FURTHER PERSPECTIVES ON THE HAIDA GWAII GLACIAL REFUGIUM

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Byun et al. (1997) reported molecular evidence supporting a purported, long-term Pleistocene glacial refugium for black bears (*Ursus americanus*) located on or near the Haida Gwaii Archipelago (Queen Charlotte Islands), British Columbia. They examined sequence data from the mitochondrial cytochrome *b* gene and uncovered two lineages, which differed by an average of 3.6%. The lineages were characterized as "coastal" (Washington to Haida Gwaii) and "continental" (Pennsylvania to central Alaska). The geographically restricted coastal lineage led them to conclude that "black bear persisted in the Hecate refugium and during early stages of deglaciation recolonized Haida Gwaii, the coastal mainland, Vancouver Island, and eventually the Olympic Peninsula" (Byun et al. 1997, p. 1651). In support of this hypothesis, they cited several lines of evidence for a coastal refugium (summarized in Scudder and Gessler 1989) and other recent molecular studies (Soltis et al. 1991; O'Reilly et al. 1993; Talbot and Shields 1996).

Our commentary does not reject the possibility of a Haida Gwaii or Hecate refugium for *U. americanus*, but we argue that the conclusions reached by Byun et al. (1997) may be premature and an artifact of limited sampling of the coastal lineage. Wooding and Ward (1997) also reported two lineages (clade A = continental, clade B = coastal) of *U. americanus* based on sequence and restriction fragment length polymorphism analysis of the mitochondrial control region. When results from both studies are combined with earlier studies (Cronin et al. 1991; Paetkau and Strobeck 1996), widespread north-south distributions for the continental and coastal lineages of *U. americanus* are observed, including areas of potential secondary contact.

We present sequence variation from the mitochondrial cytochrome *b* gene for the American pine marten (*Martes americana*) and dusky shrew (*Sorex monticolus*) that may support an alternative biogeographic hypothesis. These mammals, like *U. americanus*, have extensive distributions (Fig. 1) associated with forested habitats in North America. Our analysis uncovered two distinctive lineages in both species that overlap the coastal and continental lineages of *U. americanus*. In light of phylogeographic work on other codistributed mammals (e.g., Cronin 1992; Hogan et al. 1993; Carr and Hicks 1997; Arbogast 1999), amphibians (Good 1989; Green et al. 1996), birds (Zink 1996), and plants (Soltis et al. 1997),

comparable large-scale phylogeographic patterns among western North America flora and fauna are apparent. The origin of these patterns is not necessarily dependent upon the Haida Gwaii hypothesis.

MATERIALS AND METHODS

Complete (1140 bp, *Martes*) and partial (809 bp, *Sorex*) DNA sequences were obtained from the mitochondrial cytochrome *b* gene. The European pine marten, *Martes martes*, and vagrant shrew, *Sorex vagrans*, were used as outgroups for marten and shrew phylogenies, respectively. *Sorex bairdi*, a presumed sister species of *S. monticolus* from Oregon (Carraway 1990), was also included in our analyses. Representative samples for this study were drawn from more extensive unpublished mitochondrial and nuclear datasets (*M. americana* n = 680; *S. monticolus* n = 75). The following tissue samples are deposited in the Alaska Frozen Tissue Collection, University of Alaska Museum (AF) and the Museum of Southwest Biology Frozen Biological Materials Collection (NK): *M. americana* (n = 11): Alaska, Kantishna River quadrant (AF53); Alaska, Juneau quadrant (AF14952); Alaska, Sumdum quadrant, Admiralty Island (AF14470); British Columbia, Francois Lake (AF16020); British Columbia, Graham Island (AF20601); British Columbia, Vancouver Island (AF24477); Montana, Beaverhead County (AF23183); Montana, Gallatin County (AF23171); Montana, Park County (AF23169); Oregon, Klamath County (AF15936); Wyoming, Carbon County (AF20614); *M. martes* (n = 1): Germany (AF17559); *S. monticolus* (n = 11): Alaska, Fairbanks quadrant (AF5929); Alaska, Petersburg quadrant, Mitkof Island (AF2498); Arizona, Cochise County (NK8001); British Columbia, Dease Lake (AF12777); British Columbia, Denman Island (AF24280); British Columbia, Lakesle Lake (AF12677); Colorado, Boulder County (NK1042); Montana, Lake County (AF24262); New Mexico, Cibola County (NK11015); Utah, Wasatch County (NK55578); Washington, Kittitas County (AF14460); *S. bairdi* (n = 1): Oregon, Tillamook County (AF18983); *S. vagrans* (n = 1): Montana, Lake County (AF24263).

