	9.18 ± 0.56	7.48 ± 0.42	88.86 ± 7.23	58.28 ± 6.88	30.63 ± 4.60	10.68 ± 1.59	3.49 ± 1.21
	(15.0-16.9)49	(14.1-15.6)49	(6.3-7.0)49	(4.0-4.8)49	(2.8-3.2)49	(3.5-3.9)49	(8.7-10.3)49	(7.1-7.9)49	(79-96)65	(50-68)64	(26-38)64	(9-12)65	(2.5-4.7)19
G	16.09 ± 0.22	15.22 ± 0.61	6.74 ± 0.22	4.39 ± 0.23	3.08 ± 0.21	3.78 ± 0.22	9.34 ± 0.36	7.64 ± 0.35	94.00 ± 8.94	60.64 ± 9.94	33.36 ± 4.27	10.86 ± 0.99	3.92 ± 1.64
	(15.9-16.3)14	(14.8-15.9)14	(6.6-7.0)14	(4.1-4.5)14	(2.8-3.2)14	(3.6-4.0)14	(9.0-9.6)14	(7.4-8.0)14	(85-105)14	(52-72)14	(30-38)14	(10-11.5)14	(2.5-5.8)14
H	16.10 ± 0.64	15.25 ± 0.81	6.74 ± 0.32	4.37 ± 0.31	3.10 ± 0.22	3.76 ± 0.18	9.35 ± 0.42	7.55 ± 0.64	89.37 ± 8.18	58.10 ± 9.47	31.17 ± 6.13	9.60 ± 5.52	3.64 ± 1.10
	(15.6-16.7)27	(14.6-15.9)27	(6.5-7.1)27	(4.1-4.6)27	(2.9-3.4)27	(3.6-3.9)27	(8.9-9.7)27	(7.2-7.8)27	(82-99)30	(47-66)30	(26-38)30	(5-13)30	(3.0-5.0)23
I	15.57 ± 0.33	14.83 ± 0.35	6.50 ± 0.25	4.37 ± 0.30	3.03 ± 0.57	3.65 ± 0.17	9.07 ± 0.24	7.43 ± 0.16	92.13 ± 7.29	61.63 ± 6.67	30.50 ± 3.38	10.63 ± 1.04	3.67 ± 1.53
	(15.4-15.8)6	(14.7-15.1)6	(6.3-6.6)6	(4.1-4.5)6	(2.8-3.2)6	(3.6-3.8)6	(8.9-9.2)6	(7.4-7.6)6	(87-98)8	(58-66)8	(29-34)8	(10-11)8	(2.8-4.6)6
J	15.90 ± 0.77	15.11 ± 0.66	6.61 ± 0.47	4.29 ± 0.41	3.07 ± 0.36	3.70 ± 0.26	9.29 ± 0.34	7.52 ± 0.32	88.08 ± 4.72	57.38 ± 6.56	30.69 ± 5.44	10.67 ± 1.30	3.17 ± 2.25
	(15.4-16.4)7	(14.8-15.8)7	(6.3-7.0)7	(3.9-4.5)7	(2.8-3.3)7	(3.5-3.8)7	(9.1-9.6)7	(7.3-7.7)6	(84-92)13	(54-63)13	(26-36)13	(10-12)12	(2.4-4.4)3
K	15.4	14.65 ± 0.42	6.55 ± 0.42	4.2	3.00 ± 0.14	3.65 ± 0.14	8.85 ± 0.42	7.25 ± 0.42	90	59.50 ± 4.24	30.50 ± 4.24	10.00 ± 2.82	—
	2	(14.5-14.8)2	(6.4-6.7)2	2	(2.9-3.1)2	(3.6-3.7)2	(8.7-9.0)2	(7.1-7.4)2	2	(58-61)2	(29-32)2	(9-11)2	
L	15.36 ± 0.70	14.59 ± 0.46	6.51 ± 0.28	4.34 ± 0.22	2.97 ± 0.22	3.75 ± 0.19	8.85 ± 0.53	7.50 ± 0.43	83.77 ± 8.99	54.31 ± 8.69	29.46 ± 3.33	11	—
	(15.0-16.1)11	(14.4-15.0)11	(6.4-6.8)11	(4.1-4.5)11	(2.8-3.2)11	(3.6-3.9)11	(8.5-9.3)11	(7.2-7.9)11	(76-89)13	(46-60)13	(26-33)13	13	
M	15.15 ± 0.14	14.30 ± 0.57	6.30 ± 0.28	4.25 ± 0.42	3	3.55 ± 0.14	8.85 ± 0.42	7.5	82.67 ± 5.03	54.00 ± 2.00	28.67 ± 3.06	1	2.25 ± 0.99
	(15.1-15.2)2	(14.1-14.5)2	(6.2-6.4)2	(4.1-4.4)2	2	(3.5-3.6)2	(8.7-9.0)2	2	(80-85)3	(53-55)3	(27-30)3	3	(1.9-2.6)2
N	—	—	6.25 ± 0.12	4.22 ± 0.26	2.87 ± 0.21	3.55 ± 0.21	—	—	—	—	—	—	—
			(6.2-6.3)4	(4.1-4.4)5	(2.8-3.0)6	(3.4-3.7)6							

