

PHYLOGENETIC DIVERSIFICATION WITHIN THE *SOREX CINEREUS* GROUP (SORICIDAE)

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Phylogenetic relationships among 8 members of the *Sorex cinereus* group (*S. camtschatica*, *S. cinereus*, *S. haydeni*, *S. jacksoni*, *S. portenkoi*, *S. preblei*, *S. pribilofensis*, and *S. ugyunak*) and *S. longirostris* were estimated using DNA sequence data from 2 mitochondrial genes, cytochrome *b* (1,140 base pairs) and nicotinamide adenine dinucleotide dehydrogenase 4 (582 base pairs). *S. hoyi*, *S. monticolus*, *S. palustris*, *S. tenellus*, *S. trowbridgii*, and *S. vagrans* also were included in our analyses. Phylogenetic analyses of the combined data recovered 2 major clades within the species group: a northern clade that includes the Beringian species (*S. camtschatica*, *S. jacksoni*, *S. portenkoi*, *S. pribilofensis*, and *S. ugyunak*), *S. haydeni*, and *S. preblei* and a southern clade that includes *S. cinereus* and *S. longirostris*. Mitochondrial DNA clades generally corresponded to previously identified morphological groups with 2 exceptions: inclusion of *S. longirostris* with *S. cinereus* in the southern clade and inclusion of *S. preblei* within the northern clade. With the exception of the 5 Beringian species, taxa were readily differentiated with strong bootstrap support in our topologies. We also noted phylogenetic concordance with the general ecological affiliations of each species; the northern clade generally includes xeric-affiliated species, whereas the southern clade includes species with mesic habitat affinities.

Key words: Beringia, biogeography, mitochondrial DNA, molecular systematics, shrew

The *Sorex cinereus* group comprises 11 species of long-tailed shrews with members distributed across North America and into northeastern Asia (Hutterer 1993; Fig. 1). This group includes the only Palearctic representatives of the subgenus *Otisorex* (*S. camtschatica*, *S. leucogaster*, and *S. portenkoi*), the most widespread species of *Sorex* in North America (*S. cinereus*), and several oceanic (e.g., *S. jacksoni*) or continental (e.g., *S. lyelli*) island forms (Hall 1981). These species occur in a wide variety of habitats including deciduous, boreal and temperate rain forests, prairie, shrub-steppe,

and tundra (French 1980; Tomasi and Hoffmann 1984; Youngman 1975).

Jackson (1928) originally proposed the *S. cinereus* group to include *S. cinereus*, *S. fontinalis*, *S. lyelli*, and *S. preblei*. Later studies added *S. milleri* (Findley 1955), the Beringian species (*S. jacksoni*, *S. pribilofensis*, and Russian forms—Hoffmann and Peterson 1967; Stroganov 1956), and *S. haydeni* (van Zyll de Jong 1980) to the group. Additional studies have presented different hypotheses concerning the taxonomy, biogeography, and evolutionary relationships of the group (summarized in Table 1). However, most studies were restricted in taxonomic and geographic scope, and a

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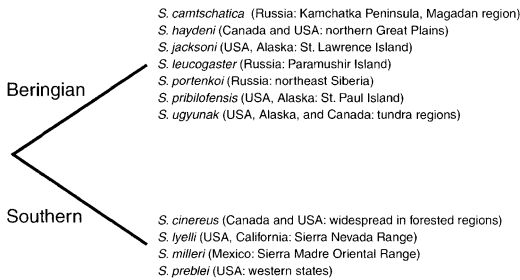


FIG. 1.—Simplified depiction of relationships within the *Sorex cinereus* group according to van Zyll de Jong (1991). Distribution information is also provided for each species. Relationships are based on a midpoint-rooted Wagner parsimony analysis of both qualitative and quantitative morphological characters. This basic topology, with the placement of *S. preblei* in the northern clade, was compared with relationships observed in the optimal maximum likelihood tree.

comprehensive evolutionary synthesis of the *S. cinereus* group was not available until the expansive morphological treatment of the group by van Zyll de Jong (1991). His cladistic examination of quantitative (13 cranial measurements) and qualitative (e.g., dental pigmentation and pelage coloration) characters revealed 2 major clades within the *S. cinereus* group: “Beringian” (*S. camtschatica*, *S. jacksoni*, *S. haydeni*, *S. leucogaster*, *S. portenkoi*, and *S. pribilofensis*) and “southern” (*S. lyelli*, *S. milleri*, *S. preblei*, and subspecies of *S. cinereus*). Taxa within the Beringian clade are generally characterized by shorter rostrums and tails and tricolored pelage (in some cases). Expanding on previous hypotheses that stressed the importance of Pleistocene glaciations (Hoffmann and Peterson 1967), van Zyll de Jong (1982, 1991) speculated that major diversification within the group coincided with the last major glacial expansion (Wisconsinan) and continued into the Holocene. van Zyll de Jong (1991) hypothesized that the Beringian clade diversified in Beringia and suggested that *S. haydeni* represented a southward migrant from this refugium to the northern Great Plains.

Biochemical and molecular evidences

have provided additional support for the close relationship of *S. cinereus*, *S. fontinalis*, *S. haydeni*, and *S. preblei* (including *S. longirostris*) within the group (Fumagalli et al. 1999; George 1988; Stewart and Baker 1994a, 1997; Stewart et al. 1993). However, these studies did not include the Beringian species, thus limiting insight into broader evolutionary and biogeographic questions for western North America and Asia. Mitochondrial DNA (mtDNA) introgression between *S. cinereus* and *S. haydeni* also has been reported that further complicates assessment of phylogenetic relationships within the group (Brunet et al. 2002; Stewart and Baker 1997).

Our goal was to provide an expanded molecular reexamination of the morphological phylogeny presented by van Zyll de Jong (1991). We estimated phylogenetic relationships on the basis of sequence variation from 2 mitochondrial genes, cytochrome *b* and nicotinamide adenine dinucleotide dehydrogenase 4, for 8 of 11 species within the *S. cinereus* group. We tested whether our mitochondrial DNA phylogeny is consistent with the existing morphological framework and examined biogeography of the *S. cinereus* group within the context of general ecological affiliations.

