



DIVERSIFICATION AND GENE FLOW IN NASCENT LINEAGES OF ISLAND AND MAINLAND NORTH AMERICAN TREE SQUIRRELS (*TAMIASCIURUS*)

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Pleistocene climate cycles and glaciations had profound impacts on taxon diversification in the Boreal Forest Biome. Using population genetic analyses with multilocus data, we examined diversification, isolation, and hybridization in two sibling species of tree squirrels (*Tamiasciurus douglasii* and *Tamiasciurus hudsonicus*) with special attention to the geographically and genetically enigmatic population of *T. hudsonicus* on Vancouver Island, Canada. The two species differentiated only about 500,000 years ago, in the Late Pleistocene. The island population is phylogenetically nested within *T. hudsonicus* according to our nuclear analysis but within *T. douglasii* according to mitochondrial DNA. This conflict is more likely due to historical hybridization than to incomplete lineage sorting, and it appears that bidirectional gene flow occurred between the island population and both species on the mainland. This interpretation of our genetic analyses is consistent with our bioclimatic modeling, which demonstrates that both species were able to occupy this region throughout the Late Pleistocene. The divergence of the island population 40,000 years ago suggests that tree squirrels persisted in a refugium on Vancouver Island at the last glacial maximum, 20,000 years ago. Our observations demonstrate how Pleistocene climate change and habitat shifts have created incipient divergence in the presence of gene flow.

KEY WORDS: Boreal, gene flow, hybridization, phylogeography, Pleistocene, refugium, speciation, species-trees, *Tamiasciurus*.

Speciation times have been shorter for many organisms in the Boreal Forest Biome when compared with similar organisms at lower latitudes (Weir and Schluter 2007). The more rapid speciation times at higher latitudes are apparently due to Pleistocene climatic cycles that drove glaciation. Full glacial advances directly displaced boreal species from most of the northern regions of the continent. Furthermore the north–south orientation of major mountain chains in western North America promoted vicariance of displaced populations into eastern and western lineages (Arbogast and Kenagy 2001; Weir and Schluter 2004) and also provided ecological gradients that promoted ecological differenti-

ation between diverging lineages. These new ecological opportunities may have produced strong divergent selection between sister lineages, which ultimately led to accelerated speciation times (Weir and Schluter 2004).

Divergence in the presence of gene flow can be an important part of the speciation process in recently divergent lineages (Pinho and Hey 2010). This may be especially true in the Boreal Forest for two reasons. First, the short divergence times likely mean that many related lineages have not evolved complete reproduction isolation through hybrid infertility or inviability (Price and Bouvier 2002). Second, the retreat of the continental ice sheets left

a “tabula rasa” at high latitudes that was reoccupied by divergent lineages from separate glacial refugia. As a consequence, many pairs of closely related lineages have met in secondary contact in the mountainous western regions of the Boreal Forest (Swenson and Howard 2005).

The location of Pleistocene refugia for boreal organisms during the last glacial maximum (LGM) has received considerable investigation. The most conspicuous refugia were south of continental ice sheets (Graham et al. 1996; Dyke 2005), but growing evidence indicates refugia in eastern Beringia and in near-shore continental islands along the northern Pacific Coastal region (Fig. 1; Brubaker et al. 2005; Cook et al. 2006; Carrara et al. 2007). The persistence of insular populations was strongly affected by historic fluctuations in sea level, expansion and contraction of continental ice sheets, glacio-isostatic adjustment of land surface, and mountainous terrain (Fedje and Josenhans 2000; Clague and James 2002; Hetherington et al. 2004). The last major advance of the Cordilleran Ice Sheet westward out of the mountains of British Columbia reached the continental shelf 20,000 years ago and eliminated nearly all terrestrial biota (Booth et al. 2003). However, recent fossil and molecular evidence indicates that some insular species persisted in a glacial refugium along the northern Pacific Coastal region (Demboski et al. 1999; Heaton and Grady 2003; Cook et al. 2006; Topp and Winker 2008).

The role of Vancouver Island as a glacial refugium is not well understood. It is the largest (460-km long) and southernmost of the series of continental islands (Fig. 1) and is separated from the mainland by as little as 2 km. Despite its proximity and similarity of habitats with the nearby mainland region, Vancouver Island’s small-mammal fauna is surprisingly depauperate compared with other organisms. The island harbors only eight of the mainland’s 23 species of small nonvolant mammals, whereas it holds 96% of the mainland’s avifauna (Campbell 1990; Nagorsen 2005). This unusually low mammal diversity may be due to the coverage of most of the island’s terrestrial exposure by the Cordilleran Ice Sheet during the LGM (Clague and James 2002; Booth et al. 2003), followed by limited postglacial recolonization.

Tree squirrels of the genus *Tamiasciurus* present a notable opportunity to examine the role of a near-shore island in lineage divergence because of their enigmatic biogeographic configuration along the northern Pacific Coastal region and on Vancouver Island in particular. Red squirrels (*Tamiasciurus hudsonicus*) on Vancouver Island are separated from the trans-continental distribution of red squirrels by a 150-km-wide coastal region that is occupied by the congeneric Douglas squirrel, *Tamiasciurus douglasii* (Fig. 1). Several testable hypotheses could explain the timing of island colonization and factors that led to this odd biogeographic arrangement. First, recent molecular evidence from coniferous tree species that are ecologically important for these squirrels suggests that forests persisted somewhere on the island

throughout the LGM (Godbout et al. 2008). Thus, red squirrels may have persisted on the island as well and then recolonized mainland regions during deglaciation (Fig. 2A). Second, it is possible that red squirrels recolonized the island from the mainland following deglaciation, dispersing out from ice-free refugia located north or south of the continental ice (Fig. 2B, C). Finally, the taxonomic description of red squirrels on Vancouver Island may be in error, and the island squirrels are actually Douglas squirrels that recolonized from the mainland during deglaciation (Fig. 2D).

We have integrated phylogenetic and population genetic analyses to test several hypotheses regarding the origin and timing of colonization of *Tamiasciurus* on Vancouver Island. To provide a broad context for understanding the origin of the Vancouver Island population, we examined phylogenetic patterns of diversification within the genus *Tamiasciurus* as a whole by using multilocus nuclear sequence data with species-tree methods. We also used mitochondrial DNA (mtDNA) to infer phylogenetic relationships and then examined factors that may contribute to the topological discordance between the nuclear and mtDNA phylogenies. Next, we explored gene flow and divergence patterns between Vancouver Island and the two squirrel species on the mainland by implementing analyses using an isolation-with-migration model. Finally, we used ecological niche modeling to measure climatic niche similarity between the two species at different times throughout the Pleistocene to show the significance of abiotic niche variables in shaping the current and past biogeographic arrangement of these squirrels.

Methods

COLLECTION OF SAMPLES AND MOLECULAR DATA

We sampled 165 specimens of *T. hudsonicus* and *T. douglasii* from 59 localities in North America from several museum collections (Fig. 1 and Table S1). We used 92 frozen tissue samples from internal organs of specimens collected between 1984 and 2010 and 73 samples obtained in 2010 from snippets of foot pads or lips of museum study specimens that were originally collected between 1937 and 1989. We extracted whole genomic DNA from frozen tissue using the protocol of DNeasy Tissue Kit (Qiagen, Valencia, CA). For samples from museum study, skins genomic DNA was extracted following recommendations in Mullen and Hoekstra (2008) for removing potential polymerase chain reaction (PCR) inhibitors.

We selected 15 nuclear introns from a panel of 40 markers identified as useful for phylogenetic analyses of closely related mammal species (Igea et al. 2010). Novel primers for screened loci were designed in conserved flanking exon regions and were based on alignments of several rodent and lagomorph genomes from the