Table 1 *continued.*

OTU	Greatest skull length	Condylobasal length	Palatal length	Maxillary breadth	Interorbital breadth	P4-M3 length	Length of braincase	Cranial breadth	Total length	Head and body length	Tail length	Length of hind foot	Body mass
O	15.12 ± 0.39	14.18 ± 0.29	6.35 ± 0.11	4.22 ± 0.34	2.87 ± 0.10	3.63 ± 0.21	8.77 ± 0.30	7.18 ± 0.43	85.30 ± 5.97	56.90 ± 7.86	28.40 ± 4.54	10.15 ± 1.77	3
	(14.9-15.4)6	(14.0-14.4)6	(6.3-6.4)6	(4.0-4.5)6	(2.8-2.9)6	(3.5-3.8)6	(8.6-9.0)6	(6.9-7.5)6	(81-90)10	(48-61)10	(24-33)10	(8.5-12)10	1
P	15.28 ± 0.14	14.40 ± 0.68	6.40 ± 0.20	4.36 ± 0.18	3.02 ± 0.26	3.60 ± 0.14	8.88 ± 0.56	7.36 ± 0.41	86.13 ± 11.08	56.50 ± 7.33	29.78 ± 2.96	10.11 ± 1.56	3.73 ± 2.53
	(14.9-15.6)5	(14.0-14.8)5	(6.3-6.5)5	(4.2-4.4)5	(2.9-3.2)5	(3.5-3.7)5	(8.6-9.2)5	(7.1-7.6)5	(74-92)8	(49-61)8	(29-32)9	(9-11)9	(2.6-5.1)3
Q	14.99 ± 0.55	14.20 ± 1.00	6.24 ± 0.43	4.29 ± 0.36	2.90 ± 0.16	3.49 ± 0.21	8.74 ± 0.30	7.29 ± 0.42	84.71 ± 11.00	56.57 ± 11.94	28.14 ± 2.69	9.86 ± 0.76	3.28 ± 1.00
	(14.6-15.4)7	(14.0-14.5)7	(5.9-6.5)7	(4.0-4.5)7	(2.8-3.0)7	(3.3-3.6)7	(8.5-8.9)7	(7.0-7.6)7	(74-91)7	(45-62)7	(26-30)7	(9-10)7	(2.8-3.8)4
R	15.11 ± 0.55	14.31 ± 0.61	6.34 ± 0.31	4.31 ± 0.21	3.01 ± 0.27	3.60 ± 0.16	8.77 ± 0.37	7.22 ± 0.42	84.24 ± 9.23	55.59 ± 10.49	28.6 ± 3.69	10.50 ± 1.41	2.70 ± 1.23
	(14.7-15.7)14	(13.9-15.0)14	(6.1-6.6)14	(4.1-4.4)14	(2.8-3.2)14	(3.5-3.7)14	(8.4-9.1)14	(6.7-7.5)14	(76-94)17	(45-63)17	(25-31)18	(10-12)18	(1.5-3.5)12
S	14.84 ± 0.55	13.96 ± 0.64	6.31 ± 0.24	4.21 ± 0.27	2.96 ± 0.20	3.59 ± 0.27	8.53 ± 0.38	7.20 ± 0.42	83.96 ± 12.49	54.25 ± 7.41	29.75 ± 7.97	10.57 ± 1.19	3.24 ± 0.86
	(14.4-15.1)7	(13.5-14.4)7	(6.2-6.5)7	(4.0-4.4)7	(2.8-3.1)7	(3.4-3.8)7	(8.2-8.7)7	(6.8-7.4)7	(70.5-91)14	(47-61)14	(20-36)14	(9.5-11.5)15	(2.4-3.8)12
T	14.71 ± 0.72	13.74 ± 0.77	6.20 ± 0.26	4.23 ± 0.32	2.87 ± 0.22	3.50 ± 0.20	8.51 ± 0.50	7.29 ± 0.18	79.00 ± 7.01	48.88 ± 6.80	29.88 ± 1.67	10.33 ± 1.41	3.56 ± 1.54
	(14.1-15.1)7	(13.2-14.2)7	(6.0-6.4)7	(4.0-4.5)7	(2.7-3.0)7	(3.4-3.7)7	(8.1-8.8)7	(7.2-7.4)7	(75-85)8	(45-54)8	(29-31)8	(9-11)9	(2.5-5.0)9
U	14.96 ± 0.50	14.20 ± 0.63	6.30 ± 0.25	4.24 ± 0.58	2.96 ± 0.11	3.60 ± 0.20	8.66 ± 0.41	7.30 ± 0.14	78.38 ± 8.14	49.63 ± 7.42	28.75 ± 4.34	9.94 ± 1.55	3.15 ± 0.71
	(14.6-15.2)5	(13.7-14.5)5	(6.2-6.5)5	(4.0-4.4)5	(2.9-3.0)5	(3.5-3.7)5	(8.4-8.9)5	(7.2-7.4)5	(73-86)8	(44-56)8	(26-33)8	(9-11)8	(2.9-3.4)2
V	14.67 ± 0.68	13.86 ± 0.76	6.18 ± 0.43	4.30 ± 0.22	2.98 ± 0.15	3.58 ± 0.29	8.48 ± 0.46	7.17 ± 0.35	77.80 ± 6.20	49.00 ± 6.85	28.80 ± 4.22	9.73 ± 0.92	2.75 ± 0.74
	(14.1-15.0)6	(13.2-14.3)6	(5.8-6.4)6	(4.1-4.4)6	(2.9-3.1)6	(3.3-3.7)6	(8.3-8.9)6	(6.9-7.3)6	(72-82)15	(42-55)15	(25-32)15	(9-10)15	(2.1-3.4)12
W	14.73 ± 0.57	13.80 ± 0.82	6.30 ± 0.16	4.15 ± 0.12	2.83 ± 0.25	3.58 ± 0.41	8.43 ± 0.60	7.08 ± 0.10	77.00 ± 5.66	47.00 ± 8.49	30.00 ± 2.83	9.75 ± 0.71	2.85 ± 0.14
	(14.4-15.1)4	(13.3-14.3)4	(6.2-6.4)4	(4.1-4.2)4	(2.7-3.0)4	(3.3-3.8)4	(8.1-8.8)4	(7.0-7.1)4	(75-79)2	(44-50)2	(29-31)2	(9.5-10)2	(2.8-2.9)2
X	14.95 ± 0.58	14.26 ± 0.78	6.31 ± 0.25	4.21 ± 0.17	2.86 ± 0.10	3.55 ± 0.15	8.64 ± 0.41	7.25 ± 0.21	84.50 ± 6.03	55.33 ± 7.45	29.17 ± 2.34	10.58 ± 0.98	3.20 ± 1.46
	(14.5-15.3)8	(13.8-14.9)8	(6.1-6.5)8	(4.1-4.4)8	(2.8-2.9)8	(3.4-3.6)8	(8.2-8.8)8	(7.1-7.4)8	(79-88)6	(49-60)6	(28-31)6	(10-11)6	(2.1-4.1)5
Y	15.29 ± 0.42	14.64 ± 0.59	6.40 ± 0.32	4.35 ± 0.24	3.10 ± 0.19	3.64 ± 0.28	8.89 ± 0.25	7.48 ± 0.45	—	—	—	—	—
	(14.9-15.6)8	(14.2-15.0)8	(6.1-6.6)8	(4.2-4.5)8	(3.0-3.2)8	(3.4-3.8)8	(8.7-9.1)8	(7.1-7.8)8					
Z	15.00 ± 0.57	14.15 ± 0.83	6.33 ± 0.35	4.30 ± 0.25	3.02 ± 0.32	3.70 ± 0.22	8.67 ± 0.27	7.42 ± 0.27	82.33 ± 8.19	52.92 ± 7.16	29.42 ± 2.17	9.96 ± 1.00	3.42 ± 0.85
	(14.5-15.3)6	(13.5-14.7)6	(6.0-6.5)6	(4.2-4.5)6	(2.8-3.2)6	(3.6-3.9)6	(8.5-8.9)6	(7.2-7.5)6	(76-91)12	(48-61)12	(28-31)12	(9-11)12	(2.6-4.0)12
a	15.96 ± 0.48	15.13 ± 0.63	6.70 ± 0.16	4.49 ± 0.38	3.20 ± 0.11	3.84 ± 0.21	9.26 ± 0.30	7.78 ± 0.39	95.64 ± 6.65	63.54 ± 7.01	32.09 ± 3.63	11.32 ± 0.92	4
	(15.7-16.3)5	(14.9-15.7)6	(6.6-6.8)7	(4.3-4.7)8	(3.1-3.3)8	(3.7-4.0)8	(9.1-9.5)5	(7.4-7.9)6	(88-100)11	(57-68)11	(29-35)11	(11-12)11	1
b	15.65 ± 0.71	14.75 ± 1.56	6.65 ± 0.14	4.50 ± 0.28	3.25 ± 0.42	3.75 ± 0.14	9.00 ± 0.57	7.80 ± 0.57	87.00 ± 12.49	55.00 ± 18.00	32.00 ± 6.93	11	3.75 ± 0.71
	(15.4-15.9)2	(14.2-15.3)2	(6.6-6.7)2	(4.4-4.6)2	(3.1-3.4)2	(3.7-3.8)2	(8.8-9.2)2	(7.6-8.0)2	(80-92)3	(46-64)3	(28-34)3	3	(3.5-4.0)3