MATERIALS AND METHODS

We examined 46 individuals (Appendix I) representing 8 species of the *S. cinereus* group recognized by van Zyll de Jong (1991). Two specimens tentatively identified as *S. cinereus* from New Mexico (J. Findley, pers. comm.) were also included. In addition, *S. longirostris* was included in our analyses based on its close relationship with *S. cinereus* (George 1988). Given a lack of unambiguous sister taxa for the *S. cinereus* group (Fumagalli et al. 1999), we included 5 additional species from within the subgenus *Otisorex*: *S. hoyi*, *S. monticolus*, *S. palustris*, *S. tenellus*, and *S. vagrans*. *S. trowbridgii* has been shown to be a basal species within *Otisorex* (Fumagalli et al. 1999) and was the designated out-group for all phylogenetic analyses.

Genomic DNA was extracted from heart, kid-

TABLE 1.—Summary of some major studies that have examined members of the *Sorex cinereus* group. Data include studies of allozymes (A), DNA sequences (D), ecology and distribution (ED), karyotype (K), cranial morphology (MC), external morphology (ME), and penile morphology (MP).

Type of data	Study	Taxonomic conclusion
MC, ME	Jackson (1928)	<i>Sorex cinereus</i> group proposed
MC, ME, ED	Hoffmann and Peterson (1967)	Beringian species allied with <i>S. cinereus</i>
K	Meylan (1967)	Specific distinction of <i>S. cinereus</i>
ME, MP	Yudin (1969)	Specific distinction of <i>S. cinereus</i> , <i>S. beringianus</i> (= <i>S. leucogaster</i>), and <i>S. hydrodromus</i> (= <i>S. pribilofensis</i>)
ME, MC, ED	Okhotina (1977)	Palaearctic subspecies of <i>S. cinereus</i> (<i>S. c. camtschatica</i> , <i>S. c. leucogaster</i> , and <i>S. c. portenkoi</i>)
ME, MC	van Zyll de Jong (1980)	Specific distinction of <i>S. haydeni</i>
MC, ME, MP, K	van Zyll de Jong (1976, 1980, 1982, 1991), Volobouev and van Zyll de Jong (1994)	Beringian species and <i>S. haydeni</i> distinct from <i>S. cinereus</i>
K	Ivanitskaya and Kozlovsky (1985)	Specific status of <i>S. camtschatica</i> , <i>S. leucogaster</i> , and <i>S. ugyunak</i>
A	George (1988)	Monophyly of <i>S. cinereus</i> , <i>S. fontinalis</i> , <i>S. haydeni</i> , and <i>S. preblei</i> , including <i>S. longirostris</i>
MC	van Zyll de Jong and Kirkland (1989)	Specific distinction of <i>S. cinereus</i> and <i>S. haydeni</i>
A	Stewart et al. (1993)	Paraphyly (<i>S. cinereus</i> and <i>S. haydeni</i>)
D	Stewart and Baker (1994b, 1997), Brunet et al. (2002)	Paraphyly or mtDNA introgression (or both) of <i>S. haydeni</i> and <i>S. cinereus</i>
K, MP	Rausch and Rausch (1995)	<i>Sorex jacksoni</i> subsumed to <i>S. c. jacksoni</i>
ED	Dokuchaev (1997)	Multiple colonization of Asia by members of the <i>S. cinereus</i> group
D	Fumagalli et al. (1999)	Sister relationship of <i>S. cinereus</i> and <i>S. haydeni</i>

ney, or liver (frozen or alcohol preserved) using a modified salt-extraction protocol (Miller et al. 1988). Genomic DNA also was isolated from 5 skin samples of *S. jacksoni* using the Qiagen DNeasy kit (Qiagen, Inc., Chatsworth, California) and following the rodent-tail protocol. DNA amplification, cycle sequencing, and purification protocols followed methods outlined in Halan-ych et al. (1999) and Lessa and Cook (1998). The following primer pairs amplified the complete cytochrome-*b* gene: MVZ04–MVZ05, MVZ14–MVZ23 (Smith and Patton 1993), and SOREX16–SOREX 37 (Demboski et al. 1999). A partial region of the nicotinamide adenine dinucleotide dehydrogenase 4 gene was amplified and sequenced with the primer pair ND4–His (Arévalo et al. 1994). Double-stranded polymerase chain reaction products were sequenced in both directions and electrophoresed on an automated sequencer (Model 373, Applied Biosystems, Inc., Foster City, California). Sequences

were edited, compiled, and aligned unambiguously in Sequence Navigator, Version 1.01 (Applied Biosystems, Inc.).

Previous analyses of both the cytochrome-*b* and nicotinamide adenine dinucleotide dehydrogenase 4 sequences by Demboski (1999) recovered the same major clades separately and in combination; therefore, all results presented in this study are based on the combined data (1,722 base pairs). Analyses were conducted using parsimony and maximum-likelihood (ML) methods. Initially, PAUP* 4.0b2-8a (Swofford 2001) was used to conduct an equal-weight parsimony search (heuristic, stepwise addition, 10 random addition replicates, and tree-bisection–reconnection branch swapping) using all sequences ($n = 46$). Nodal support was estimated using bootstrap analysis with 500 replicates (Felsenstein 1985). Unequal base composition of sequences was tested using the chi-square test implemented in PAUP*.

Due to the computational constraints of ML, the data set was pruned to 32 unique haplotypes. A neighbor-joining topology based on p -distances served as the starting point for evaluating different models of sequence substitution. These included the Jukes–Cantor (Jukes and Cantor 1969), Kimura 2-parameter (Kimura 1980), Hasegawa–Kishino–Yano (Hasegawa et al. 1985), Tamura–Nei (Tamura and Nei 1993), and general time-reversible (Lanavé et al. 1984) models. Additional parameters estimated with each model included the proportion of invariable sites (Hasegawa et al. 1985), discrete approximation to the Γ -distribution (Yang 1994), and a mixed distribution model (Gu et al. 1995). Because all 20 models evaluated were hierarchically nested, likelihood-ratio tests were used to determine the most appropriate model from among those evaluated (Yang et al. 1995). A fully defined ML search (heuristic, stepwise addition, and tree-bisection–reconnection branch swapping) was then conducted using the chosen model (general time-reversible+I+ Γ). Model parameters were reestimated from the 1st tree recovered and then used in a subsequent ML search (e.g., Sullivan et al. 1997). This strategy continued until the likelihood score and parameter estimates stabilized. Nodal support for the ML tree was assessed using both ML (general time-reversible+I+ Γ ; 100 replicates) and parsimony (500 replicates) bootstrap analyses (Felsenstein 1985). We also tested the molecular clock hypothesis for our data using a likelihood-ratio test (Felsenstein 1988).