To increase geographic sampling of marten, the level of divergence (p) between a partial sequence (402 bp) of *M. americana* from Maine (Hosoda et al. 1997) and the interior Alaska sequence (AF53) was determined. However, the Maine sample was not included in the dataset used to construct phylogenetic trees. Sequences have been submitted to

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(A) *Martes americana*   (B) *Sorex monticolus* and *S. bairdi*
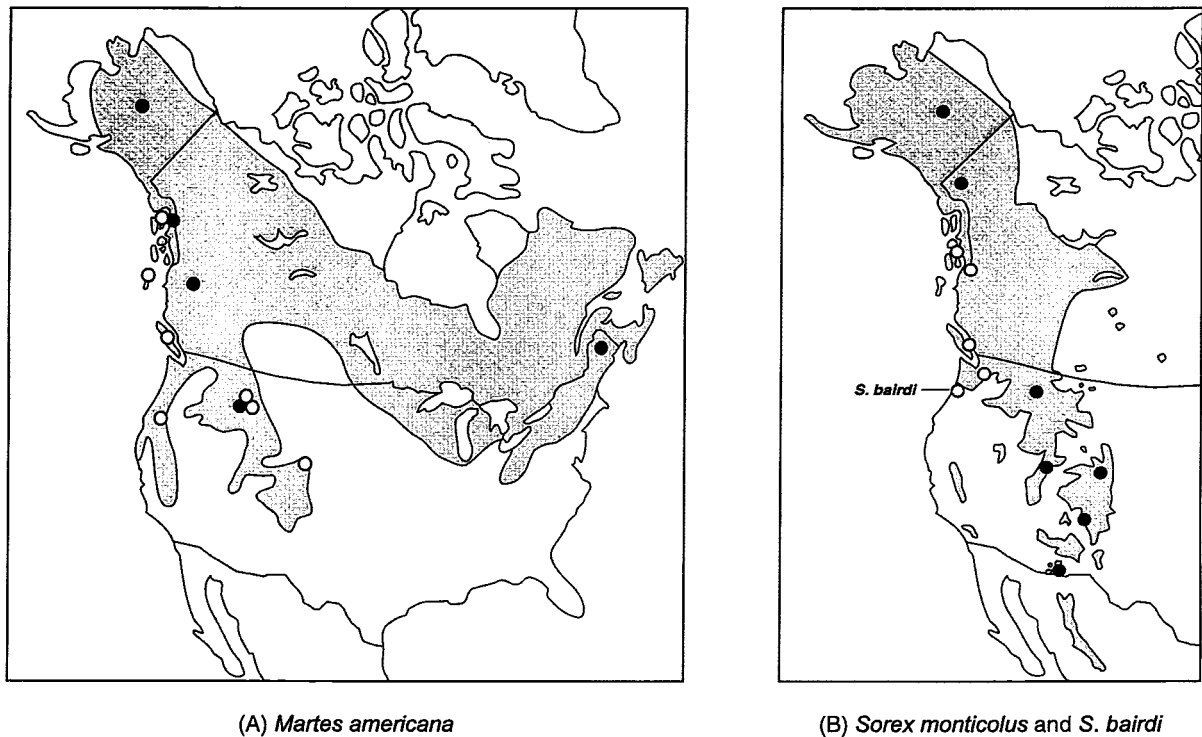
FIG. 1.   Distribution maps for depicting sampling locations and mtDNA lineages (○, coastal; ●, continental) discussed in the text. (A) *Martes americana*; (B) *Sorex monticolus* and *S. bairdi*.

the GenBank database with the following accession numbers: *Martes* (AF154964–AF154975) and *Sorex* (AF154539–AF154551).