Table 2. Eigenvector loadings for eight cranial characters in *Sorex longirostris* and the percent variation explained by the first two principal components.

Character	I	II
Greatest skull length	0.370	-0.305
Condylobasal length	0.366	-0.304
Palatal length	0.367	-0.271
Maxillary breadth	0.324	0.579
Interorbital breadth	0.336	0.500
P^4-M^3 length	0.347	-0.007
Length of braincase	0.363	-0.315
Cranial breadth	0.353	0.240
Percent of variance explained	85.580	7.660

4.0 to 12.0 and averaged 7.43%. The mean number of alleles per locus was 1.0 for 16 OTUs, 1.1 for 7 OTUs, and 1.2 for 2 OTUs.

Heterozygosities over all OTUs ranged from 0.000 to 0.080 and averaged 0.021 (Table 3). Among OTUs containing >4 individuals, average heterozygosities ranged from 0.010 to 0.031 and averaged 0.021 (Table 3). Deviation from Hardy-Weinberg expected heterozygosity occurred in only three OTUs and at only four loci. Chi-square analysis for conformity to Hardy-Wienberg expected equilibrium using Levene's (1949) correction for small sample size (data not shown) revealed that the following populations were heterozygote deficient at the loci indicated: Isle of Wight, **1** (PEPA and ACN1); Chesapeake, **3** (6PGD); and Wayne, **21** (MPI).

Fourteen OTUs clustered together within the 0.06 distance level in the phenogram based on modified Rogers' (1972) genetic distance matrix (Fig. 2), and 13 of these were from the Coastal Plain physiographic province. The cophenetic correlation coefficient for this phenogram was 0.953.

Genetic distances between OTUs (data not shown) ranged from 0.000 to 0.206 with the largest value between Pitt County (**22**), in the Coastal Plain of eastern North Carolina, and Moore County (**17**), in the Piedmont of North Carolina. OTUs with 0.0 distance included Hertford (**23**) and Beaufort (**8**), and Dare (**6**), Robeson (**14**), Columbus (**13**), Richmond (**16**), Stumpy Lake (**2**), and Duplin South (**11**), all of which are in the Lower Coastal Plain of southeastern Virginia and eastern North Carolina. There was relatively high genetic similarity (97.1%) between shrews from Pender County (**12**), in southeastern North Carolina, and the City of Chesapeake (**3**), Virginia, the type locality of *S. l. fisheri*, whereas the similarity between shrews from Pender County (**12**) and Henry County (**24**), in the foothills of the Blue Ridge Mountains in south-central Virginia, was relatively low (90.3%). When analyzing populations with sample sizes of >4 individuals, genetic distances ranged from 0.024 between Perquimans/Chowan counties (**5**), immediately south of the Great Dismal Swamp in North Carolina, and the City of Chesapeake (**3**) in Virginia, to 0.098 between Beaufort County (**8**), North Carolina, and Henry County (**24**), Virginia.

Shrews from nine of 18 OTUs in the Coastal Plain physiographic province of eastern North Carolina and southeastern Virginia exhibited the C allele at MPI (Table 3). The C allele was also present in specimens from Nash (**20**) and Wayne (**21**) counties, which lie between the Coastal Plain and Piedmont physiographic provinces in central North Carolina, but it was not found in shrews from the foothills of the Blue Ridge Mountains of Virginia (**24**) and North Carolina (**25**) or from the Sandhills and Upper Coastal Plain of south-central North Carolina (**13-17**).

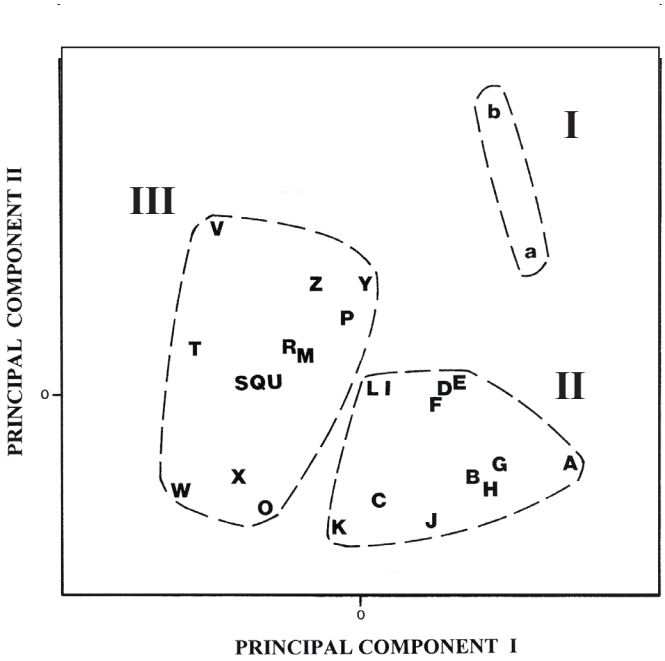

Fig. 1. Two-dimensional plot of Principal Components I and II for 27 OTUs of *Sorex longirostris*. Three groups of OTUs, labeled I, II, and III, are indicated with dashed lines. OTU **N** was not included due to missing data. See Fig. 3a and Appendix 1 for key to sample locations.

Table 3. Alphabetic designations for electromorphs, mean heterozygosity (*H*), number of expected heterozygotes (H_{exp}; Nei, 1978), and percent polymorphism (*P*) at two polymorphic loci assayed across 25 OTUs of *Sorex longirostris*. Allelic frequencies for polymorphic loci are indicated in parentheses. Abbreviations for loci are provided in Appendix 2. See Fig. 3b and Appendix 1 for key to sample locations.