We used the Shimodaira–Hasegawa test (Shimodaira and Hasegawa 1999) as implemented in PAUP* (Swofford 2001) to compare van Zyll de Jong’s (1991) Wagner parsimony topology (Fig. 1) with the best ML tree recovered in our analysis. The Shimodaira–Hasegawa test allowed us to compare both an a priori–selected and a posteriori–selected relationships; the appropriate use of this test is discussed in Goldman et al. (2000). We were specifically interested in the placement of *S. preblei* within the southern clade, a finding reported by van Zyll de Jong (1991). We estimated the optimal ML tree constrained to fit relationships revealed by van Zyll de Jong’s (1991) midpoint-rooted topology [*preblei*, *cinereus*, *longirostris*, remaining taxa]. The likelihood score of the constrained tree (L_{VZDJ}) was then compared with the score of the best ML tree (L_{ML}) using the Shimodaira–

Hasegawa test. To reduce computational time associated with full likelihood optimizations for each of the 10,000 replicates, bootstrap data sets, we used resampling-estimated log-likelihood optimization. This approach bypasses reestimation of model parameters for each bootstrap replicate (Kishino et al. 1990).

RESULTS

The complete cytochrome-*b* gene had 1,140 base pairs. Partial nicotinamide adenine dinucleotide dehydrogenase 4 sequences (582 base pairs) corresponded to positions 10914–11495 in *Mus* (Bibb et al. 1981). GenBank accession numbers for these sequences are listed in Appendix I. Levels of variation between cytochrome *b* and nicotinamide adenine dinucleotide dehydrogenase 4 were similar. Within the complete data set ($n = 46$), 482 (28%) sites were observed to vary. Of these, 333 (19%) were parsimony informative. Variation was distributed among codon positions such that 1st- (18%) and 3rd-position (81%) sites accounted for 99% of the total variation. The null hypothesis of base stationarity across sequences, as determined in PAUP*, was not rejected ($\chi^2 = 12.60$, $d.f. = 135$, $P = 1.0$; ignoring correlation due to phylogenetic structure). Nuclear copies of mtDNA genes (pseudogenes) have been documented in some species of mammals (Smith et al. 1992); however, characteristics of pseudogenes such as a relaxation of compositional biases or sequences truncated with stop codons were not observed in our data.

The parsimony search conducted with all sequences ($n = 46$) recovered 165 equally parsimonious trees of 965 steps (consistency index [CI] = 0.595, retention index [RI] = 0.835, rescaled CI = 0.497). A strict consensus of these trees was similar to the 1st of the trees (Fig. 2) except for resolution of tip relationships within the *S. cinereus* group. Twenty models of sequence substitution were evaluated with the reduced data set ($n = 32$). The likelihood score obtained under the general time-reversible+I+ Γ model was the best overall ($-\ln L =$