Genomic DNA was extracted from frozen tissues, tissues in ethanol, or museum skins using a salt-extraction method modified from Miller et al. (1988). Segments of the cytochrome *b* gene were amplified by the polymerase chain reaction (PCR) and sequenced following methods outlined in Lessa and Cook (1998) and Halanych et al. (1999). The following primers were used for both PCR amplification and cycle sequencing of cytochrome *b*: MVZ04, MVZ05, MVZ14, MVZ16, MVZ23 (Smith and Patton 1993); MARTEN37 (5'-TATATATACCCCGAAACATGGA-3'), SOREX16 (5'-GCRAATAGGAAATATCAYTCDGGYTTAAT-3'), and SOREX37 (5'-TAYATRTTYYTAGATACATGAA-3'). PCR products were sequenced on an ABI model 373 automated sequencer in both directions. Sequences were translated and segments aligned with Sequence Navigator, Version 1.01 (ABI, Foster City, CA).

Phylogenetic trees were constructed under frameworks of maximum parsimony and distance (neighbor-joining, NJ) using PAUP*, version 4.0b2a (Swofford 1999). Both equal-weighted and weighted parsimony analyses were conducted using the branch-and-bound search option in PAUP*. Weighted searches employed transversion:transition ratios of 2:1, 5:1, and 10:1 based on other intraspecific analyses of the mammalian cytochrome *b* gene (Lessa and Cook 1998; Halanych et al. 1999). The Kimura two-parameter distance (Kimura 1980) was used for neighbor-joining searches also employing these transversion:transition ratios. Support of phylogenetic

relationships was assessed with 1000 bootstrap replicates for both equal-weighted and weighted analyses.

RESULTS

Base composition for cytochrome *b* was similar to values reported for other mammals (e.g., Irwin et al. 1991; Johns and Avise 1998), including carnivores (Talbot and Shields 1996) and insectivores (Fumagalli et al. 1996). We found a low overall percentage of guanine residues in both *Martes* (14.5%) and *Sorex* (13.6%), especially notable in the third position of codons.

Nonrandom signal (g_1 skewness statistic) in both datasets was detected from 1000 random trees, irrespective of weighting schemes ($P < 0.01$ using table 2, Hillis and Huelsenbeck 1992). The topological relationships in trees and levels of bootstrap support for various clades were comparable across phylogenetic methods and weighting schemes for the clades defined below. These relationships included the recovery of two major clades, continental and coastal, in both marten and dusky shrew datasets.

Levels of divergence (p) between the coastal and continental clades of *Martes* were 2.5–2.8%. Divergence values were no greater than 0.5% within coastal and continental clades of *Martes*; however, two subclades within the coastal clade were supported (Fig. 2A). The interior Alaska and Maine (Hosoda et al. 1997) sequences differed by less than 0.5%, therefore, the Maine sample was included in the continental clade (Fig. 1A).