OTU Number	Name	n	MPI	ACN1	*H*	H_{exp}	*P*
1	Isle of Wight	23	A(0.65) B(0.17) C(0.11) D(0.07)	A(0.80) B(0.20)	0.024	0.040	8.0
2	Stumpy Lake	1	A	A	0.000	0.000	0.0
3	Chesapeake	12	A(0.75) B(0.08) C(0.17)	A(0.92) B(0.08)	0.027	0.029	12.0
4	Camden	3	A(0.83) C(0.17)	A	0.027	0.027	8.0
5	Perquimans and Chowan	8	A(0.79) C(0.21)	A(0.93) B(0.07)	0.016	0.025	12.0
6	Dare	1	A	A	0.000	0.000	0.0
7	Tyrrell	1	C(0.50) D(0.50)	A(0.50) C(0.50)	0.080	0.080	8.0
8	Beaufort	8	A(0.75) C(0.25)	A	0.010	0.016	4.0
9	Greene	1	A(0.50) B(0.50)	A(0.50) B (0.50)	0.080	0.080	8.0
10	Duplin North	1	A(0.50) C(0.50)	A	0.040	0.040	4.0
11	Duplin South	1	A	A	0.000	0.000	0.0
12	Pender	6	A(0.66) B(0.17) C(0.17)	A	0.020	0.022	4.0
13	Columbus	1	A	A	0.000	0.000	0.0
14	Robeson	3	A	A	0.000	0.000	0.0
15	Scotland	3	A(0.83) B(0.17)	A	0.013	0.013	4.0
16	Richmond	3	A	A	0.000	0.000	0.0
17	Moore	2	A	A(0.75) B(0.25)	0.020	0.020	4.0
18	Sampson	1	B	A	0.000	0.000	0.0
19	Johnston	2	A(0.50) D(0.50)	A	0.040	0.027	4.0
20	Nash	1	A(0.50) C(0.50)	A	0.040	0.040	4.0
21	Wayne	2	A(0.50) C(0.25) D(0.25)	A	0.020	0.033	4.0
22	Pitt	1	D	A	0.000	0.000	0.0
23	Hertford	2	A(0.75) C(0.25)	A	0.020	0.020	4.0
24	Henry	9	A(0.83) B(0.06) D(0.11)	A(0.56) B(0.44)	0.031	0.033	8.0
25	Rutherford and Polk	5	A(0.70) D(0.30)	A	0.024	0.019	4.0

DISCUSSION

Morphometric data demonstrate that the southeastern shrew is comprised of three well-defined subspecies. This pattern conforms to that found by Jones et al. (1991), but our results indicate that shrews assignable to *S. l. fisheri* occupy a much larger geographic distribution than was previously documented (Fig. 3). Shrews with large but relatively narrow crania were widespread throughout eastern North Carolina and southeastern Virginia. Southeastern shrews from immediately east and west of the present Great Dismal Swamp were slightly smaller than shrews from the Great Dismal Swamp in cranial and external measurements, as was noted by Padgett (1991), Padgett et al. (1987), and Rose (1983). When compared to specimens from throughout the range of the species, however, these shrews had relatively long narrow rostra, and we assign them to *S. l. fisheri*.

Southeastern shrews from the Mountain and Piedmont physiographic regions of Virginia and North Carolina were more similar to individuals from the Mississippi

and Ohio River basins in cranial proportions than they were to shrews from the mid-Atlantic coast. They were only slightly smaller than specimens from the type locality of *S. l. longirostris* in coastal South Carolina, and we assign them to *S. l. longirostris* (Fig. 3).

Intergradation between *S. l. fisheri* and *S. l. longirostris* was evident in specimens from immediately west of the Suffolk Scarp in southeastern Virginia and northeastern North Carolina and in specimens from the Upper Coastal Plain of southeastern North Carolina. Shrews from the western edge of the Lower Coastal Plain in both states typically had crania that were relatively long and narrow; these specimens were assignable to *S. l. fisheri*, even though some had measurements approaching those of *S. l. longirostris* for some characters. Shrews from the Upper Coastal Plain, however, had crania that were generally short and stocky. These individuals were assignable to *S. l. longirostris*, even though some had dimensions approaching those of *S. l. fisheri*.

Morphometric data indicated that southeastern shrews with long, relatively wide crania and short tails (all referable to *S. l. eionis*) were distributed throughout the northern two-thirds of peninsular Florida (OTU **a**) and as far west as the Apalachicola River in the Florida panhandle and as far north as southern Georgia (OTU **b**). The latter specimens (OTU **b**) were assigned to *S. l. longirostris* by Jones et al. (1991); however, we judge these specimens to be virtually indistinguishable in cranial and external dimensions, albeit slightly smaller, from the holotype and a topotypical series of *S. l. eionis* from Homosassa Springs, Florida (OTU **a**).

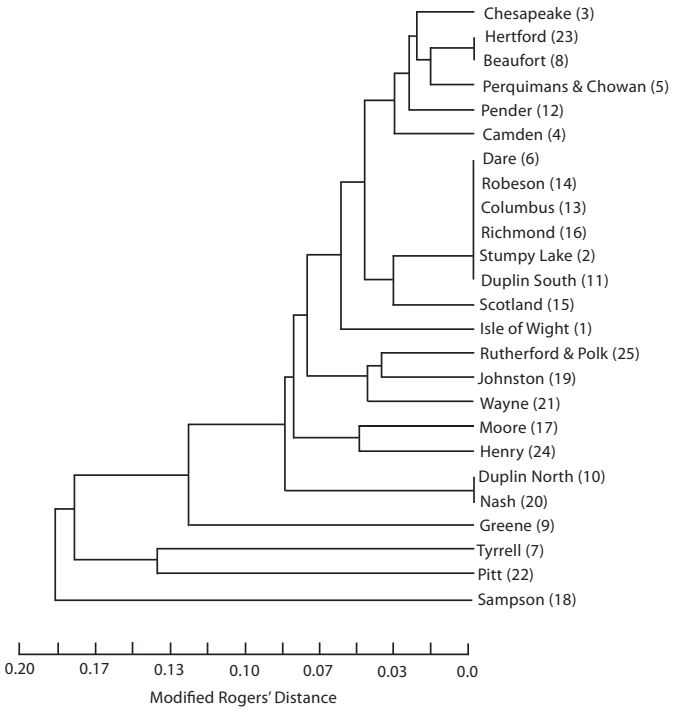

Fig. 2. Phenogram based on UPGMA cluster analysis using Rogers' (1972) modified genetic distance among 25 OTUs of *Sorex longirostris* (cophenetic correlation is 0.953). See Fig. 3b and Appendix 1 for key to sample locations.