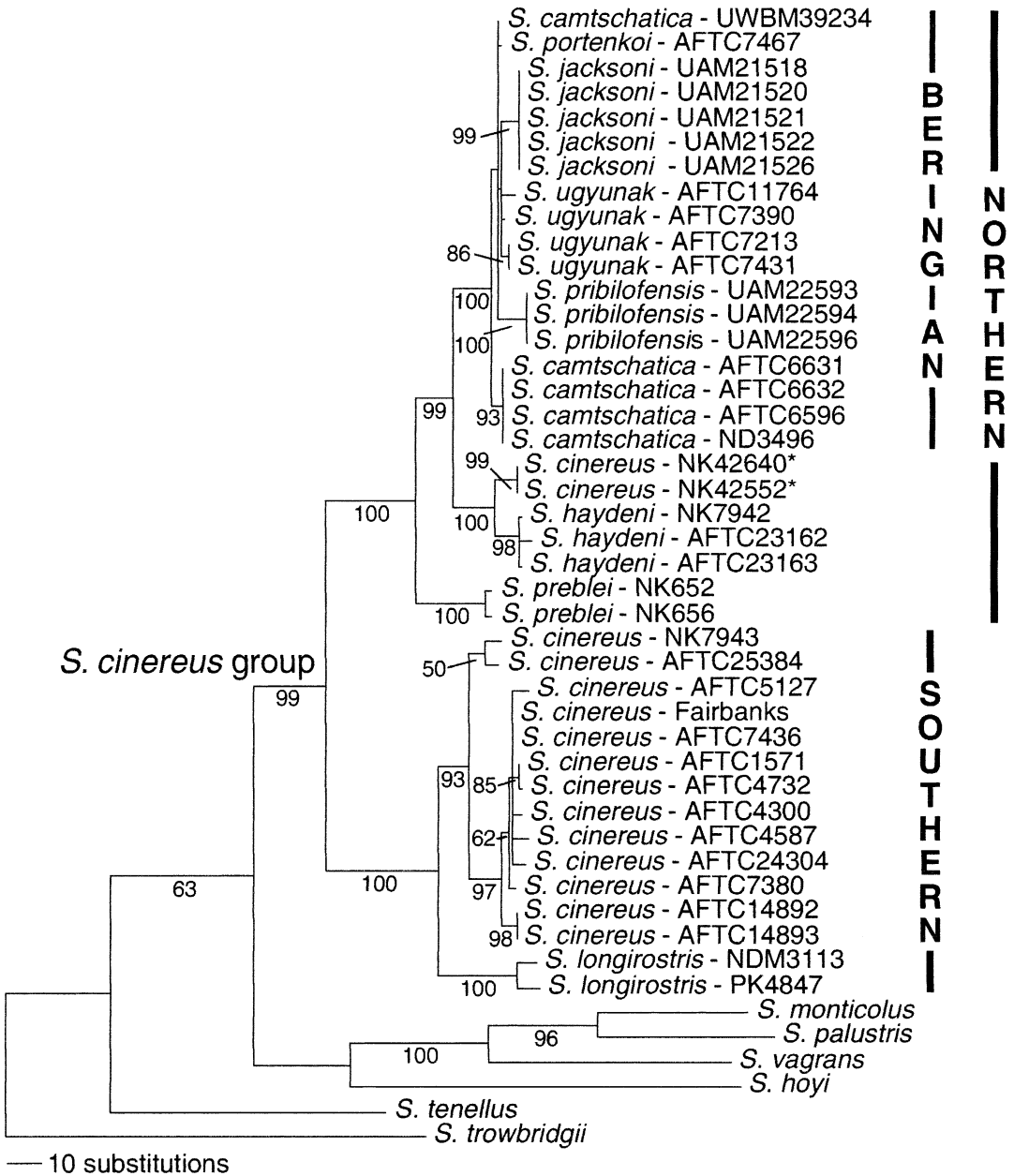


FIG. 2.—Equal-weight parsimony tree (heuristic search) recovered using the complete data set ($n = 46$). This is 1 of 165 equally parsimonious trees of 965 steps (consistency index [CI] = 0.595, retention index = 0.835, rescaled CI = 0.497). Tree was rooted with *Sorex trowbridgii*. Bootstrap values of $\geq 50\%$ (500 replicates) are shown below branches. The *S. cinereus* group, northern–southern dichotomy, and Beringian clades are depicted. Two tentatively identified specimens of *S. cinereus* from New Mexico are designated with an asterisk. Specimen numbers are given after specific names (Appendix I).

6,441.37) and when compared with the next simplest model, general time-reversible+ Γ , was significantly better ($-\ln L = 6,448.77$; $\chi^2 = 14.80$, $d.f. = 1$, $P < 0.0001$). The remaining models evaluated also were significantly worse. A subsequent search under the optimized general time-reversible+I+ Γ model ($r_{AC} = 2.77$, $r_{AG} = 20.88$, $r_{AT} = 2.99$, $r_{CG} = 0.24$, $r_{CT} = 45.28$, $\alpha = 2.42$, $p_{inv} = 0.64$) recovered 2 equally likely trees ($-\ln L = 6,428.82$). The trees differed only with regard to placement of the branch uniting the 3 *S. haydeni* sequences (AFTC23162, AFTC23163, and NK7942).

Congruence between parsimony and ML topologies included the recovery of a strongly supported clade ($\geq 92\%$ bootstrap support) corresponding to the *S. cinereus* group with the inclusion of *S. longirostris* (Figs. 2 and 3). The major bifurcation corresponds to southern (*S. cinereus*–*S. longirostris*) and northern (*S. prebleii*–*S. haydeni*–Beringian species) clades. Within the northern clade, 3 additional subclades were recovered. One of these consisted of the closely related Beringian species, *S. camtschatica*, *S. jacksoni*, *S. portenkoi*, *S. pribilofensis*, and *S. ugyunak* (Figs. 2 and 3). Sister to the Beringian species were *S. haydeni* and 2 samples tentatively identified as *S. cinereus* from northern New Mexico (J. Findley, pers. comm.). The basal subclade within the northern group consisted of the 2 samples of *S. prebleii* from Oregon. Within the southern clade, subclades composed of *S. cinereus* and *S. longirostris* were apparent.

Members of the “*S. monticolus*–*va-grans*” group were monophyletic in both analyses (Figs. 1 and 2), and a weakly supported relationship between *S. hoyi* and this group was observed. *S. tenellus* was basal to all taxa excluding *S. trowbridgii*, the designated out-group. An unambiguous sister taxon to the *S. cinereus* group was not apparent in our analyses. Results of the molecular clock tests with both ML topologies indicated that we must reject the assump-

tions of clocklike evolution in our data ($\chi^2 = 60.88$, $d.f. = 30$, $P < 0.005$).

Results of the Shimodaira–Hasegawa test led us to reject van Zyll de Jong’s (1991) hypothesis that *S. prebleii* is nested within the southern clade. The difference in likelihood scores between the best ML tree and an ML tree constrained to fit van Zyll de Jong’s hypothesis was $\delta = L_{ML} - L_{VZDJ} = -6,428.82 - (-6,591.52) = 162.70$. The result of the Shimodaira–Hasegawa test indicates that the inclusion of *S. prebleii* within the mtDNA southern clade can be rejected ($P < 0.0001$).

DISCUSSION

Phylogenetic and taxonomic considerations.—Taxa within the *S. cinereus* group were readily differentiated in both parsimony and ML topologies with the exception of the 5 Beringian species (Figs. 2 and 3). The northern–southern mtDNA dichotomy (about 6% uncorrected sequence divergence) that we observed within the *S. cinereus* group generally corresponds to the major morphological clades recognized by van Zyll de Jong (1991). One major difference is our placement of *S. prebleii* within the mtDNA northern clade, which contrasts with the morphological phylogeny (van Zyll de Jong 1991). van Zyll de Jong (1991) allied *S. prebleii* with the southern clade but noted that it was the most divergent taxon within this clade in the cladistic analysis. When we constrain *S. prebleii* to the mtDNA southern clade, to reflect the existing morphological framework, we are able to easily reject this relationship based on the results of the Shimodaira–Hasegawa test. In addition, our results indicate that *S. longirostris* is the sister taxon to *S. cinereus* in the southern clade.