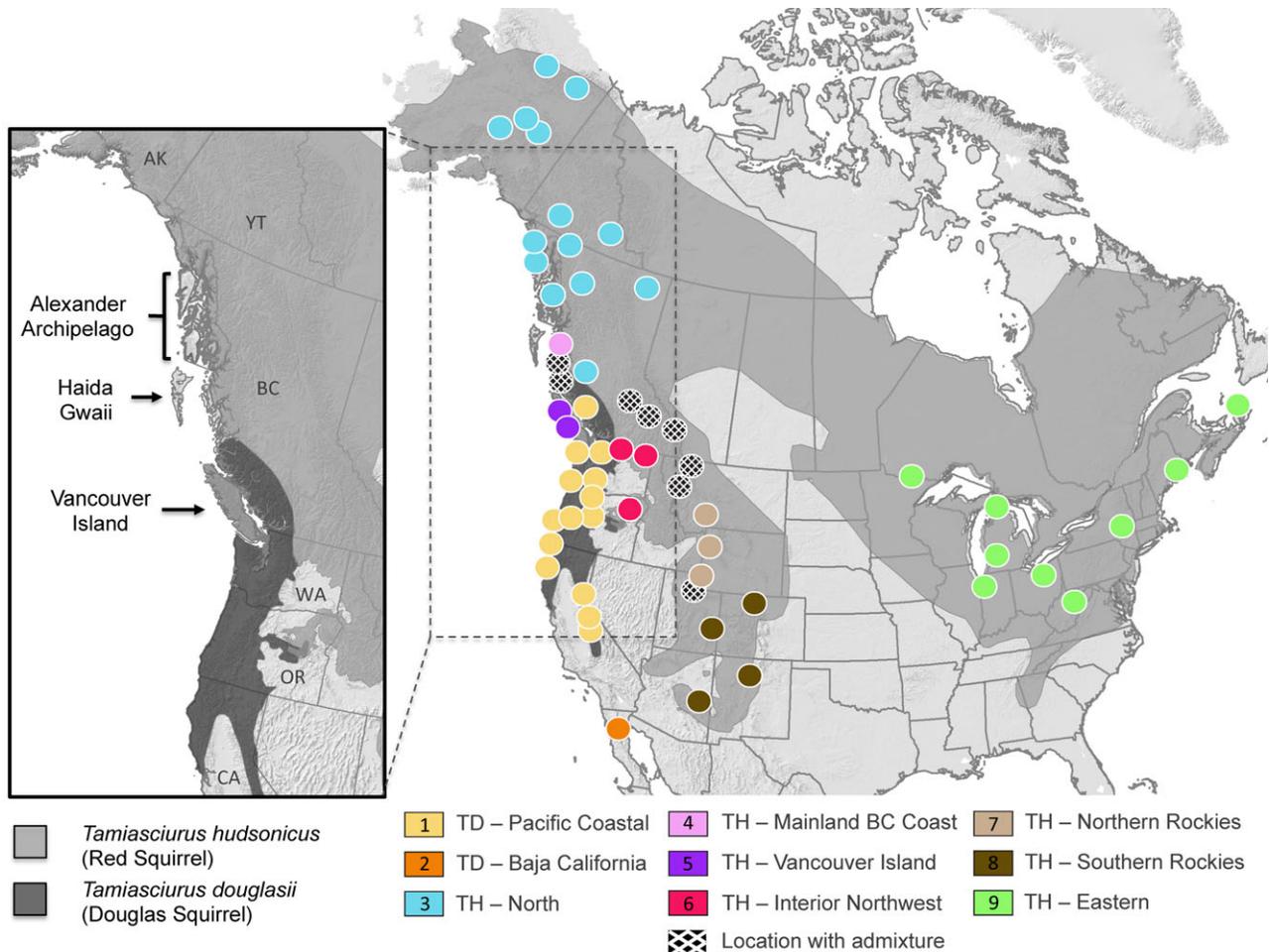


Figure 1. North American map depicting geographic ranges of pine squirrels (*Tamiasciurus* spp.), with enlargement panel showing detail of Vancouver Island and other west-coast island groups. Dark gray on map indicates *Tamiasciurus douglasii* and medium gray is *Tamiasciurus hudsonicus* (redrawn from Hall 1981; Nagorsen 2005). Colored circles mark 59 sampling localities, and associated color scheme indicates nine geographically discrete ancestral populations based on nuclear DNA using STRUCTURE. Numbered color codes and names of the nine populations are: (1) TD-Pacific Coastal: *T. douglasii*, Pacific coastal North America from southern British Columbia southward through California; (2) TD-Baja California: *T. douglasii* (*mearnsi*), San Pedro Martir mountains of Baja California; (3) TH-North: *T. hudsonicus* (TH), Alaska, Yukon Territory, and northern British Columbia; (4) TH-Mainland BC Coast: coastal mountains of mainland British Columbia; (5) TH-Vancouver Island: Vancouver Island; (6) TH-Interior Northwest: southern interior British Columbia southward through eastern Washington and Oregon; (7) TH-Northern Rockies: northern Rocky Mountains region from Montana southward to northern Utah; (8) TH-Southern Rockies: southern Rocky Mountains from northern Utah to Arizona; (9) TH-Eastern: eastern North America. Checkered circles represent localities with populations containing individuals with an admixture of genotypes from adjacent areas (Table S1).

ENSEMBL database (<http://www.ensembl.org>). Primers were designed using PRIMER3 (Rozen and Skaletsky 2000) in flanking exonic regions with degenerate bases at sites where reference genomes differed. After initial sequencing, we improved marker performance by designing new internal primers that were more specific for *Tamiasciurus* samples and that reduced the length of amplicons to less than 800 base pairs (bp). We also amplified a 312–328 bp sequence of the mtDNA control region using PCR with primers OSU5020L and OSU5021H (Wilson et al. 2005). Primer sequences, product lengths, optimal annealing temperatures, magnesium chloride volumes, and PCR conditions for both

nuclear and mtDNA markers are listed and described in Table S2. Capillary sequencing was performed on an ABI 3730 genetic analyzer (Applied Biosystems Inc.) with manual editing and alignments performed using SEQUENCHER 4.6 (Gene Codes Corp.). Nuclear intron sequences with multiple heterozygous sites were probabilistically phased into haplotypes using the PHASE (Stephens et al. 2001) model without recombination (-MS flag) in DnaSP version 4.9 (Rozas et al. 2003). We used an acceptance probability of greater than 0.7 for phase calls (Harrigan et al. 2008) and inferred haplotypes for 97% of the ambiguous nucleotide positions. Sequences were deposited in GenBank under accession

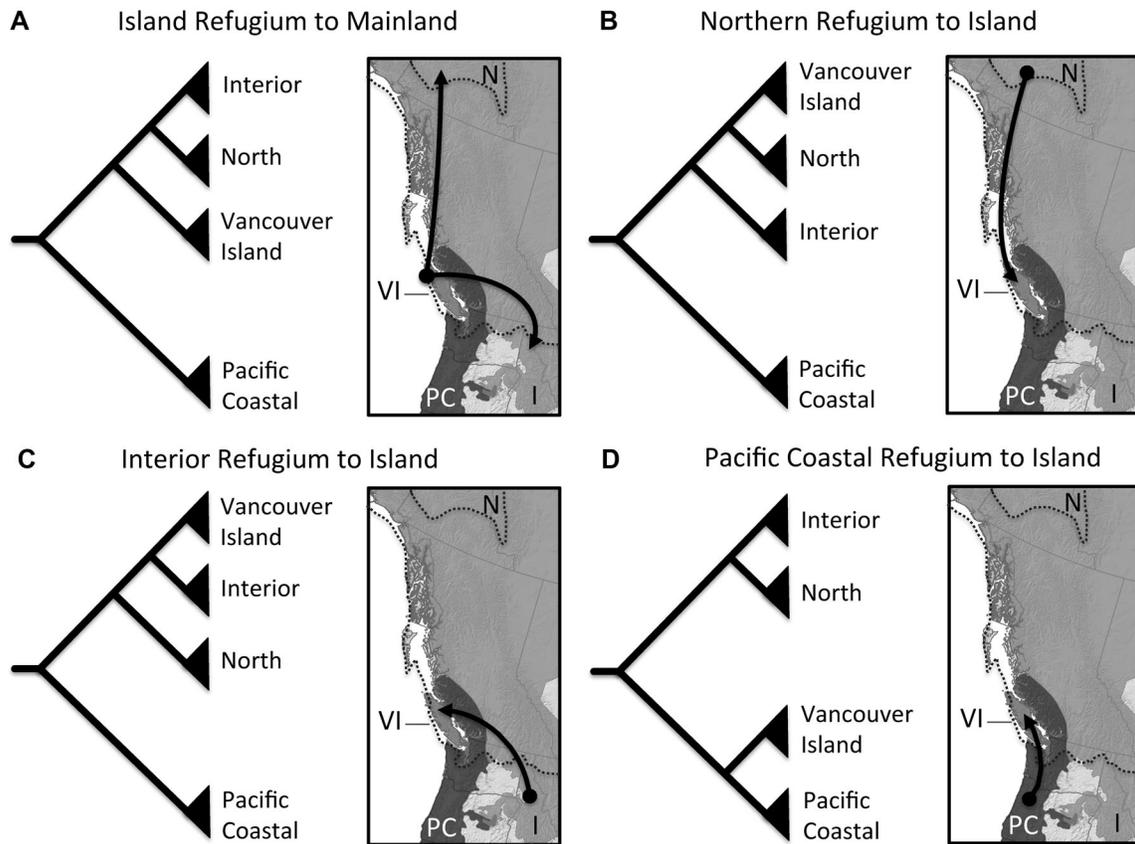


Figure 2. Phylogenetic hypotheses representing four alternative dispersal routes (arrows on maps) between Vancouver Island and mainland populations of pine squirrels (*Tamiasciurus hudsonicus* medium gray, *Tamiasciurus douglasii* dark gray). Dotted line represents approximate margin of the Cordilleran Ice Sheet during the LGM (Booth et al. 2003).

numbers KF882736–KF885216. We also acquired sequence data for 8 rodent and lagomorph taxa for the same 15 introns from the Ensembl Genome Browser (<http://www.ensembl.org/index.html>) to serve as outgroup taxa.

POPULATION STRUCTURE

To clearly identify the number of populations (major lineages) and their assignment, we performed population structure and assignment test analyses for each species (*T. hudsonicus* and *T. douglasii*) in STRUCTURE version 2.3.3 (Pritchard et al. 2000) with allelic data from the phased nuclear intron sequences. *Tamiasciurus mearnsi* samples were grouped with *T. douglasii* because of their close genetic similarity (Arbogast et al. 2001). STRUCTURE is a Bayesian method that uses a model-based Markov-chain Monte-Carlo (MCMC) approach to cluster individuals by minimizing Hardy–Weinberg disequilibrium and gametic phase disequilibrium between loci within groups. We set the model parameters in this analysis to “admixture” with correlated allele frequencies among populations and performed 8 replicate runs for each value of *K* with a burn-in of 1×10^4 followed by 1×10^5 repetitions. We performed these runs for values of *K* ranging 1–15

for *T. hudsonicus* samples and 1–5 for *T. douglasii* samples. We also defined sampling location for each individual to assist with the clustering by implementing the LOCPRIOR model (Hubisz et al. 2009). To select the most appropriate number of *K* from our data we plotted the average “log-likelihood of the STRUCTURE model” $\text{Ln}P(D)$ for each value of *K* and chose the value of *K* associated with a peak in the $\text{Ln}P(D)$ or if the $\text{Ln}P(D)$ plateaued we chose the smallest value of *K* at the beginning of the plateau (Pritchard et al. 2007).