Our allozymic analyses produced estimates of variation (percentages of polymorphic loci and heterozygosity) in *S. longirostris* that were similar to those reported for other small mammals where adequate sample sizes were analyzed (Nevo, 1978). Only three other studies of allozymic variation in *S. longirostris* are known to us, and they have focused on single populations (Driskell, 1992; Tolliver and Robbins, 1987) or included only a few individuals (George, 1988). Driskell (1992) found variability in eight of 23 loci in two specimens from Land Between the Lakes, Kentucky and Tennessee; 17.2% of the loci were polymorphic and mean heterozygosity was 0.069. Tolliver and Robbins (1987) found variation in four of 25 loci in 14 specimens from one site in South Carolina; 18.5% of the loci were polymorphic and mean heterozygosity was 0.021. George (1988) reported allozymic variation in two of 24 loci in 10 specimens from Florida (n = 4), Louisiana (n = 2), and Virginia (n = 4); 7.69% of the loci were polymorphic and mean heterozygosity was 0.04. Our polymorphism estimates are most similar to those reported by George (1988) and our heterozygosity estimates are most similar to those reported by Tolliver and Robbins (1987), studies that focused, like ours, on individuals from the easternmost part of the range of *S. longirostris*. These studies, however, lacked the sample sizes necessary to compute genetic distances among populations.

There was good agreement between the allozymic results and the morphological assignment of specimens to either *S. l. longirostris* or *S. l. fisheri*. Twelve of 14 OTUs clustering at the 0.06 distance level were assignable to *S. l. fisheri* on the basis of cranial morphology and size (Fig. 2). The two exceptions were OTUs from Hertford County (**M**, **23**), North Carolina, which included intergrades that were marginally closer to *S. l. longirostris* than to *S. l. fisheri*, and Richmond County (**R**, **16**), North Carolina, which included animals that were clearly referable to *S. l. longirostris*. Eight of 11 OTUs of shrews that joined the cluster after Isle of Wight were referable to *S. l. longirostris* on the basis of cranial morphometrics (Fig. 2). The remaining three OTUs (Tyrrell, **7**; Greene, **9**; Duplin North, **10**) were represented by a total of only three shrews, all referable to *S. l. fisheri* on the basis of cranial morphometrics.

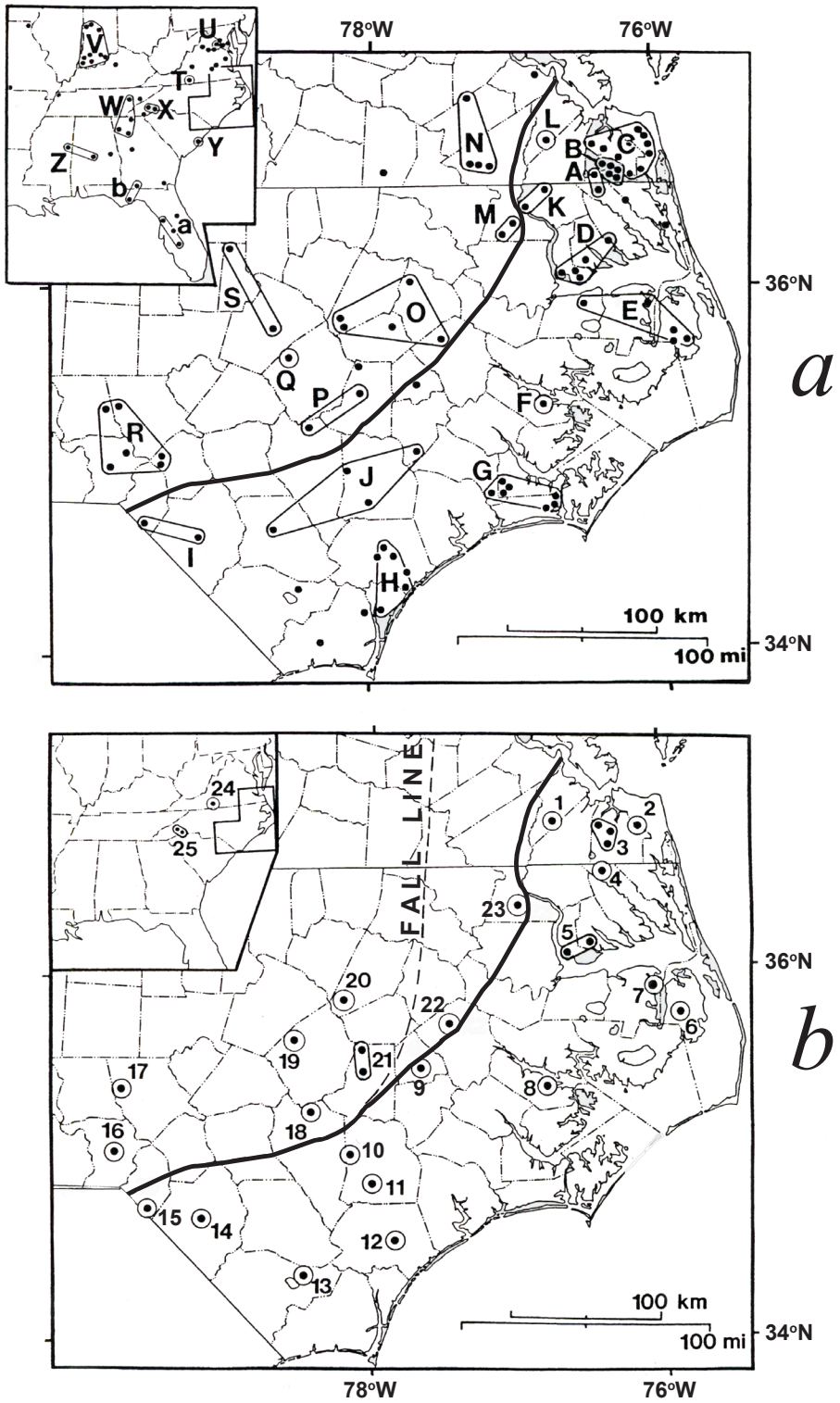

Fig. 3. Distribution of *Sorex longirostris fisheri and S. l. longirostris*. a).— Locations of specimens examined (dots) and samples (enclosed) included in morphometric analyses (letters). Some dots represent more than one locality; those not enclosed represent damaged specimens or locations with small sample sizes, which were omitted from the morphometric analysis. Inset shows geographic distribution of *Sorex longirostris* in the southeastern United States. b).—Locations of samples used in the allozymic analysis. The boundary between the Piedmont and Coastal plain physiographic provinces (labeled "Fall Line") is indicated with a dashed line. In each case, we assign samples in Virginia and North Carolina east of the solid heavy line to *S. l. fisheri*; samples to the west are *S. l. longirostris.* This line is coincident with the Fall Line in south-central North Carolina.