At this stage, we suggest no major taxonomic revisions for the *S. cinereus* group other than the inclusion of *S. longirostris* in this species group. In addition, we note that there is a lack of resolution among the 5 Beringian species (Figs. 2 and 3). The maximum level of uncorrected sequence diver-

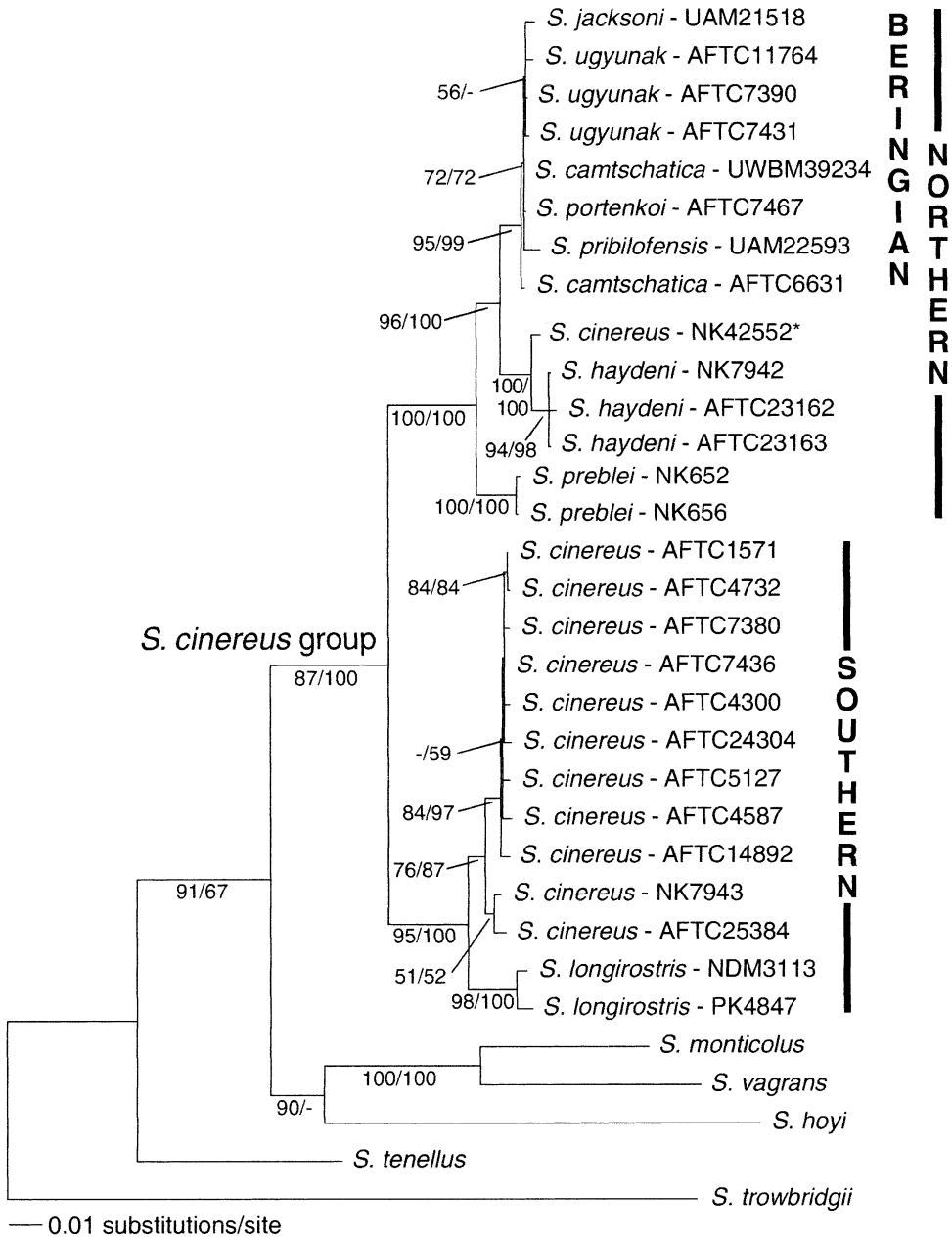


FIG. 3.—One of 2 maximum-likelihood trees recovered ($-\ln L = 6,428.82$) for the pruned data set ($n = 32$) using general time-reversible+I+ Γ model. The 2 trees differed only with regard to placement of the node uniting *Sorex haydeni* samples. Tree was rooted with *S. trowbridgii*. Maximum-likelihood (100 replicates) and parsimony (500 replicates) bootstrap values ($\geq 50\%$) are shown below the branches. The *S. cinereus* group, northern-southern dichotomy, and Beringian clades are depicted. A tentatively identified specimen of *S. cinereus* from New Mexico is designated with an asterisk. Specimen numbers are given after specific names (Appendix I).

gence within the Beringian clade (0.81%) is less than that in most interspecific comparisons previously reported in *Sorex* (Demboski and Cook 2001; Fumagalli et al. 1999) and in comparisons among different populations of *S. cinereus* examined in this study (1.34%). *S. jacksoni* and *S. pribilofensis* are characterized by slightly longer terminal branches (Fig. 2), and this is probably indicative of their isolation on St. Lawrence and St. Paul islands, respectively, with the flooding of the Bering Strait (about 10,000–16,000 years ago—Hopkins et al. 1982).

It might be tempting to suggest taxonomic changes within the Beringian clade based on our data; however, these taxa have an unsettled taxonomic history with many conflicting conclusions (Table 1). Rausch and Rausch (1995) concluded that *S. jacksoni* was a subspecies of *S. cinereus* (*S. c. jacksoni*) based on analysis of karyotypes ($2n = 66$, $FN = 70$) that were identical to *S. cinereus* from mainland Alaska. This designation requires recognition of polyphyletic relationships when compared with our mtDNA results, which indicate a nonsister relationship between *S. cinereus* and *S. jacksoni* combined with about 6% uncorrected sequence difference (Figs. 2 and 3). In contrast, *S. portenkoi*, which is indistinguishable from *S. jacksoni* and other Beringian species on our analysis, possesses a karyotype ($2n = 60$, $FN = 62$ —Ivanitskaya and Kozlovsky 1985) that is distinct from that of both *S. jacksoni* and *S. cinereus*. Known karyotypes for members of the *S. cinereus* group, viewed within the context of the mtDNA results, suggest that the distinct karyotypes of *S. portenkoi* and *S. haydeni* ($2n = 64$, $FN = 66$) may represent derived states. The difficulty of identifying an unambiguous sister taxon to the *S. cinereus* group and the absence of karyological information for some taxa prevent characterization of an ancestral karyotype for the group. Taxonomic revisions within the Beringian clade should await information from additional molecular characters, ex-

panded geographic sampling within taxa, and the inclusion of *S. leucogaster* ($2n = 66$, $FN = 70$ —Ivanitskaya and Kozlovsky 1985).