NUCLEAR SPECIES-TREE INFERENCE

We used *BEAST (Heled and Drummond 2010) as implemented in BEAST version 1.7.3 (Drummond and Rambound 2007) to reconstruct a *Tamiasciurus* species trees from the 15-nuclear-intron dataset. *BEAST is a Bayesian MCMC method that coestimates multiple gene trees embedded in a shared species tree along with the effective population size and divergence times of both extant and ancestral lineages. For this method, the term “species” is not necessarily the same as the taxonomic rank and instead designates a group of individuals that likely have no recent history of breeding with individuals outside of that group (Heled

and Drummond 2010). Furthermore, the method requires that the assignment of individuals to species (major lineages) be given a priori. Therefore, we used the results from the STRUCTURE analysis to inform the *BEAST analysis that there were 9 major lineages within *Tamiasciurus* and to which lineage each specimen was assigned. *BEAST assumes incomplete lineage sorting (ILS) rather than hybridization or horizontal gene transfer as the main cause of phylogenetic discordance among gene trees. We attempted to minimize the possible effects of introgression on our species-tree estimation by selecting exemplar samples that were located in the core of each lineage's geographic distribution and samples that were not assigned with mixed ancestry as determined by STRUCTURE. This filtering process reduced the number of samples for each intron marker to a maximum of 64 specimens (128 phased sequences). Finally, *BEAST also assumes no recombination within loci. We checked for recombination breakpoints using the difference of sums of squares (DSS) method with a sliding window of 100 and a 10 bp step size in TOPALi version 2.5 (Milne et al. 2009). Only two of the 15 loci showed a recombination breakpoint. Therefore, we trimmed a combined 280 bp of 1110 bp from these two loci. Overall, we analyzed 7729 bp across 15 nuclear loci for each sample.

We used a two-step species-tree inference process to estimate intraspecific divergence times within each *Tamiasciurus* species to reduce issues associated with time-dependent mutation rate from having calibration points from very distantly related outgroup taxa (Ho et al. 2008). First, we used fossil calibration points from eight rodent and lagomorph outgroup taxa (rodent-lagomorph species tree; Fig. S1) outgroup taxa to estimate the interspecific divergence time between the sister *Tamiasciurus* species. For this analysis, we used five fossil calibrations with hard minimum and soft maximum bounds (with γ or exponential distributions) as priors (Table S3). We used soft maximum bounds to allow the molecular data to correct for conflicting fossil information (Yang and Rannala 2006). For the second step, we used the estimated 95% highest probability density (HPD) interval representing the split between *T. hudsonicus* and *T. douglasii* with a normal distribution (Ho 2007) as a secondary calibration prior for the root of the *Tamiasciurus*-only species tree (Table S3). Secondary calibrations can be useful when primary calibration points are not available (Blair Hedges and Kumar 2004).

The program BEAUTi (part of BEAST) was used to create the input XML file for *BEAST. For all species-tree analyses, we compared strict versus relaxed molecular clock models using likelihood ratio tests in PAUP* (Swofford 2003) and found a significant departure from a strict clock model for the rodent-lagomorph dataset, but no significant departure for the *Tamiasciurus* dataset. A strict-molecular clock is appropriate for datasets that are used to estimate intraspecific relationships and divergence times for a couple of reasons, including (1) the low levels of rate variation

between branches (Brown and Yang 2011), and (2) the overparameterization of the species-tree model when using a relaxed clock due to the low levels of phylogenetically informative sites in intraspecific datasets. The best-fitting model for this analysis according to AIC model selection in jModeltest 0.1.1 (Posada 2008) and that is available in BEAST was the Hasegawa–Kishino–Yano (HKY) sequence evolution model (Hasegawa et al. 1985) + Gamma model of nucleotide substitution. We also provided a starting species-tree for all analyses, which was assumed to follow a Yule speciation process. Analyses were run for 2 billion steps for the rodent-lagomorph species tree and 1.5 billion steps for the *Tamiasciurus* species tree, were logged at every 100,000 steps, and had the first 10% of the run discarded as burn-in. We assessed stationarity by examining trace plots and whether effective sample size (ESS) values exceeded >200 using TRACER 1.5 (Rambaut and Drummond 2007). Three independent runs were performed for each species-tree estimate to assure convergence in the MCMC. We also checked if the priors had undue influence on the posterior estimates by running the analysis for each species-tree with an empty alignment (generated by BEAUTi). Summary trees were generated with TreeAnnotator version 1.6.1, part of the BEAST package.

MITOCHONDRIAL GENE-TREE INFERENCE

We used mtDNA control region data from 73 *Tamiasciurus* specimens to infer a mtDNA gene tree in BEAST version 1.7.3. The 73 samples included 54 of the 64 samples that were used in the nuclear species-tree analysis plus 19 additional samples from Vancouver Island (Table S1). The best-fitting model for this analysis according to AIC model selection in jModeltest 0.1.1 (Posada 2008) and that is available in BEAST was the HKY + Gamma model of nucleotide substitution. The phylogenetic inference was analyzed for 100×10^6 generations (with trees sampled every 10,000 generations). The first 25% of sampled trees was discarded as burn-in after visual inspection using TRACER 1.5 revealed stationarity. To estimate divergence times, we used the 95% HPD interval from the fossil-calibrated species-tree analysis representing the split between *T. hudsonicus* and *T. douglasii* as a secondary calibration prior for the root of the mtDNA gene tree (Table S3).

INVESTIGATING CAUSES OF MITOCHONDRIAL-NUCLEAR PHYLOGENETIC DISCORDANCE

To distinguish whether hybridization or ILS explains discordant relationships between the mtDNA gene tree and nuclear species tree, we used a posterior predictive checking method (Joly et al. 2009) implemented in JML 1.0.1 (Joly 2012). We specifically examined the hypothesis that mitochondrial introgression explains the closer relationship between the Vancouver Island mtDNA

lineage with the Douglas squirrel mtDNA clade rather than the red squirrel clade. JML uses posterior predictive checking to test whether the observed minimum distance between sequences of two species is smaller than expected under a scenario that does not account for hybridization. Replicate datasets are simulated using the coalescent from the posterior distribution of species trees from *BEAST outputs with branch lengths and population sizes. JML samples the species trees to generate a gene tree from which DNA sequences are then simulated. A test quantity, the minimum distance between sequences of two species, is then calculated for all replicated datasets to generate a posterior predictive distribution. The observed distance from the empirical dataset is finally compared with the posterior predictive distribution to calculate the probability that the observed distance is caused by hybridization (Joly et al. 2009). If the observed distance is smaller than 95% of the simulated values, then we can reject ILS and conclude that hybridization explains the topological discordance.

We used the output file containing the posterior distribution of 10,000 nuclear species trees from our previous *BEAST analysis as the input file for the analysis in JML. We also included the mtDNA alignment as our reference sequence file. We used the mean clock rate from our previous mtDNA gene tree reconstruction in BEAST as a relative mutation rate for the JML control file.

ESTIMATING MIGRATION

We tested for the occurrence of postdivergence gene flow between the *T. hudsonicus* population on Vancouver Island and each species (*T. hudsonicus* and *T. douglasii*) on the mainland with IMA2 (Hey 2010) using a combined sequence dataset from 15 nuclear intron loci and the one mtDNA locus. IMA2 uses a coalescent-based model of isolation-with-migration under a Bayesian framework to coestimate the multilocus effective population sizes (present and ancestral), divergence times, and migration rates (Nielsen and Wakeley 2001; Hey and Nielsen 2004). IMA2 was recently modified to infer demographic parameters for multiple populations, that is, two or more at a time including ancestral populations, rather than just two populations at a time (Hey 2010). We defined populations based on three geographically discrete regions (Table S1): TD, 20 mainland *T. douglasii* phased haplotypes from within the contiguous range of the species from British Columbia to California, as well as from the isolated population in Baja California; TH, 20 mainland *T. hudsonicus* haplotypes from the Coast Mountains of British Columbia southward to the Southern Rocky Mountains and to eastern North America; VI, 20 *T. hudsonicus* haplotypes found only on Vancouver Island. We also used the HKY mutation model of nucleotide substitution for all loci. To obtain demographic parameter estimates from model parameter estimates, we provided a mutation rate/site/year/lineage of 6.7×10^{-5} for the mtDNA locus that

was calculated from our calibrated mtDNA gene tree analysis in BEAST. We also assumed an average generation time of 4 years (McAdam et al. 2007). Inheritance scalars were set at 1 for the nuclear loci and 0.25 for the mtDNA locus.

We performed several exploratory runs in IMA2 using “MCMC mode” to determine the values for most efficient swapping of MCMC chains, but that also allowed for appropriate prior settings for population parameters (i.e., t [divergence time], Θ [theta], and m [migration rate]). We then performed three independent runs with different starting seeds in “MCMC mode” to sample genealogies and obtain model parameter estimates. We determined that a sufficient burn-in period of sampled genealogies was achieved after burn-in trend plots had reached a plateau. We assessed convergence by checking for consistent parameter values from multiple long runs, monitoring ESS values, and trend lines. Next, we used sampled genealogies from the “MCMC mode” in a new analysis “Load Genealogies Mode” to statistically evaluate whether the fully parameterized migration model ranked as a better model than 15 simpler nested models with fewer migration scenarios using Akaike Information Criterion (AIC; table 1: Carstens et al. 2009). Due to enormity of possible nested models in a three population model, we only examined 16 nested models that represent migration scenarios between the *T. hudsonicus* island population and each of the mainland species (*T. hudsonicus* and *T. douglasii*), and not the migration scenarios between mainland species (Table 1). Moreover, we also did not analyze migration scenarios between the ancestral population of *T. hudsonicus* and *T. douglasii* because of the lack of convergence in parameter estimates for ancestral migration rates. We also calculated two related information theoretical statistics to provide objective measures of model support: Akaike weights (ω_i), which is the normalized relative likelihoods of the model, and the evidence ratio ($E_{\min/i} = \omega_{\min}/\omega_i$), which compares each model to the best model.