In conclusion, the Dismal Swamp southeastern shrew (*Sorex longirostris fisheri*) has a much broader geographic distribution than previously reported, extending from southeastern Virginia southward throughout the Lower Coastal Plain as far south as New Hanover, Brunswick, and Columbus counties in southern North Carolina (Fig. 3). In southeastern Virginia, shrews from Isle of Wight County, the City of Chesapeake, and the City of Virginia Beach are referable to *S. l. fisheri*, whereas those from Surry, Sussex, and Southampton counties are assignable to *S. l. longirostris* (Fig. 3). Shrews from the Piedmont and Mountain regions of Virginia and North Carolina are clearly assignable to *S. l. longirostris* (Fig. 3). Thus, the zone of intergradation between *S. l. longirostris* and *S. l. fisheri* is relatively narrow in southeastern Virginia (where the Coastal Plain is relatively narrow), but it is relatively wide in southeastern North Carolina, where the Coastal Plain is relatively wide.

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APPENDIX 1
SPECIMENS EXAMINED

All specimens are deposited in the Vertebrate Collections at the University of North Carolina Wilmington (UNCW) unless otherwise noted. See *Acknowledgments* for institutional abbreviations. OTU designations for specimens used in the morphometric analysis are indicated by bold letters, and those used in the allozymic analysis are indicated by bold numerals. Specimens housed by VCU at the time of this study are now part of the VMNH Collection of Mammals.

Sorex longirostris eionis (15).— FLORIDA. *Citrus Co*.: Homosassa Springs, head of Homosassa River (9 AMNH **a**). *Highlands Co*.: 6-8 mi S Lake Placid (1 AMNH **a**). *Polk Co*.: 1.5 mi NE Davenport (1 AMNH **a**). *Volusia Co*.: 5-6 mi N De Land, Hwy 11 (1 AMNH). *Wakulla Co*.: Saint Marks National Wildlife Refuge (1 NMNH **b**). GEORGIA. *Grady Co*.: Beachton (1 NMNH **b**); Beachton, Sherwood Plantation (1 NMNH **b**).

Sorex longirostris fisheri (395).— NORTH CAROLINA. *Beaufort Co*.: 4 mi N Aurora (73 **F 8**). *Bladen Co*.: Salters Lake (11 NCSM **J**); 5 mi ESE White Oak, Salters Lake (2 NCSM). *Brunswick Co*.: Leland (2); *ca* 4 mi N Supply, Green Swamp, Hwy 211 (1 NCSM). *Camden Co*.: Dismal Swamp State Natural Area (74 **A 4**); 4.2 mi NE South Mills (1 NCSM). *Carteret Co*.: 3 mi ENE Harlowe (2 NCSM **G**); *ca* 5.5 mi ESE Harlowe (2 NCSM **G**); *ca* 3.25 mi ESE Newport (1 NCSM). *Chowan Co*.: 4.5 mi SE Edenton, Hwy 32 (3 NCSM **D**); 2 km W Edenton, Hwy 17 (1 **5**); 3 km NNW Edenton, Hwy 32 (4 **D 5**). *Columbus Co*.: 2 km NW Bolton, Hwy 211 (1 **13**). *Craven Co*.: *ca* 7 mi WSW Croatan (5 NCSM **G**); *ca* 8.9 mi SW Croatan (5 NCSM **G**); 11.25 mi WSW Havelock (1 NCSM **G**). *Currituck Co*.: Coinjock (1 NCSM); 5 mi W Moyock, SR 1218 (2). *Dare Co*.: 7 km WNW Stumpy Point (4 **E**); 17 km W Stumpy Point (3); 17 km WNW Stumpy Point (4 **E 6**). *Duplin Co*.: 3 mi ESE Rose Hill, SR 1148 (2 **J 11**); 4 km W Warsaw, Hwy 24 (2 **J 10**). *Gates Co*.: Jct Hwy 13 and SR 1300, 1 mi S Virginia-NC Line (1 **K**); 3.3 mi NE Chowan River at Hwy 13, SR 1200 (4 **K**). *Greene Co*.: 7 km S Snow Hill, Hwy 258 (2 **9**). *Jones Co*.: *ca* 6 mi SE Maysville (1 NCSM **G**). *Lenoir Co*.: 5 km SW Woodington, SR 1925 (4 **J**). *New Hanover Co*.: Wilmington (2 **H**). *Pender Co*.: 3 mi E Burgaw (1); 5 km S Burgaw, I-40 (4); Holly Shelter Game Lands (23 **12**); Scotts Hill, Hwy 17 (9 **H**). *Perquimans Co*.: Chapanoke (1 ANSP); 5 km SSW Hertford, Hwy 17/37 (9 **D**); 6.5 km SSW Hertford, Hwy 17/37 (5 **D 5**). *Robeson Co*.: 6 km WSW Lumberton, SR 2503 (4 **I 14**). *Scotland Co*.: 8 km SW Laurinburg, Hwy 15/401 (4 **I 15**). *Tyrrell Co*.: 16 km E Columbia, Hwy 64 (2 **E 7**). *Washington Co*.: 1 km NW Scuppernong, Hwy 64 (1 **E**). VIRGINIA. *City of Chesapeake*: Bower's Hill (1 **C 3**); Dismal Swamp (1 NMNH); 12.75 km S, 5.75 km E Chesapeake Municipal Center (5 VCU **B**); 17 km S, 5 km E Chesapeake Municipal Center (3 VCU **B**); 15.25 km S, 0.75 km E Chesapeake Municipal Center (3 VCU **B**); 13 km S, 1.25 km W Chesapeake Municipal Center (4 VCU **B**); 15 km S, 6.5 km W Chesapeake Municipal Center (12 VCU **B**); 11 km S, 2 km W Chesapeake Municipal Center (3 VCU **B**); 6.25 km S, 3.25 km W Chesapeake Municipal Center (2 VCU **B**); 10 km S, 6.25 km W Chesapeake Municipal Center (2 VCU **B**); 5 km S, 6 km W Chesapeake Municipal Center (3 VCU **B**); 6.5 km S, 10 km W Chesapeake Municipal Center (4 VCU **B**); 2 mi S Deep Creek (1 **C 3**); Dismal Swamp, Lake Drummond (1 AMNH, 8 NMNH **A**); Great Bridge (1 VCU **C**); Stumpy Lake (2 **C 2**); 4.7 mi NNE Wallaceton, Hwy 17 (1 NMNH **B**); *ca* West Landing, Hwy 17 (28 **B 3**). *City of Virginia Beach*: 2 mi E Princess Anne (2 **C**); 5 km N, 0.75 km E Princess Anne Courthouse (2 VCU **C**); 1.5 km N, 2 km E Princess Anne Courthouse (1 VCU); 6 km S, 1 km W Princess Anne Courthouse (4 VCU **C**); 16.25 km S, 2.25 km W Princess Anne Courthouse (2 VCU **C**); 20 km S, 4 km W Princess Anne Courthouse (2 VCU **C**). *Isle of Wight Co*.: *ca* Windsor (13 VMNH **L 1**).