Specific status for *S. haydeni* has been supported by previous biochemical, chromosomal, molecular, and morphological studies (Fumagalli et al. 1999; George 1988; van Zyll de Jong 1980; Volobouev and van Zyll de Jong 1994). Our mtDNA data corroborate those earlier studies and suggest the possibility of previously undetected phylogenetic and geographic diversities within this species (Figs. 2 and 3). The tentative classification of 2 New Mexico specimens as *S. cinereus* (NK42552 and NK42640—J. Findley, pers. comm.) appears incorrect based on the close sister relationship of these individuals to *S. haydeni* from the northern Great Plains. These may be the 1st records of “*S. haydeni*” from New Mexico, but additional sampling of the southern Rockies is needed to expand on these preliminary results. In Alberta and Minnesota, bidirectional, mitochondrial introgression between *S. cinereus* and *S. haydeni* has been reported (Brunet et al. 2002; Stewart and Baker 1994b, 1997). These species are not sister taxa based on our analyses, do not appear to exhibit morphological intergradation (van Zyll de Jong 1980), and possess distinct karyotypes (Volobouev and van Zyll de Jong 1994). Analysis of nuclear loci would provide information regarding levels of gene flow at these hybrid zones and an insight into species boundaries in *Sorex*.

Although morphologically similar to *S. cinereus* (Klippel and Parmalee 1982), *S. longirostris* was considered by Findley (1955) to be part of a group allied with western taxa; *S. vagrans*, *S. ornatus*, and Mexican species. On the other hand, Junge and Hoffmann (1981) opted not to include *S. longirostris* within any proposed species groups in *Sorex*. Our analyses corroborate the allozyme study of George (1988) that identified a close relationship between *S. longirostris* and the *S. cinereus* group.

However, contrary to the allozyme data, our results place *S. longirostris* sister to *S. cinereus*, not basal to *S. cinereus*, *S. fontinalis* (= *S. c. fontinalis*), *S. haydeni*, and *S. preblei*. These differences may reflect sampling biases or differential sorting of mtDNA relative to nuclear genes in rapidly evolving taxa (Avice 1994).

Previous biochemical and molecular work has been inconclusive regarding identification of a sister taxon for the *S. cinereus* group. The most expansive treatments of *Sorex* have concluded that deeper nodes within the subgenus *Otisorrex* were the result of a rapid radiation that obscured these relationships (Fumagalli et al. 1999; George 1988). Stewart and Baker (1994a) suggested that *S. fumeus*, which was not sampled for this study, was sister to *S. cinereus* and *S. haydeni*; however, their sampling was limited to 7 species of *Sorex*. Our limited survey of other species of *Sorex* was also inconclusive. Inclusion of additional North American species of *Sorex* may shed light on this question; however, the polytomy that characterizes early diversification within *Otisorrex* may still obscure resolution at internal nodes (Fumagalli et al. 1999).

Implications for historical biogeography.—Phylogenetic diversity within *Sorex* is thought to be a result of repeated climatic and geological changes that led to large-scale diversification across the Northern Hemisphere (Findley 1955; George 1988; Reumer 1989). Late Pleistocene climatic fluctuations have been postulated as having an important role in this diversification (Findley 1955; George 1988; Reumer 1989; van Zyll de Jong 1991). Indeed, it is tempting to suggest that climatic oscillations during the late Pleistocene shaped many of the phylogenetic relationships within the *S. cinereus* group as has been previously postulated (George 1988; van Zyll de Jong 1991). Fossil estimates for the 1st appearance of members of the *S. cinereus* group are also within a Pleistocene time frame (Kurtén and Anderson 1980). Unfortunately, violation of the molecular clock as-

sumption for our data prohibits estimation of divergence dates within the *S. cinereus* group. However, with this caveat in mind, we speculate that initial divergence leading to the northern–southern dichotomy most likely predates the late Pleistocene. The beginning of extreme climatic oscillations, after a long period of relative stasis during the Pliocene, may have been the catalyst for phylogenetic diversification within the *S. cinereus* group.

Our results and those of other molecular studies suggest that multiple southern refugia were available during glacial advances in the Pleistocene (Conroy and Cook 2000a; Cook et al. 2001; Demboski and Cook 2001; Good and Sullivan 2001; Hayes and Harrison 1992). Within the northern clade, divergence between *S. preblei* and *S. haydeni*–Beringian clades could be the result of a general east–west segregation of ancestral populations. During a later climatic shift, ancestral populations leading to *S. haydeni* and members of the Beringian clade may have become isolated north and south of continental ice sheets. Given the moderate level of divergence (about 2%) between the Beringian clade and *S. haydeni*, the hypothesis that *S. haydeni* represents a late Pleistocene off-shoot of the Beringian clade that has recently colonized southward into the Great Plains through a Wisconsinan ice-free corridor is not supported (van Zyll de Jong 1991). The observation that samples of the tentatively identified “*S. cinereus*” from New Mexico (NK42552 and NK42640) are geographically separate, yet minimally differentiated (0.87%), from *S. haydeni* of the northern Great Plains suggests a recent (possibly late Pleistocene–Holocene timeframe) subdivision of a previously widespread ancestral population that was partially displaced to the southwestern United States. This level of divergence is similar to levels observed within the Beringian species. A similar biogeographic scenario leading to relictual isolates of the northern jumping mouse, *Zapus hudsonius*, in the southwestern United

States was previously observed (Hafner et al. 1981) and provides an insight into the possible assembly of continental biotas in this region (Riddle 1998).

Within the southern clade, divergence of *S. cinereus* and *S. longirostris* (about 2.6%) may represent a mid-Pleistocene north-south geographic segregation in eastern North America. During the late Pleistocene-early Holocene, western forms of *S. cinereus* may have tracked the movement of boreal forest northward into central Alaska and Canada after recession of continental ice sheets. The east-west dichotomy observed within *S. cinereus* (Fig. 2) appears to be relatively recent based on levels of sequence divergence (1.34%) but will require expanded sampling throughout the range of *S. cinereus* to be fully characterized.