ECOLOGICAL NICHE MODELING

We gathered locality information from museum collections by searching VertNet (vertnet.org) and MaNIS (manisnet.org) for “*Tamiasciurus*” and downloaded available records. We removed records that: (1) had coordinate uncertainty greater than 10 km and (2) were sampled before 1950. To account for spatial autocorrelation in sampling, the occurrence dataset was reduced by identifying pairwise distances of 10 km or less, and removal of one of the points until all occurrences were at least 10 km apart. From an initial ~16,000 museum records, we selected 350 localities of *T. hudsonicus* and 171 localities of *T. douglasii* for our dataset.

Bioclim variables (Hijmans et al. 2005) were obtained through WorldClim (worldclim.org), representing current and past climate conditions. Current conditions were estimated as

Table 1. Ranked results of 16 forward-migration models within a three-population model in “Load Genealogies Mode” in IMA2. The 16 models include nested migration scenarios between the Vancouver Island *Tamiasciurus hudsonicus* population (VI) and each mainland *Tamiasciurus* species: mainland *Tamiasciurus douglasii* (TD) and mainland *T. hudsonicus* (TH). Joint parameter estimates for each forward migration direction are shown, including values that were fixed at 0 (in brackets) for each listed model.

No.	Model description	Forward migration VI to TD	Forward migration TD to VI	Forward migration VI to TH	Forward migration TH to VI	$\log(P)$	K	AIC	Δ_i	ω_i	$E_{\min/i}$
16	VI to/from TD; VI to/from TH	0.049	0.233	0.895	0.147	7.0	4	-5.2	0.0	0.7	1.0
15	VI to TD and TH; TD to VI	0.068	0.211	0.783	[0.000]	5.0	3	-3.6	1.6	0.3	2.3
13	VI to TD and TH; TH to VI	0.150	[0.000]	0.413	0.086	3.2	3	0.1	5.2	0.0	13.8
12	VI to TH; TD and TH to VI	[0.000]	0.130	0.708	0.087	-6.6	3	19.7	24.8	0.0	>100
10	VI to TD and TH	0.212	[0.000]	1.230	[0.000]	-9.0	2	22.2	27.3	0.0	>100
8	VI to TH; TD to VI	[0.000]	0.226	0.763	[0.000]	-19.5	2	43.1	48.3	0.0	>100
9	VI to TD; TH to VI	0.111	[0.000]	[0.000]	0.813	-22.0	2	48.2	53.3	0.0	>100
14	VI to TD; TD and TH to VI	0.111	0.000	[0.000]	0.813	-22.0	3	50.4	55.5	0.0	>100
6	VI to/from TH	[0.000]	[0.000]	1.052	0.234	-30.0	2	63.5	68.6	0.0	>100
5	VI to TD	0.085	[0.000]	[0.000]	[0.000]	-31.6	1	65.2	70.3	0.0	>100
11	VI to/from TD	0.085	0.000	[0.000]	[0.000]	-31.6	2	67.3	72.5	0.0	>100
3	VI to TH	[0.000]	[0.000]	0.447	[0.000]	-33.2	1	68.5	73.6	0.0	>100
4	TD to VI	[0.000]	[0.000]	[0.000]	[0.000]	-35.2	1	72.5	77.7	0.0	>100
7	TD and TH to VI	[0.000]	[0.000]	[0.000]	0.000	-35.2	2	74.7	79.8	0.0	>100
2	TH to VI	[0.000]	[0.000]	[0.000]	0.109	-49.2	1	100.5	106	0.0	>100
1	All migration equal zero	[0.000]	[0.000]	[0.000]	[0.000]	-111.1	0	222.2	227	0.0	>100

No. = model number, K = number of model parameters, Δ_i = difference in AIC, ω_i = Akaike weights, $E_{\min/i}$ = evidence ratio.

trends from 1950 to 2000 and were available at 2.5 arc-minute resolutions. Data for the LGM were available for two scenarios, The Community Climate System Model (CCSM) and The Model for Interdisciplinary Research on Climate (MIROC) reconstructions, and available at 2.5 arc-minutes, whereas the last interglacial (LIG) reconstruction was a representation of the CCSM scenario at 10 arc-minutes. For each era, we used 7 climate variables (annual mean temperature, mean diurnal temperature range, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation of wettest month, and precipitation of driest month) that have been shown to be relatively uncorrelated at large spatial scales (Jiménez-Valverde et al. 2009).

To estimate the potential distribution of tree squirrels, we used an ecological niche model (ENM) approach, where we built correlative models of occurrence and climate and projected these into geographic space. We implemented MAXENT 3.3.3k (Philips et al. 2006), which results in a probability distribution of occurrence from constraints, in this case the environmental values associated with localities. Tests of our ability to predict points in novel environments are described in Tables S4 and S5. Because model complexity can inhibit predictions for novel environmental space (Warren and Seifert 2011), we used the model selection feature of ENMTools (Warren et al. 2010) that determines β settings for Maxent. We generated models for each spatial unit using

the β with the lowest AIC score (Burnham and Anderson 2002) and projected these models onto the requisite partner background while converting the logistic output (Philips and Dudik 2008) to a presence/absence map using a minimum training presence threshold (Pearson et al. 2007). If the models were able to correctly predict points outside the spatial range, we were more confident in the ability to predict areas of potential occurrence in different eras. As such, we determined the positive predictive value, that is, the proportion of correctly predicted points, in the novel space.

To compare potential distributions at the different eras, we first repeated for each species the buffering of occurrence points, clipping of environmental data, splitting into training and testing sets, and model selection. We then generated MAXENT models under the requisite β value, but used 10-fold cross-validation of the training set, and determined the positive predictive value of the aggregated thresholded (by minimum training presence) maps. Again, if we expect to mimic the potential distribution of the species, the positive predictive value should be high. The models were projected onto the extent of North America to cover the geographic range of both species, both LGM reconstructions, and LIG reconstruction. Results were summarized as the sum of the cross-validation models and clipped based on the limiting novel climate (Elith et al. 2010) and estimates of the extent of the glacial extent at LGM (Aber et al. 1995; Manley and Kauffman 2002)

using a script and the R package raster (R Development Core Team 2012; Hijmans and van Etten 2012). Similarity measures (Warren et al. 2008) were calculated through ENMTools at 3 scales: current climate, LGM reconstructions (CCSM and MIROC), and LIG, at an extent focused on Vancouver Island and surrounding mainland region.

Results

POPULATION STRUCTURE OF *TAMIASCIURUS*

Our STRUCTURE analysis of 15 nuclear introns revealed that the inferred number of ancestral populations of *Tamiasciurus* in North America is nine, consisting of seven geographically segregated populations within *T. hudsonicus* ($\text{Ln}P(D) = -1812.65$) and two populations representing *T. douglasii* ($\text{Ln}P(D) = -4017.5$; Figs. 1, S2 and Table S1). We also found that about 7% of the samples possess genetic contributions from two or three different geographically proximate populations (Fig. 1, checkered circles and Table S1).

NUCLEAR SPECIES-TREE AND DIVERGENCE TIMES

Our fossil-calibrated species-tree placing *Tamiasciurus* within other rodent and lagomorph taxa using *BEAST for the 15 nuclear-intron loci supported a middle Miocene divergence of *Tamiasciurus* from its sister genus *Sciurus*, and perhaps more significantly a split between *T. douglasii* and *T. hudsonicus* that did not occur until the Pleistocene. The median age for the most recent common ancestor (MRCA) of *Tamiasciurus* and *Sciurus* was around 8.52 million years ago (Ma; 95% HPD interval [HPD]: 8.00–9.55 Ma; Fig. S1). The median age for the MRCA of *T. hudsonicus* and *T. douglasii* was estimated to be 0.457 Ma (HPD: 0.09–0.865 Ma).

Our species tree for the previously defined 9 lineages of *Tamiasciurus* using the same 15 nuclear loci in *BEAST with a secondary calibration point (based on our previous estimate of the 95% HPD interval for the split between *T. douglasii* and *T. hudsonicus*) indicated a Late Pleistocene diversification (Fig. 3). The median age for divergence between *T. douglasii* and *T. hudsonicus* was 422,900 years ago (HPD: 297,900–553,800 years ago). Within the seven lineages of *T. hudsonicus*, the TH-Eastern lineage split first from the remaining six lineages around 134,500 years ago. The second split was the TH-North lineage from remaining lineages located mostly in western North America about 117,100 years ago. The most recent divergence within this clade was that of the TH-Vancouver-Island lineage from the more northerly TH-Mainland-BC-Coast lineage, which occurred only around 41,100 years ago (HPD: 22,500–65,400 years ago).