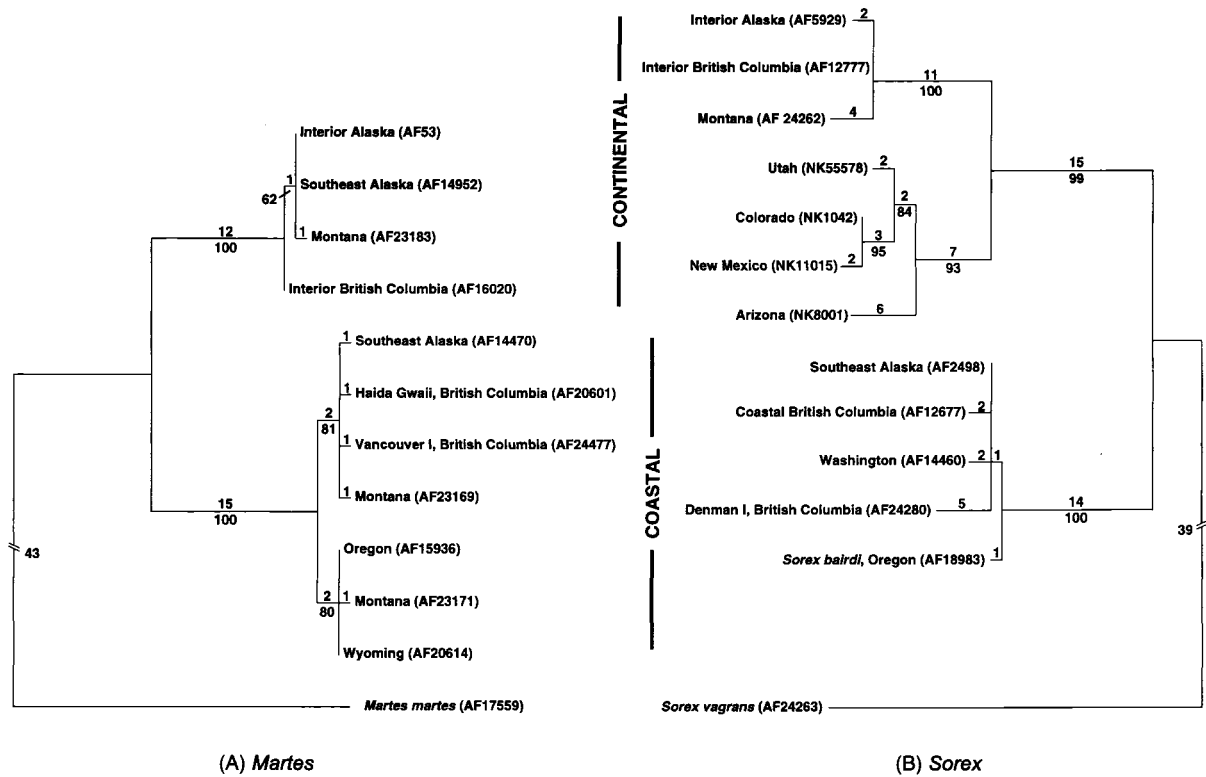Levels of divergence between the coastal and continental

FIG. 2. Maximum-parsimony trees for (A) *Martes* and (B) *Sorex*. One tree was recovered for *Martes*, and one of eight most parsimonius trees is shown for *Sorex*. Branch lengths (steps) are depicted above the branches and bootstrap values (> 50%) are depicted below the branches.

clades of *Sorex* were 4.7–5.7%. Divergence values within the two clades of *Sorex* were greater than within clades of *Martes*. Values within the coastal clade of *Sorex*, including *S. bairdi*, were between 0.3% and 0.9%. The continental clade consisted of two subclades (Fig. 2B), corresponding to northern and southern populations of *S. monticolus*, that differed by 2.7–3.5%. Within the southern subclade, values ranged from 0.3–1.6%, and within the northern subclade from 0.3–0.7%.

DISCUSSION

Insight into regional biogeographic history has benefited from studies of comparative phylogeography, where multiple codistributed taxa have been examined (Avise 1992; Riddle 1995; Moritz and Faith 1998; Taberlet et al. 1998). Preliminary investigation of 12 mammalian taxa from western North America (Table 1) suggests a common biogeographic history across coastal and continental lineages. However, some widespread North American taxa may not exhibit these coastal and continental phylogeographic patterns (e.g., Zink 1996). The geographic extent of two major mtDNA clades identified within both *M. americana* and *S. monticolus* (Fig. 1) was similar to coastal and continental lineages of black bears (Byun et al. 1997; Wooding and Ward 1997) and similar to mtDNA lineages identified in *Glaucomys sabrinus* (Demboski et al. 1998; Arbogast 1999), *Peromyscus* spp. (Hogan et al. 1993), *Odocoileus hemionus* (Cronin 1992), *Ursus arctos* (Talbot and Shields 1996), and other mammals (Table 1). These data suggest the possibility that one or more significant

phylogeographic events in western North America gave rise to these codistributed mtDNA lineages. The role of the Haida Gwaii refugium in the origin of these coastal lineages, however, remains unclear.

Sequence divergence in marten between coastal and continental lineages was similar to black bear lineages (2.7% vs. 3.6%; Byun et al. 1997). More extensive geographic sampling of marten indicated that the coastal lineage extended from Oregon, Montana, and Wyoming northward beyond the Haida Gwaii region to southeast Alaska. Within this coastal marten lineage (Fig. 2A), the two well-supported subclades may indicate the effects of isolation during late Pleistocene glacial advances. However, the location of potential refugia would be speculative without further sampling, given the association of a Montana marten (AF23169) with coastal samples. The continental lineage was more widespread than the coastal lineage, extending from interior Alaska southward through British Columbia to Montana and eastward to Maine (Fig. 1A), yet little intralineage differentiation was detected.