Amphiberian diversification.—A lack of divergence among populations on opposite sides of the Bering Strait reflects the recent separation of Beringian forms by the late Pleistocene-early Holocene marine transgression of the Bering Land Bridge. As continental ice sheets contracted, *S. ugyunak* probably colonized eastward out of Beringia to occupy its current range across northern Canada and Alaska. Biogeographic hypotheses invoking multiple invasions of Asia have been posited based on ecological and morphological data (Dokuchaev 1997; Král and Ivanitskaya 1973; Okhotina 1977; Yudin 1973). These studies have suggested that *S. camtschatica*, *S. leucogaster*, and *S. portenkoi* are differentiated as a result of 2 or 3 unidirectional invasions of Asia. However, genetic divergence is minimal among taxa in the Beringian clade (Figs. 2 and 3), indicating that geographic, morphological, and ecological differentiation among these taxa is recent. Biogeographic scenarios that involve multiple amphiberian invasions are not supported by our data. Biochemical and molecular studies of other mammals (e.g., *Lemmus*, *Lepus*, and *Microtus*) also have reported minimal amphiberian differentiation, and these

findings are consistent with the most recent flooding of the Bering Strait (Conroy and Cook 2000b; Fedorov et al. 1999; Halanych et al. 1999; Lance and Cook 1998).

The role of Beringia as a filter between the North American and Asian continents has been an important paradigm (Simpson 1940). However, the Beringian refugium also has been suggested as a major region of diversification for high-latitude organisms (Hoffmann 1981, 1984; Hopkins et al. 1982). Other genetic studies provide support for this hypothesis (Lance and Cook 1998; Stepan et al. 1999) and still others provide evidence that various refugia were available across Beringia (Abbott et al. 2000; Holder et al. 2000). The distinct Beringian clade includes members that span the 2 continents, are endemic to the Bering Sea region, and apparently originated in this high-latitude refugium.

Ecological implications.—Current habitat affiliations, coupled with our mtDNA phylogeny, indicate a fundamental division of the *S. cinereus* group into mesic- and xeric-affiliated clades. These broad ecological classifications generally correspond to the major mtDNA dichotomy within the *S. cinereus* group (Fig. 4). A postulated late Pliocene or early Pleistocene time frame (about 2×10^6 years ago) for initial divergence between the northern and southern clades would coincide with the general cooling trend that preceded the glacial-interglacial cycles characterizing much of the Pleistocene. During cooler glacial periods, the presence of large continental ice sheets contributed to the development of heterogeneous landscapes found in refugia. For example, xeric habitats (e.g., tundra and shrub-steppe) were found in Beringia and the southern fringe of continental ice sheets, whereas more mesic habitats (e.g., boreal and deciduous forest) were found farther south in North America (Davis 1983). Our results suggest that isolation in distinct mesic and xeric refugia may explain the primary subdivision found in this group.

Members of the Beringian clade inhabit

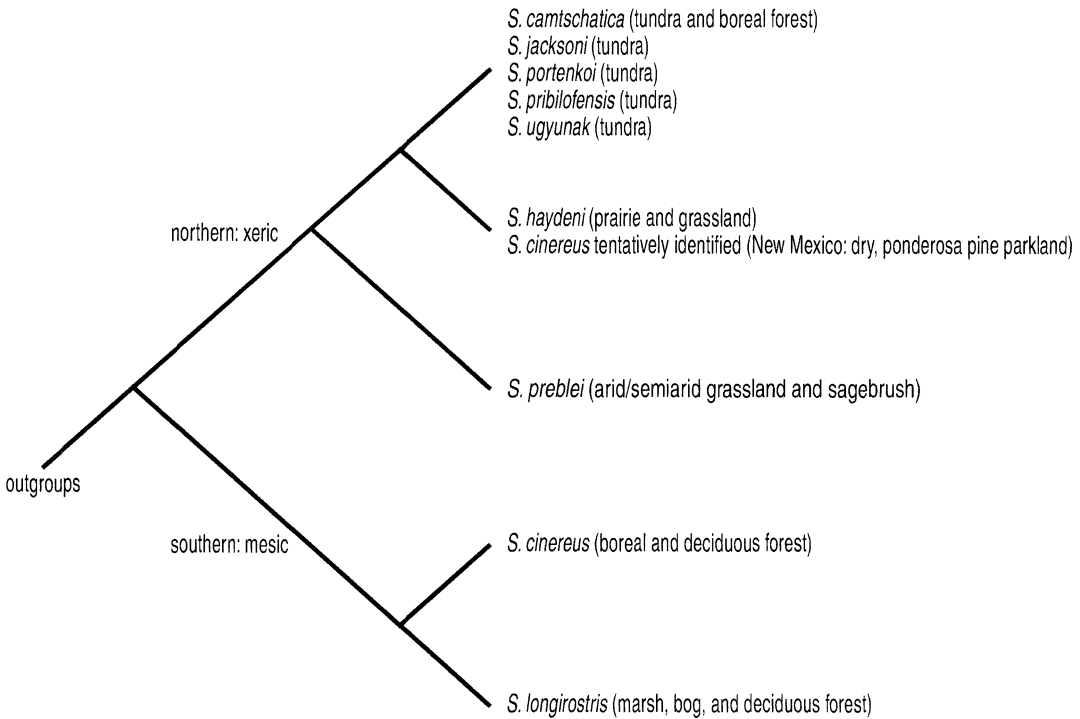


FIG. 4.—Simplified cladogram of phylogenetic relationships within the *S. cinereus* group with general habitat affiliations noted for each taxon. Branch lengths are not shown to scale.