MITOCHONDRIAL GENE TREE INFERENCE

Our mtDNA gene tree for 54 *Tamiasciurus* specimens reveals structure that is largely congruent with the nuclear species-tree, with the exception of the relationship between the Vancouver Island lineages and the mainland species. The first major split is between two major clades that generally correspond with the two species (Fig. 4): (1) a *T. douglasii* clade consisting of 8 specimens (described as *T. hudsonicus*) from Vancouver Island and 14 specimens representing the entire geographic range of *T. douglasii*; and (2) a large and geographically expansive continental clade of *T. hudsonicus* represented by 32 specimens that span from Alaska, throughout the Rocky Mountains, and across the continent to eastern North America. The Vancouver Island mtDNA lineages of *T. hudsonicus* (Fig. 4) are discordant with those of the nuclear species tree (Fig. 3) and are composed of two subclades that experienced two well-supported (>0.90 posterior probability) splits from the *T. douglasii* clade. One subclade shows a basal split from the *T. douglasii* clade around 132,000 years ago (HPD: 26,200–374,700 years ago) and the other subclade shows a more derived split from *T. douglasii* individuals located nearby in the mainland coast of British Columbia around 36,000 years ago (HPD: 38,000–117,600 years ago). In addition, our data showed no haplotype sharing between Vancouver Island and the mainland, suggesting an absence of modern gene flow of mtDNA haplotypes between these regions.

A well-supported split occurred within the *T. hudsonicus* clade around 135,900 years ago (HPD: 22,500–373,000 years ago) between northern lineages ranging from Alaska to the Northern Rockies and more southerly lineages ranging from central British Columbia to the southern Rockies and to eastern North America.

DISTINGUISHING HYBRIDIZATION FROM ILS

Posterior predictive checking of topological discordance between gene trees and species trees in JML demonstrated that ILS is not the best explanation for the data, thus sustaining the interpretation that hybridization has occurred. The analysis specifically demonstrated introgression of *T. douglasii* mtDNA haplotypes into the Vancouver Island population. The observed pairwise genetic distance between Vancouver Island mtDNA lineages and *T. douglasii* lineages was smaller than 99% of the simulated minimum distance values (P -value < 0.001).

DEMOGRAPHIC ESTIMATES FROM ISOLATION-WITH-MIGRATION MODEL

Our L-Mode analysis in IMA2 of historical gene flow using the 15 nuclear introns and the mtDNA loci revealed that the best supported model was bidirectional gene flow (Model 16) between the Vancouver Island *T. hudsonicus* population and both species on the mainland following their divergence (Table 1). Demographic estimates of rate of gene flow from the marginal distribution in

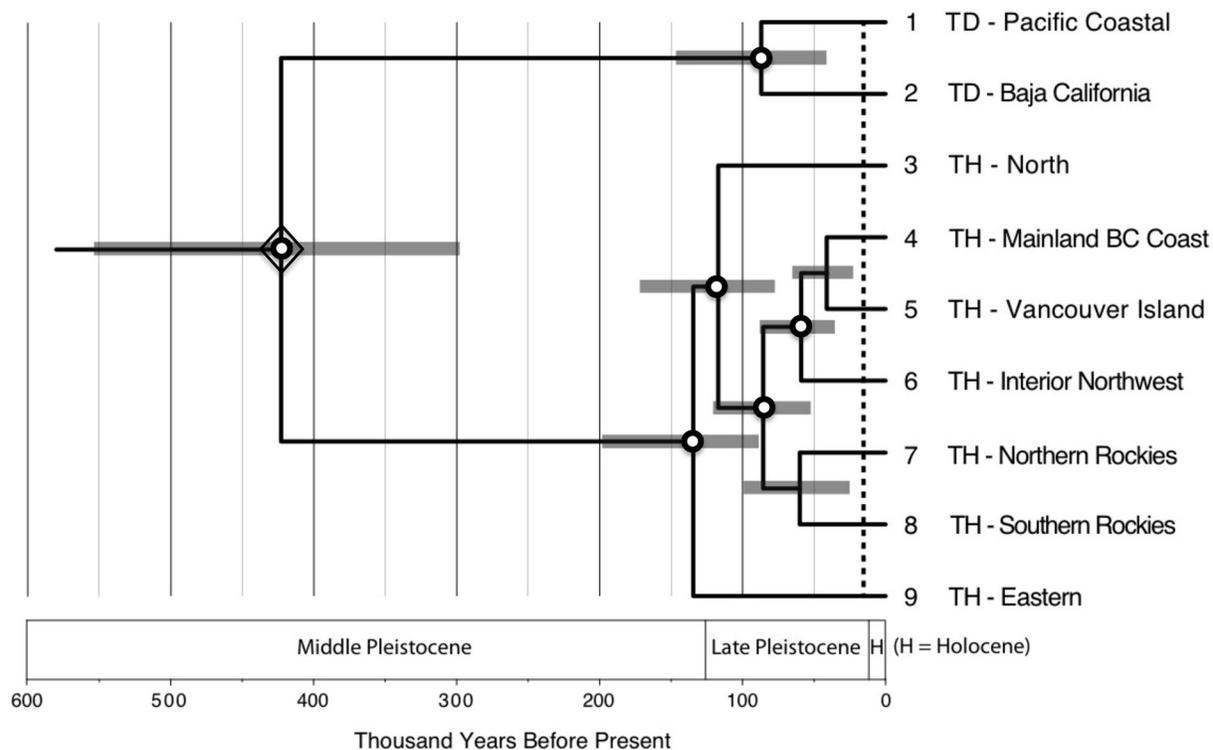


Figure 3. Time-calibrated species tree for the nine *Tamiasciurus* lineages based on 15 nuclear introns and computation with *BEAST. Nodes with white circles represent strong posterior probability (pp) support ($pp \geq 0.95$). Gray-shaded bars represent 95% highest probability density of estimated node age. Diamond indicates secondary calibration (Table S3). Dotted vertical line represents approximate age of last glacial maximum (~18,000 years ago; Blaise et al. 1990).

M-Mode was greater from the Vancouver Island population into the mainland population of *T. hudsonicus* (0.0955 migration rate per year per gene copy) than in the opposite direction (0.0087). The gene flow rate was lower from Vancouver Island to the mainland population of *T. douglasii* (0.0039) than in the opposite direction (0.0055).

Estimates of effective population sizes from M-Mode were highest for the mainland *T. hudsonicus* population ($N_1 = 119,592$; HPD: 80,968–198,257), next highest for the mainland *T. douglasii* population ($N_0 = 37,738$; HPD: 26,753–52,266), and smallest for the *T. hudsonicus* population on Vancouver Island ($N_0 = 8,681$; HPD: 4,075–15,060). The estimate of divergence between the *T. hudsonicus* population on Vancouver Island and the mainland *T. hudsonicus* population was 130,400 years ago (HPD: 62,365–1,173,597). The divergence estimate between *T. hudsonicus* and *T. douglasii* was 1,037,528 years ago (HPD: 629,320–1,423,057).

ECOLOGICAL NICHE MODELING

Our application of bioclimatic envelope modeling estimated broad geographic overlap in the potentially suitable ecological spaces of *T. hudsonicus* and *T. douglasii* over the past 130,000 years, that is, from the time of the LIG, through the LGM, and con-

tinuing through the present (Figs. 5, S2 and Table S6). Variable contributions to models were different between species, where maximum temperature of the warmest month was important for *T. douglasii* (25% contribution) and minimum temperature of the coldest month was important for *T. hudsonicus* (32.6% contribution; Table S7). However, changes in accuracy were associated most with precipitation of the wettest month for *T. douglasii* and annual mean temperature for *T. hudsonicus*. Both species were predicted to have occupied habitat in suitable climatic space across much of western North America. Importantly, the environment of Vancouver Island and surrounding mainland appears to have been suitable for both species throughout the entire Late Pleistocene.

Discussion

RAPID PLEISTOCENE SPECIATION OF BOREAL FOREST TAXA

The speciation history within the genus *Tamiasciurus* has unfolded surprisingly rapidly and recently over the past 300,000 to 600,000 years. This timing is more recent than the previously estimated speciation time of 2 million years for temperate-zone mammals in North America (Avice et al. 1998). Our finding, combined with the lack of fossil records of other *Tamiasciurus*