The coastal lineage of *S. monticolus* (including *S. bairdi*) extended along the Pacific Coast from Oregon to southeastern Alaska (Fig. 1B). Further geographic subdivision was found in the continental lineage and indicated northern and southern populations of *S. monticolus* (Fig. 2B). Uncorrected divergence values between the coastal and continental lineages of *S. monticolus* (4.7–5.7%) were about twice those for *M. americana* and *U. americanus*, but comparable to lineage divergence (4.2–7.2%) in the northern flying squirrel (Demboski

TABLE 1. Examples of mammal taxa with suggested coastal and continental lineages based on morphology and biochemical/molecular evidence.

Species	Kind of data	
	Morphological	Biochemical/molecular
Clethrionomys californicus/C. gapperi	Dalquest 1948	
Odocoileus hemionus		Cronin 1992
Glaucomys sabrinus	Dalquest 1948	Demboski et al. 1998; Arbogast 1999
Martes americana	Davis 1939	Carr and Hicks 1997; this paper
Mustela erminea	Dalquest 1948	
Peromyscus keeni/P. maniculatus		Hogan et al. 1993
Sorex monticolus	Findley 1955	this paper
Sorex palustris/S. bendirii	Dalquest 1948	
Tamiasciurus hudsonicus/T. douglasii	Dalquest 1948	
Ursus americanus		Cronin et al. 1991; Paetkau and Strobeck 1996; Byun et al. 1997; Wooding and Ward 1997
Ursus arctos		Talbot and Shields 1996; Heaton et al. 1996
Zapus trinotatus/Z. princeps	Dalquest 1948	

et al. 1998; Arbogast 1999). Discrepancies between these carnivore and insectivore/rodent divergence values may be due to several processes such as (1) different phylogeographic events (i.e., a deeper time frame for the divergence between coastal and continental lineages in *Sorex* and *Glaucomys*, when compared to *Martes* or *Ursus*); or (2) a higher mutation rate for smaller mammals, such as insectivores and rodents (Wu and Li 1985; Martin and Palumbi 1993; Lessa and Cook 1998).

Morphological differences between coastal and interior forms of some Washington mammals have been attributed to diversification during the Pleistocene (Dalquest 1948). Others have hypothesized as many as four major glacial refugia as sources for postglacial colonization of western North America (Rand 1954; Klein 1965; Hoffmann 1981; Scudder and Gessler 1989; Rogers et al. 1991; MacDonald and Cook 1996); however, the possibility of coastal refugia in Alaska and British Columbia is still debated (Scudder and Gessler 1989; Josenhans et al. 1995; Mann and Hamilton 1995). Paleobotanical and archaeological evidence indicates that ice-free areas were present in the now submerged Hecate Strait following glacial retreat toward the end of the Pleistocene (Josenhans et al. 1995). Such an ice-free corridor may have allowed both northward (Wooding and Ward 1997) and southward (Byun et al. 1997) colonization. However, the duration and extent of this coastal corridor is controversial (Mann and Hamilton 1995; Barrie and Conway 1999). Continuous mammalian occurrence in a coastal refugium throughout glacial cycles in the Pleistocene has yet to be demonstrated. In cases where fossils have been recovered along the coast, they have been dated to either periods before or after glacial maxima (Nagorsen et al. 1995; Heaton et al. 1996), suggesting the possibility of movement along the coast during interstadial periods (MacDonald and Cook 1996; Lance and Cook 1998).

The proposed Haida Gwaii refugium (Foster 1965; Scudder and Gessler 1989) has relied on evidence from distributional, morphological, and molecular analyses (Foster 1965; Klein 1965; Cowan 1989; Rogers et al. 1991; O'Reilly et al. 1993; Heaton et al. 1996; MacDonald and Cook 1996; Byun et al. 1997). Proposed survival of black bears in an ice-free refugium along the Alaska and British Columbia coast is based on similar indirect lines of evidence (Scudder and Gessler

1989) or limited geographic sampling (Byun et al. 1997). Biogeographic reconstruction is difficult because direct evidence for refugia (e.g., dated fossils) is usually lacking, but we caution that limited sampling of a widespread species can add an additional layer of uncertainty.

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