the xeric conditions of the “arctic desert” that have characterized Beringia during the Pleistocene and into the Holocene (Elias et al. 1996; Hopkins et al. 1982). *S. haydeni* and *S. preblei* also are found in distinctly arid habitats such as areas of the Great Plains (van Zyll de Jong 1980) and shrub-steppe regions of the western United States (Cornely et al. 1992), respectively. The observation that tentatively identified *S. cinereus* from New Mexico may actually represent a western population of the prairie-affiliated *S. haydeni* is logical. These individuals were collected in xeric Ponderosa pine stands of the Jemez Mountains (Kirkland and Findley 1996). General ecological affiliation is also a better predictor of phylogeny than is morphology with regard to *S. preblei* (Fig. 4). This species is most commonly found in arid shrub-steppe habitats in the western United States (Cornely et al. 1992). Within the mesic southern clade, *S. longirostris* is associated with

marsh areas and deciduous forests (French 1980). *S. cinereus*, with the largest range of any North American shrew, is found across the continental boreal forest, with northern expansion into forest-tundra fringe and southern reaches into deciduous forest (Junge and Hoffmann 1981). There are exceptions to this general pattern of mesic and xeric diversification. For example, lack of divergence between the forest-affiliated *S. camtschatica* and tundra-affiliated shrews within the Beringian clade suggests that *S. camtschatica* has colonized boreal forest along the Sea of Okhotsk and the Kamchatka Peninsula since the late Pleistocene. MtDNA does not provide support for divergence of *S. camtschatica* in a forest refugium as suggested by Dokuchaev (1997) and van Zyll de Jong (1991). There also are other examples of mesic-xeric diversification within *Sorex* in North America. The known members of the unnamed subgenus identified by George (1988) comprise 2 xe-

ric-affiliated sister species (*S. arizonae* and *S. merriami*) and a 3rd, mesic-affiliated species, *S. trowbridgii*. Two closely related western United States species, *S. nanus* and *S. tenellus*, also represent xeric-affiliated taxa, but the phylogenetic relationships of these 2 species with other members of *Sorex* remain unclear (George 1988).

Our study provides a preliminary molecular framework of phylogenetic relationships within this widespread group. Expanded sampling of the *S. cinereus* group should include *S. leucogaster*, *S. lyelli*, and *S. milleri*, in conjunction with more extensive intraspecific sampling of eastern forms of *S. cinereus*.

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APPENDIX I

Specimens examined.—Specimens or sequences were obtained from the following institutions or individuals (with abbreviations): Alaska Frozen Tissue Collection or University of Alaska Museum (AFTC or UAM); University of Washington Burke Museum (UWBM); Museum of

Southwestern Biology (NK); Virginia Museum of Natural History (VMNH); P. Kennedy (PK); N. Dokuchaev (ND). GenBank numbers are indicated by AF and AY. Sample size in parentheses follows specific name. Localities are followed by specimen, cytochrome *b* GenBank, and nicotinamide adenine dinucleotide dehydrogenase 4 GenBank numbers in parentheses.

Sorex camtschatica (5).—RUSSIA, Magadan (AFTC6631, AY014917, AF250426), (AFTC6632, AY014918, AF250427), (AFTC6569, AY014919, AF250425), (ND3496, AY014920, AF250428); RUSSIA, Kamchatka Peninsula (UWBM39234, AY014916, AF250424).

Sorex cinereus (15).—ALASKA, Alaska Peninsula (AFTC1571, AY014946, AF250454); ALASKA, Chandalar Shelf (AFTC5127, AY014942, AF250450); ALASKA, Cleveland Peninsula (AFTC4732, AY014947, AF250455); ALASKA, Fairbanks (no number, AY014944, AF250452); ALASKA, Kanuti National Wildlife Refuge (AFTC24304, AY014951, AF250460); ALASKA, Misty Fiords (AFTC4300, AY014949, AF250458); ALASKA, Haines (AFTC4587, AY014950, AF250459); ALASKA, Seward Peninsula (AFTC7380, AY014943, AF250451), (AFTC7436, AY014945, AF250453); MONTANA, Carbon County (AFTC14892, AY014948, AF250456), (AFTC14893, AF238038, AF250457); MINNESOTA, Clay County (NK7943, AY014941, AF250449); Goodhue County (AFTC25384, AY014952, AF250461); NEW MEXICO, Sandoval County, tentative identification (NK42552, AY014935, AF250442), (NK42640, AY014934, AF250443).

Sorex haydeni (3).—MINNESOTA, Clay County (NK7942, AY014938, AF250446); SOUTH DAKOTA, Davison County (AFTC-

23162, AY014939, AF250447), (AFTC23163, AY014940, AF250448).

Sorex hoyi (1).—ALASKA, Hughes Quadrangle (AFTC7982, AF238040, AF250467).

Sorex jacksoni (5).—ALASKA, Saint Lawrence Island (UAM21518, AY014922, AF250430), (UAM21520, AY014923, AF250431), (UAM21521, AY014924, AF250432), (UAM21522, AY014925, AF250433), (UAM21526, AY014926, AF250434).

Sorex longirostris (2).—TENNESSEE, Perry Co. (PK4847, AY014954, AF250463); VIRGINIA, Mecklenburg County (NDM3113, AY014953, AF250462).

Sorex monticolus (1).—CANADA, Yukon Territory (AFTC10905, AF238014, AF250464).

Sorex palustris (1).—ALASKA, Petersburg Quadrangle (AFTC2806, AF238033, AF250466).

Sorex portenkoi (1).—RUSSIA, Provideniya (AFTC7467, AY014921, AF250429).

Sorex preblei (2).—OREGON, Harney County (NK652, AY014936, AF250444), (NK656, AY014937, AF250445).

Sorex pribilofensis (3).—ALASKA, St. Paul Island (UAM22593, AY014931, AF250440), (UAM22594, AY014932, AF250439), (UAM22596, AY014933, AF250441).

Sorex tenellus (1).—CALIFORNIA, Mono County (NK5904, AY014955, AF250468).

Sorex trowbridgii (1).—WASHINGTON, Kittitas County (AFTC14146, AY014956, AF250469).

Sorex ugyunak (4).—ALASKA, Barrow (AFTC11764, AY014927, AF250435); ALASKA, Galbraith Lake (AFTC7213, AY014929, AF250437); ALASKA, Seward Peninsula (AFTC7390, AY014928, AF250436), (AFTC7431, AY014930, AF250438).

Sorex vagrans (1).—MONTANA, Lake County (AFTC24263, AF154551, AF250465).