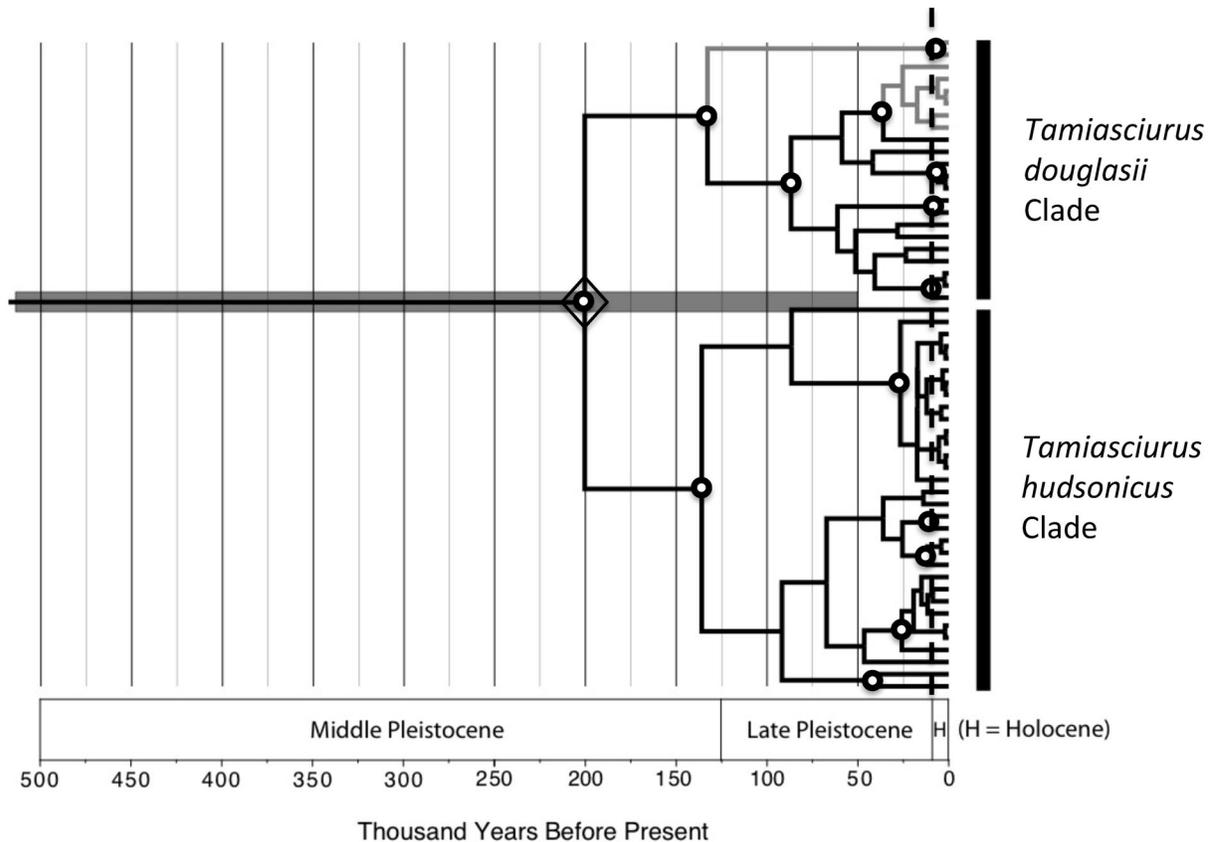


Figure 4. Time-calibrated Bayesian gene tree of 54 unique *Tamiasciurus* mtDNA haplotypes using BEAST. Analysis revealed strong support for two major clades corresponding to the two species, as indicated by vertical bars. All Vancouver Island lineages are shown in light gray shade and are nested within the *Tamiasciurus douglasii* clade. In contrast, all Vancouver Island samples were nested within a group of *Tamiasciurus hudsonicus* lineages in the nuclear intron species-tree analysis. White circles represent nodes with $pp \geq 0.95$. Gray-shaded bars represent 95% highest probability density (HPD) of estimated node age. Diamond indicates secondary calibration (Table S3). Dashed vertical line represents approximate age of last glacial maximum ($\sim 18,000$ years ago; Blaise et al 1990).

species, suggests that the genus *Tamiasciurus* experienced a long period of stasis before it diverged into the two contemporary species in the Late Pleistocene. Speciation was also suspended until the Late Pleistocene in several boreal birds and trees (Weir and Schluter 2004; Levsen et al. 2012), which may have resulted from displacement of the Boreal Forest Biome to the northern margin of the continent during the drier and warmer conditions of the Miocene and Pliocene (Axelrod et al. 1991; Thompson and Fleming 1996; Williams et al. 2008). Pleistocene speciation in boreal taxa in general was likely induced by repeated glaciation cycles that prompted extensive contraction and expansion of species ranges (Booth et al. 2003). This historic movement is reflected by the presence of the modern Boreal Forest Biome within areas that were covered by continental ice sheets during the LGM and the distribution of extralimital fossils of many of these boreal taxa, including *Tamiasciurus*, in areas of the southern United States that no longer support the boreal biome (Graham et al. 1996; Steele 1998, 1999).

POPULATION GENETICS AND BIOGEOGRAPHY OF ISLAND COLONIZATION

Our nuclear and mitochondrial data show conflicting patterns for the origin of Vancouver Island's squirrels, suggesting that both species colonized the island and subsequently hybridized. Based on the nuclear genome, Vancouver Island squirrels have the closest affinity to interior-montane populations of *T. hudsonicus*, rather than the geographically most proximate mainland *T. douglasii*. The split between the island and interior-montane lineages of *T. hudsonicus* occurred only about 41,000 years ago, and this is therefore the most recently derived divergence within all of *T. hudsonicus*. In contrast, the mtDNA phylogeny shows that all Vancouver Island lineages are more closely related to the *T. douglasii* clade than the *T. hudsonicus* clade. Moreover, these data indicate two distinct colonization events involving mtDNA lineages on Vancouver Island, the first representing a basal mtDNA lineage that split from the mainland *T. douglasii* clade around 132,000 years ago and the second, more derived split of only about 36,000

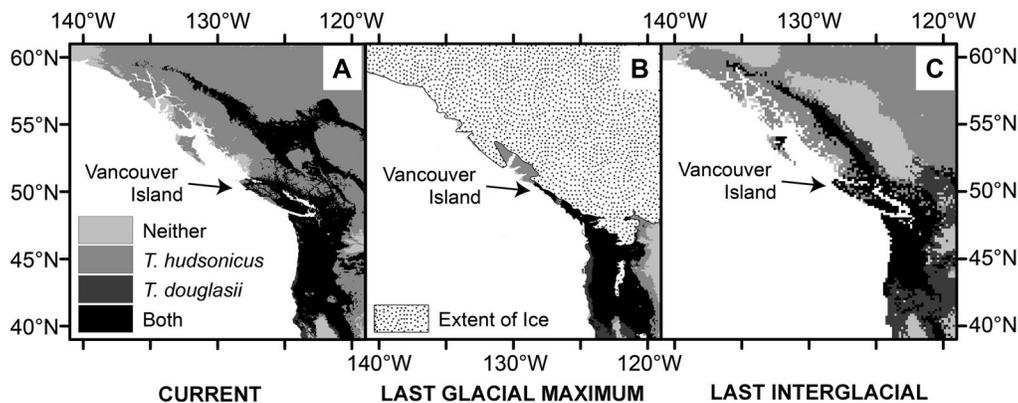


Figure 5. Bioclimatic envelope models for *Tamiasciurus hudsonicus* and *Tamiasciurus douglasii* under three historical climate scenarios, based on MAXENT: (A) Current, contemporary conditions; (B) last glacial maximum (18,000 years before present), and (C) last interglacial (114,000–131,000 years before present). Potentially suitable climatic space, defined by a species-specific minimum presence threshold, is indicated by shading: neither species (lightest gray), *T. hudsonicus* only (gray), *T. douglasii* only (darkest gray), both species overlapping (black).

years ago. Our ENMs show that island colonization by both mainland species throughout the last 130,000 years should have been feasible, because the physical environment would have allowed either species to inhabit mainland areas near the island. Nonetheless, we are still left with the question of why the historical *T. douglasii* mtDNA haplotypes on Vancouver Island completely displaced *T. hudsonicus* mtDNA haplotypes. Male-dominated colonization by *T. hudsonicus* may not be the best explanation for this mysterious pattern of the maternally inherited mtDNA, because *Tamiasciurus* do not show sex-biased dispersal (Berteaux and Boutin 2000). Furthermore, interspecific differences in male competitive ability to procure mates (Pearson and Rowher 2000) may also not be likely given that the nearby hybrid zone between the two species on the mainland exhibits a pattern of bidirectional introgression (Chavez et al. 2011).

Topological discordance between gene trees and species trees is commonplace (Edwards et al. 2007; Knowles 2009), especially for shallow species trees (Degnan and Rosenberg 2009), as we have shown in *Tamiasciurus*. Introgressive hybridization and ILS are two of the main processes that produce such discordances (Maddison 1997). However, these two processes produce different expectations for the distribution of coalescent times of gene genealogies within a species tree (Holder et al. 2001), particularly because in cases of ILS an incongruent sequence will always coalesce with a sequence from another species prior to the speciation event, whereas in cases of gene flow, coalescence can occur before or after the speciation event (Joly et al. 2009). We demonstrated, using two different analytical approaches (isolation-with-migration [IM] model and phylogenetic posterior predictive checking) that hybridization between the two mainland species on the island, rather than ILS, best explains the discordance between the mtDNA gene tree and the nuclear

species tree. Furthermore, the IM model showed that bidirectional gene flow has occurred between the Vancouver Island population and both mainland *Tamiasciurus* species. We suspect that gene flow is no longer occurring between the island population and either mainland species because mtDNA haplotypes are not shared. However, an alternative explanation for the origin of the hybrid island population is that the colonizing squirrels already possessed admixed ancestry; this appears reasonable given that the contemporary hybrid zone on the mainland occurs less than 200 km from Vancouver Island (Chavez et al. 2011).

Our observed pattern of complex island colonization by two mainland squirrel species provides a new example of the importance of hybridization in the evolutionary history of northern-latitude taxa. This is apparent from the observation that hybrid zones for many closely related lineages of plants and animals cluster in the mountainous region of northwestern North America (Stone et al. 2002; Bennuah et al. 2004; Peacock et al. 2007; Brelsford and Irwin 2009; Jaramillo-Correa et al. 2009; Krosby and Rohwer 2009; Runck et al. 2009; Gugger et al. 2010). Furthermore, the pattern of historical hybridization in our data is similar to the historical hybridization between polar bears (*Ursus maritimus*) and brown bears (*Ursus arctos*) in this region (Cahill et al. 2013). All modern brown bears from Alaska's Admiralty, Baranof, and Chichagof (ABC) Islands are surprisingly fixed with mtDNA haplotype that are very closely related to polar bears (Talbot and Shields 1996). A more recent genome-wide analysis shows that continuing postglacial dispersal of male brown bears onto the ABC Islands and historical hybridization with the now-extinct polar bears gradually converted this hybrid bear population into an almost genetically pure brown bear population that still possesses the maternally inherited mtDNA and X-chromosome region that traces back to polar bears (Cahill et al. 2013). We

suspect that a similar process of genomic erosion may have led to the current pattern on Vancouver Island, where island squirrels are phenotypically and genotypically more similar to *T. hudsonicus* except for their mtDNA, which is more closely related to *T. douglasii*.