Sorex longirostris longirostris (216).— ALABAMA. *Autauga Co*.: Autaugaville (1 NMNH). *Chambers Co*.: 2 mi N Gold Hill, Hwy 147 (12 NMNH). DISTRICT OF COLUMBIA. Washington (1 NMNH). GEORGIA. *Charlton Co*.: Okefinokee Swamp, Chesser's Prairie, 1 mi SW Lake Sego (1 ANSP). *Floyd Co*.: 3 mi from Rome (1 NMNH **W**). *Fulton Co*.: Roswell (1 AMNH **W**). *Taylor Co*.: Butler (1 NMNH). *Town Co*.: Young Harris (1 NMNH **W**). INDIANA. *Boone Co*.: 4 mi E Whitestown (1 NMNH **V**). *Dubois Co*.: Cuzco (1 NMNH). *Fountain Co*.: 3 mi E, 2 mi N Attica (1 NMNH **V**). *Knox Co*.: Bicknell (3 NMNH). *Marion Co*.: Indianapolis (1 NMNH **V**). *Martin Co*.: Crane NAD (1 NMNH **V**). *Pike Co*.: 2 mi SE Coe (2 NMNH **V**). *Tippecanoe*

Co.: 6 mi E Lafayette (1 NMNH **V**); 10 mi W Lafayette (6 NMNH **V**); West Lafayette (1 NMNH **V**). *Washington Co*.: 4 mi S Pekin (1 NMNH **V**); 3 mi N Smedley (1 NMNH **V**). KENTUCKY. *Franklin Co*.: Union Ridge Rd (1 NMNH). MARYLAND. *Anne Arundel Co*.: Shady Side (1 NMNH). *Calvert Co*.: Camp Roosevelt (2 NMNH); Chesapeake Beach (1 NMNH). *Charles Co*.: Nanjemoy, Hwy 224 (1 NMNH). *Prince Georges Co*.: 4 mi W Hall, West Branch of Patuxent River (1 NMNH). MISSISSIPPI. *Noxubee Co*.: Macon (1 NMNH **Z**). MISSOURI. *Barry Co*.: Roaring River State Park (1 NMNH). *Clark Co*.: 3 mi W, 2 mi S Alexandria (1 NMNH). NORTH CAROLINA. *Buncombe Co*.: Bent Creek Experimental Forest, Pisgah Forest (2 NMNH **X**). *Durham Co*.: Rougemont (1 UMMZ **S**). *Edgecombe Co*.: *ca* 4 mi ESE Battleboro (1 NCSM **O**). *Hertford Co*.: 2 km NW Ahoski, Hwy 11 (2 **M 23**); 3 km SW Winton, Hwy 13 (1). *Hoke Co*.: McCain (1 NCSM **R**); *ca* 1.5 mi SW McCain, Hwy 211 (1 NCSM); no specific locality (1 NCSM). *Johnston Co*.: 10 km WSW Clayton, Jct Hwy 42 and I-40 (12 **Q 19**). *Macon Co*.: 2 mi SW Highlands, 3280 ft (1 AMNH). *Montgomery Co*.: 2 km E Biscoe, Hwy 24/27 (2 **R**). *Moore Co*.: 7 km SW Robbins, Hwy 24/27 (5 **R 17**). *Nash Co*.: 3 km WNW Bailey, SR 1108 (3 **O**); 3 km ENE Middlesex, SR 1109 (2 **O 20**). *Pitt Co*.: 3 km WSW Dupree Crossroads, Hwy 222 (4 **O 22**). *Polk Co*.: 6 km NE Saluda, SR 1151, 1100 ft (1 **X**); 8 km NE Saluda, SR 1151, 1100 ft (3 **X 25**). *Richmond Co*.: 4.3 mi SE Norman, Jct SR 1424 and SR 1458 (1 NCSM **R**); 6 km NNE Rockingham, SR 1443 (12 **R 16**). *Rutherford Co*.: *ca* Lake Lure, 1410-1860 ft (3 **X 25**). *Sampson Co*.: 2 km SW Newton Grove, SR 1648 (9 **P 18**). *Wake Co*.: Raleigh (4 NCSM, 8 UMMZ, 3 NMNH **S**); no specific locality (2 NCSM). *Wayne Co*.: 10 km NNW Goldsboro, Hwy 581 (3 **P 21**); 7 km E Kenly, Hwy 581 (2 **21**). *Wilson Co*.: 3 km SE Elm City, SR 1420 (1 **O**). *No Specific Locality*: (1 UMMZ). SOUTH CAROLINA. *Charleston Co*.: 4 km SW Awendaw, Iron Swamp (7 NMNH **Y**); 3.3 km NW McClellanville, head of Mill Branch (15 NMNH **Y**). *Georgetown Co*.: Swamps of Santee River, Hume Plantation on Cat Island (1 ANSP). TENNESSEE. *Knox Co*.: 10 mi SW Knoxville (1 NMNH **W**). *Lake Co*.: 12 mi E Phillippy, Reelfoot Lake (1 NMNH). *Sevier Co*.: Sevierville (1 NMNH). VIRGINIA. *Amelia Co*.: Amelia Court House (4 NMNH). *Arlington Co*.: Little Pimmett Run, 2 mi SW Chain Bridge (1 NMNH). *Brunswick Co*.: Triplett, Seward Forest (2 NMNH). *Chesterfield Co*.: 4 mi N Midlothian, Powhatan County Line (1 NMNH). *Culpeper Co*.: 10 mi SE Culpeper, Lignum (1 NMNH). *Essex Co*.: 3.5 mi NW Center Cross (2 NMNH). *Fairfax Co*.: near Burke (1 NMNH **U**); Falls Church (1 NMNH **U**); Fort Belvoir (11 NMNH **U**); 2 mi NW center of Vienna, 410 ft (1 NMNH **U**). *Fauquier Co*.: Casanova (1 NMNH). *Hanover Co*.: 1.5 mi S Montpelier (1 NMNH). *Henry Co*.: 1.5 mi S, 1.25 mi W Martinsville City Hall (9 VMNH **T 24**). *Page Co*.: 4.7 mi ENE Luray, Shenandoah National Park, 1200 ft (1 NMNH); Shenandoah National Park, 1200 ft (2 NMNH). *Prince William Co*.: 4 mi SE Manassas (2 NMNH). *Rockbridge Co*.: Vesuvius (1 NMNH). *Southampton Co*.: 4 mi W Capron (1 VCU **N**); 8 mi W Capron (2 VCU **N**); 5.7 mi W Courtland (1 VCU **N**); 7 mi W Courtland (1 VCU **N**). *Surry Co*.: 4 mi NE Surry (1 NMNH). *Sussex Co*.: 1.4 mi SE Warwick Swamp, Sussex-Prince George Line (1 VCU **N**).