The contemporary enigmatic biogeographic arrangement of *T. hudsonicus* on Vancouver Island together with intervening *T. douglasii* on the nearby mainland coast (Fig. 1) likely reflects different periods of occupancy by each species on the coastal mainland next to Vancouver Island due to historic turnover of forest types following deglaciation. Our ENMs for *T. hudsonicus* and *T. douglasii* show support for broad overlap of their abiotic niches, which suggests that spatial segregation between the two species was not due to gross climatic differences, but rather to other factors such as differential competitive abilities in different forest types (Smith 1968, 1970, 1981). *Tamiasciurus hudsonicus* typically inhabits drier forests with cold winters, and *T. douglasii* inhabits mesic forests with milder winters (Steele 1998, 1999). Paleocological records from Vancouver Island and nearby mainland areas show dramatic changes in forest composition during the Holocene that are attributed to regional climate changes (Whitlock 1992; Brown and Hebda 2003; Dyke 2005). The warmer climate since the LGM led to the development of a more mesic forest in this region, whereas cold-coniferous species shifted further north, east, or upslope. On the mainland, the two squirrel species apparently responded to these changes by following the shifts in their associated forests. The fossil record shows that *Tamiasciurus*, like many other boreal mammals, showed strong niche conservatism (Martínez-Meyer et al. 2004) and moved northward with major northward re-establishment of boreal forests following the LGM (Paleobiology Database, <http://www.paleodb.org>).

THE ROLE OF REFUGIA IN LINEAGE DIVERSIFICATION

Our age estimates of the Vancouver Island population suggest that tree squirrels remained present in a refugium on Vancouver Island at the LGM (~20,000 years ago). This result is counter to an important hypothesis that the Cordilleran Ice Sheet completely covered the entire island 20,000 years ago (Blaise et al. 1990; Porter and Swanson 1998; Dallimore et al. 2008; Mackie et al. 2011) and that all terrestrial organisms were eliminated from the island (Clague and James 2002; Ward et al. 2003). However, proponents of a coastal refugium hypothesis on Vancouver Island claim that both unglaciated high-elevation sites (nunataks) and some sites that are now submerged by elevated sea levels could have supported terrestrial biota (Haggarty and Hebda 1997). Our findings provide compelling evidence that a refugium on Vancouver Island must have supported coniferous forest, because tree squirrels are strongly associated with this type of habitat. In addition, this finding has important relevance to the location of

ice-free coastal regions during the LGM and how these ice-free regions may have provided a coastal-migration corridor for many organisms, including early human populations (Dixon 2013).

Considerable evidence for the “North Pacific Coastal Refugium,” based on fossil and molecular data, has shown that Haida Gwaii and the Alexander Archipelago were a major coastal refugium during the LGM (Warner et al. 1982; Hansen and Engstrom 1996; Byun et al. 1999; Conroy and Cook 2000; Fleming and Cook 2002; Janzen et al. 2002; Heaton and Grady 2003; Lucid and Cook 2004; Burg et al. 2005, 2006; Pruett and Winker 2005; Cook et al. 2006; Godbout et al. 2008; Shafer et al. 2010). Notably, natural populations of *Tamiasciurus* are absent from the outer islands of the Alexander Archipelago and Haida Gwaii, but are present in nearby mainland areas (MacDonald and Cook 2007; Palmer et al. 2007), suggesting that these islands did not serve as a coastal refugium for *Tamiasciurus* through the LGM. In fact, fossil records show that many small mammal species, unlike some large mammals such as bears, were extirpated by continental ice sheets during the LGM and were unable to recolonize these islands once favorable habitats returned (Conroy et al. 1999; Heaton and Grady 2003). The close genetic similarity of all northern *T. hudsonicus* populations (Fig. 3, number 3 TH-North) suggests that tree squirrels persisted in the Beringian Refugium, further to the north, rather than in the North Pacific Coastal Refugium (Cook et al. 2006) during the LGM. This finding reinforces an emerging hypothesis that a boreal ecosystem existed in Beringia throughout the LGM (Anderson et al. 2006, 2011; Zazula et al. 2006; Godbout et al. 2008; van Els et al. 2012).

Conclusion

Most previous phylogeographic studies of boreal forest organisms in North America have been based solely on a single, mitochondrial genetic marker. With our multilocus study using both nuclear and mtDNA, we have demonstrated rapid and recent late-Pleistocene speciation within a genus that contains only a Pacific coastal and a trans-continental species. On Vancouver Island, we also found that the nuclear and mitochondrial markers demonstrated conflicting phylogeographic patterns, which we have interpreted as a result of historical hybridization between the two mainland species on the island and gene flow between the Vancouver Island population and both mainland species. Our findings, combined with recent observations on other boreal taxa, show that hybridization has played an important role in the speciation process of boreal organisms in general. Our results also demonstrate that tree squirrels likely persisted in a refugium on Vancouver Island during the LGM, which is contrary to the hypothesis that terrestrial biota were eliminated from the island by the continental ice sheet during the LGM.

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DATA ARCHIVING

The doi for our data is 10.5061/dryad.j15q6. Sequence data have been archived in GenBank—Accession numbers: KF882736–KF885216.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

- Table S1.** Localities and other identifying information of the 165 specimens of *Tamiasciurus douglasii* and *Tamiasciurus hudsonicus* used in this study.
- Table S2.** Markers used in this study with summary statistics and laboratory conditions for PCR.
- Table S3.** Fossil and secondary calibrations used in this study.
- Table S4.** Model selection results for ecological niche modeling.
- Table S5.** ENM summary.
- Table S6.** ENM similarities.
- Table S7.** Variable assessment for Maxent models for each species.
- Figure S1.** Time-calibrated species-tree for rodents and lagomorph.
- Figure S2.** STRUCTURE plots of assignment probabilities for *Tamiasciurus douglasii* and *Tamiasciurus hudsonicus* samples.