APPENDIX 2

Buffer systems and enzymes used to analyze *Sorex longirostris* were as follows: tris-citrate, pH 8.0 (TC8) for malic enzyme (ME, Enzyme Commission number 1.1.1.40), malate dehydrongenase (MDH1, MDH2, 1.1.1.37), glutamate oxaloacetate transaminase (GOT1, GOT2, 2.6.1.1), lactate dehydrogenase (LDH1, LDH2, 1.1.1.27), glucose-6-phosphate dehydrogenase (G6PD, 1.1.1.49), phosphoglucomutase (PGM1, PGM2, PGM3, 2.7.5.1), 6-phosphogluconate dehydrogenase (6PGD, 1.1.1.44), glycerol-3-phosphate dehydrogenase (G3PD, 1.1.1.8), isocitrate dehydrogenase (IDH1, IDH2, 1.1.1.42), tris-citrate, pH 7.0 (TC7) for aconitase (ACN1, ACN2, 4.2.1.3), adenosine deaminase (ADA, 3.5.4.4), creatine kinase (CK1, CK2, 2.7.3.2), peptidase A (valyl-leucine used as substate; PEPA, 3.4.11), peptidase B (leucyl-glycyl-glycine used as substrate; PEPB, 3.4.11), peptidase D (phenylalanyl-proline used as substrate; PEPD, 3.4.13.9), peptidase S (leucyl-glycyl-glycine or valyl-leucine used as substrate; PEPS, 3.4.11), phosphoglucose isomerase (PGI, 5.3.1.9), nucleoside phosphorylase (NP, 2.4.2.1), manose phosphate isomerase (MPI, 5.3.1.8), sorbitol dehydrogenase (SDH, 1.1.1.14), and xanthine dehydrogenase (XDH-1, -2, 1.1.1.204).

Parts published to date

1 On the taxonomy of the milliped genera *Pseudojulus* Bollman, 1887, and *Georgiulus*, gen. nov., of southeastern United States. Richard L. Hoffman. Pp. 1-19, figs. 1-22. 1992. $2.00

2. A striking new genus and species of bryocorine plant bug (Heteroptera: Miridae) from eastern North America. Thomas J. Henry. Pp. 1-9, figs. 1-9. 1993. $1.00.

3. The American species of *Escaryus*, a genus of Holarctic centipeds (Geophilo-morpha: Schendylidae). Luis A. Pereira & Richard L. Hoffman. Pp. 1-72, figs. 1-154, maps 1-3. 1993. $7.00

4. A new species of *Puto* and a preliminary analysis of the phylogenetic position of the *Puto* Group within the Coccoidea (Homoptera: Pseudococcidae). Douglass R. Miller & Gary L. Miller. Pp. 1-35, figs. 1-7. 1993. $4.00.

5. *Cambarus (Cambarus) angularis*, a new crayfish (Decapoda: Cambaridae) from the Tennessee River Basin of northeastern Tennessee and Virginia. Horton H. Hobbs, Jr., & Raymond W. Bouchard. Pp. 1-13, figs. 1a-1n. 1994. $2.00.

6. Three unusual new epigaean species of *Kleptochthonius* (Pseudoscorpionida: Chthoniidae). William B. Muchmore. Pp. 1-13, figs. 1-9. 1994. $1.50.

7. A new dinosauromorph ichnogenus from the Triassic of Virginia. Nicholas C. Fraser & Paul E. Olsen. Pp. 1-17, figs. 1-3. 1996. $2.00.

8. “Double-headed” ribs in a Miocene whale. Alton C. Dooley, Jr. Pp. 1-8, figs. 1-5. 2000. $1.00.

9. An outline of the pre-Clovis Archeology of SV-2, Saltville, Virginia, with special attention to a bone tool dated 14,510 yr BP. Jerry N. McDonald. Pp. 1-60, figs. 1-19. 2000. $3.00.

10. First confirmed New World record of *Apocyclops dengizicus* (Lepishkin), with a key to the species of *Apocyclops* in North America and the Caribbean region (Crustacea: Copepoda: Cyclopidae). Janet W. Reid, Robert Hamilton, & Richard M. Duffield. Pp. 1-23, figs. 1-3. 2002. $2.50

11. A review of the eastern North American Squalodontidae (Mammalia:Cetacea). Alton C. Dooley, Jr. Pp. 1-26, figs. 1-6. 2003. $2.50.

12. New records and new species of the genus *Diacyclops* (Crustacea: Copepoda) from subterranean habitats in southern Indiana, U.S.A. Janet W. Reid. Pp. 1-65, figs. 1-22. 2004. $6.50.

13. *Acroneuria yuchi* (Plecoptera: Perlidae), a new stonefly from Virginia, U.S.A. Bill P. Stark & B. C. Kondratieff. Pp. 1-6, figs. 1-6. 2004. $0.60.

14. A new species of woodland salamander of the *Plethodon cinereus* Group from the Blue Ridge Mountains of Virginia. Richard Highton. Pp. 1-22. 2005. $2.50.

15. Additional drepanosaur elements from the Triassic infills of Cromhall Quarry, England. Nicholas C. Fraser & S. Renesto. Pp. 1-16, figs. 1-9. 2005. $1.50.

16. A Miocene cetacean vertebra showing partially healed compression fracture, the result of convulsions or failed predation by the giant white shark, *Carcharodon megalodon*. Stephen J. Godfrey & Jeremy Altmann. Pp. 1-12. 2005. $1.50.

17. A new *Crataegus*-feeding plant bug of the genus *Neolygus* from the eastern United States (Hemiptera: Heteroptera: Miridae). Thomas J. Henry. Pp. 1-10. $1.50.

18. Barstovian (middle Miocene) Land Mammals from the Carmel Church Quarry, Caroline Co.,Virginia. Alton C. Dooley, Jr. Pp. 1-17. $2.00.

19. Unusual Cambrian Thrombolites from the Boxley Blue Ridge Quarry, Bedford County, Virginia. Alton C. Dooley, Jr. Pp 1-12, figs. 1-8, 2009. $ 3.00.

20. Injuries in a Mysticete Skeleton from the Miocene of Virginia, With a Discussion of Buoyancy and the Primitive Feeding Mode in the Chaeomysticeti. Brian L. Beatty and Alton C. Dooley, Jr. Pp. 1-27.2009.

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