Tissue Source	Date	Genus species	Museum Number	Museum	Prep ID:	Country	StateOrProv	County	Locality	Latitude (decimal)	Longitude (decimal)
Liver/Kidney/Heart	November 7, 2007	Tamiasciurus douglasii	HSUVM_8218	Humboldt State University Vertebrate Museum	..	USA	California	Del Norte	41.631N 124.039W	41.631	-124.039
Liver/Kidney/Heart	October 3, 2007	Tamiasciurus douglasii	HSUVM_8220	Humboldt State University Vertebrate Museum	..	USA	California	Del Norte	41.491N 124.917W	41.491	-124.917
Liver/Kidney/Heart	October 8, 2008	Tamiasciurus douglasii	HSUVM_8235	Humboldt State University Vertebrate Museum	..	USA	California	Humboldt	41.027N 123.903W	41.027	-123.903
Liver/Kidney/Heart	October 17, 2008	Tamiasciurus douglasii	HSUVM_8237	Humboldt State University Vertebrate Museum	..	USA	California	Humboldt	41.017N 124.015W	41.017	-124.015
Skin	May 23, 1982	Tamiasciurus douglasii	MSB_47459	Museum of Southwest Biology	..	MEXICO	Baja California		SIERRA SAN PEDRO MA	31.017	-115.533
Skin	May 23, 1982	Tamiasciurus douglasii	MSB_47460	Museum of Southwest Biology	..	MEXICO	Baja California		SIERRA SAN PEDRO MA	31.017	-115.533
Skin	May 23, 1982	Tamiasciurus douglasii	MSB_47461	Museum of Southwest Biology	..	MEXICO	Baja California		SIERRA SAN PEDRO MA	31.017	-115.533
Liver/Kidney/Heart	June 10, 2007	Tamiasciurus douglasii	MVZ_201566	Museum of Vertebrate Zoology, University of California	..	USA	California	Mariposa	Crane Flat, Yosemite Na	37.751	-119.791
Liver/Kidney/Heart	June 11, 2007	Tamiasciurus douglasii	MVZ_201567	Museum of Vertebrate Zoology, University of California	..	USA	California	Mariposa	Crane Flat (junction Tio	37.752	-119.797
Liver/Kidney/Heart	September 4, 2008	Tamiasciurus douglasii	MVZ_222808	Museum of Vertebrate Zoology, University of California	..	USA	California	Nevada	2.4 km N, 8.8 km W Hg	39.421	-120.291
Liver/Kidney/Heart	September 5, 2008	Tamiasciurus douglasii	MVZ_222809	Museum of Vertebrate Zoology, University of California	..	USA	California	Nevada	2.4 km N, 8.8 km W Hg	39.421	-120.291
Liver/Kidney/Heart	June 24, 2009	Tamiasciurus douglasii	MVZ_223974	Museum of Vertebrate Zoology, University of California	..	USA	California	Tulare	Horse Corral Meadow,	36.745	-118.772
Liver/Kidney/Heart	June 27, 2009	Tamiasciurus douglasii	MVZ_223975	Museum of Vertebrate Zoology, University of California	..	USA	California	Tulare	Horse Corral Meadow,	36.745	-118.772
Liver/Kidney/Heart	August 10, 2009	Tamiasciurus douglasii	MVZ_224506	Museum of Vertebrate Zoology, University of California	..	USA	California	Fresno	Bullfrog Lake, Kings Ca	36.770	-118.402
Liver/Kidney/Heart	August 11, 2009	Tamiasciurus douglasii	MVZ_224507	Museum of Vertebrate Zoology, University of California	..	USA	California	Fresno	Bullfrog Lake, Kings Ca	36.770	-118.402
Liver/Kidney/Heart	September 24, 2009	Tamiasciurus douglasii	MVZ_224633	Museum of Vertebrate Zoology, University of California	..	USA	California	Placer	Cisco	39.303	-120.547
Liver/Kidney/Heart	September 22, 2009	Tamiasciurus douglasii	MVZ_224634	Museum of Vertebrate Zoology, University of California	..	USA	California	Placer	Cisco	39.303	-120.549
Skin	00-Sep-84	Tamiasciurus douglasii	RBCM_013116	Royal BC Museum	..	CANADA	British Columbia	Redonda Island	East Redonda Island	50.233	-124.725
Skin	00-Sep-84	Tamiasciurus douglasii	RBCM_013117	Royal BC Museum	..	CANADA	British Columbia	Redonda Island	East Redonda Island	50.233	-124.725
Skin	July 21, 1989	Tamiasciurus douglasii	RBCM_016992	Royal BC Museum	..	CANADA	British Columbia		Pemberton Meadows	50.148	-122.933
Liver/Kidney/Heart	September 19, 1997	Tamiasciurus douglasii	UWBM_41850	Burke Museum, University of Washington	GJK 379	USA	Washington	Island	Whidbey Island	47.935	-122.398
Liver/Kidney/Heart	October 20, 1997	Tamiasciurus douglasii	UWBM_49091	Burke Museum, University of Washington	BSA 215	USA	Oregon	Deschutes	Sisters	44.189	-121.691
Liver/Kidney/Heart	October 20, 1997	Tamiasciurus douglasii	UWBM_49092	Burke Museum, University of Washington	BSA 216	USA	Oregon	Klamath	Crescent	43.471	-121.863
Liver/Kidney/Heart	October 20, 1997	Tamiasciurus douglasii	UWBM_49093	Burke Museum, University of Washington	BSA 217	USA	Oregon	Klamath	Crescent	43.471	-121.863
Liver/Kidney/Heart	September 7, 1997	Tamiasciurus douglasii	UWBM_74107	Burke Museum, University of Washington	EEM 299	USA	Washington	Island	Clinton, 4267 E Barba	47.985	-122.382
Liver/Kidney/Heart	June 5, 1997	Tamiasciurus douglasii	UWBM_74110	Burke Museum, University of Washington	EEM 302	USA	Washington	Skamania	Mt. Adams	46.362	-121.729
Liver/Kidney/Heart	June 5, 1997	Tamiasciurus douglasii	UWBM_74114	Burke Museum, University of Washington	EEM 306	USA	Washington	Lewis	Ashford	46.722	-121.893
Liver/Kidney/Heart	October 17, 1995	Tamiasciurus douglasii	UWBM_74139	Burke Museum, University of Washington	DP95023	USA	Washington	Thurston		46.530	-123.090
Liver/Kidney/Heart	July 18, 2001	Tamiasciurus douglasii	UWBM_75142	Burke Museum, University of Washington	GJK 607	USA	Washington	Clallam	road into Olympic Natio	48.038	-123.254
Liver/Kidney/Heart	September 27, 2000	Tamiasciurus douglasii	UWBM_75455	Burke Museum, University of Washington	XGZ 340	CANADA	British Columbia		Log Creek vicinity	50.031	-121.423
Liver/Kidney/Heart	September 27, 2000	Tamiasciurus douglasii	UWBM_75461	Burke Museum, University of Washington	XGZ 346	CANADA	British Columbia		Log Creek vicinity	50.031	-121.423
Liver/Kidney/Heart	January 13, 2000	Tamiasciurus douglasii	UWBM_75828	Burke Museum, University of Washington	JR 1243	USA	Washington	Clallam	Sequim	48.078	-123.105
Liver/Kidney/Heart	October 26, 2000	Tamiasciurus douglasii	UWBM_78345	Burke Museum, University of Washington	JEB 493	USA	Washington	Skamania	Gifford Pinchot Nationa	46.225	-121.350
Liver/Kidney/Heart	January 2, 2001	Tamiasciurus douglasii	UWBM_78685	Burke Museum, University of Washington	HH 002	USA	Washington	Clallam	Sequim	48.044	-123.064
Liver/Kidney/Heart	July 29, 2005	Tamiasciurus douglasii	UWBM_80404	Burke Museum, University of Washington	CMH 414	USA	Oregon	Clackamas	Mt. Hood, Government	45.163	-121.439
Liver/Kidney/Heart	September 14, 2006	Tamiasciurus douglasii	UWBM_80630	Burke Museum, University of Washington	CMH 512	USA	Washington	Snohomish	Stillaguamish Drainage	48.085	-121.761
Liver/Kidney/Heart	July 25, 2007	Tamiasciurus douglasii	UWBM_80685	Burke Museum, University of Washington	ASC 076	USA	Oregon	Clackamas	Mt. Hood	45.303	-121.746
Liver/Kidney/Heart	April 29, 2008	Tamiasciurus douglasii	UWBM_81939	Burke Museum, University of Washington	ASC 217	CANADA	British Columbia	Cortes Island	Whaletown Rd.	50.112	-124.955
Liver/Kidney/Heart	April 29, 2008	Tamiasciurus douglasii	UWBM_81940	Burke Museum, University of Washington	ASC 218	CANADA	British Columbia	Cortes Island	Whaletown Rd.	50.112	-124.955
Liver/Kidney/Heart	September 23, 2009	Tamiasciurus douglasii	UWBM_81941	Burke Museum, University of Washington	ASC 219	USA	Washington	Whatcom	Baker Lk.	48.683	-121.758
Liver/Kidney/Heart	September 23, 2009	Tamiasciurus douglasii	UWBM_81942	Burke Museum, University of Washington	ASC 220	USA	Washington	Whatcom	Baker Lk.	48.683	-121.758
Liver/Kidney/Heart	May 6, 2010	Tamiasciurus douglasii	UWBM_82026	Burke Museum, University of Washington	RPL 015	USA	Washington	Snohomish	Stanwood	48.141	-122.282
Liver/Kidney/Heart	August 29, 2010	Tamiasciurus douglasii	UWBM_82029	Burke Museum, University of Washington	ASC 248	USA	Oregon	Douglas	Siuslaw N.F.	43.899	-123.867
Liver/Kidney/Heart	August 29, 2010	Tamiasciurus douglasii	UWBM_82030	Burke Museum, University of Washington	ASC 249	USA	Oregon	Douglas	Siuslaw N.F.	43.899	-123.867
Liver/Kidney/Heart	September 4, 2010	Tamiasciurus douglasii	UWBM_82048	Burke Museum, University of Washington	ASC 267	USA	Oregon	Lane	Umpqua N.F. - Oakridg	43.725	-122.696
Liver/Kidney/Heart	September 4, 2010	Tamiasciurus douglasii	UWBM_82049	Burke Museum, University of Washington	ASC 268	USA	Oregon	Lane	Umpqua N.F. - Oakridg	43.725	-122.696
Liver/Kidney/Heart	September 7, 2010	Tamiasciurus douglasii	UWBM_82058	Burke Museum, University of Washington	ASC 277	USA	Oregon	Deschutes	Newberry Crater	43.707	-121.327
Liver/Kidney/Heart	September 7, 2010	Tamiasciurus douglasii	UWBM_82059	Burke Museum, University of Washington	ASC 278	USA	Oregon	Deschutes	Newberry Crater	43.707	-121.327
Liver/Kidney/Heart	September 9, 2010	Tamiasciurus douglasii	UWBM_82091	Burke Museum, University of Washington	ASC 310	USA	Oregon	Wheeler	Ochoco N.F. - Mitchell	44.452	-119.942
Liver/Kidney/Heart	September 9, 2010	Tamiasciurus douglasii	UWBM_82092	Burke Museum, University of Washington	ASC 311	USA	Oregon	Wheeler	Ochoco N.F. - Mitchell	44.452	-119.942
Liver/Kidney/Heart	August 10, 2010	Tamiasciurus douglasii	UWBM_82110	Burke Museum, University of Washington	ASC 329	USA	Oregon	Klatsop	Arcadia State Beach	45.840	-123.958
Liver/Kidney/Heart	September 23, 1989	Tamiasciurus hudsonicus	BYU_13761	Monte L. Bean Life Science Museum at Brigham Young University	DSR 3073	USA	Utah	San Juan	La Sal Mtns, 9,900 ft. e	38.447	-109.272
Liver/Kidney/Heart	July 10, 1995	Tamiasciurus hudsonicus	FHSM-M_35931	Sternberg Museum of Natural History, Fort Hays State University	PDS 463	USA	Wyoming	Teton	2 mi S of Turpin Meado	43.826	-110.262
Skin	July 9, 1969	Tamiasciurus hudsonicus	KU_120015	University of Kansas Natural History Museum	..	CANADA	Yukon		FRANCIS LAKE, W END	61.446	-129.432
Liver/Kidney/Heart	May 9, 1990	Tamiasciurus hudsonicus	MSB_62078	Museum of Southwest Biology	NK 17871	USA	Arizona	Apache County	GREENS PEAK, FROM A	34.112	-109.574
Liver/Kidney/Heart	May 9, 1990	Tamiasciurus hudsonicus	MSB_62079	Museum of Southwest Biology	NK 17872	USA	Arizona	Apache County	GREENS PEAK, FROM A	34.112	-109.574
Liver/Kidney/Heart	August 24, 1990	Tamiasciurus hudsonicus	MSB_66244	Museum of Southwest Biology	NK 21987	USA	Alaska		Chatanile River,4 mi E	65.294	-146.337

Tissue Source	Date	Genus species	Museum Number	Museum	Prep ID:	Country	StateOrProv	County	Locality	Latitude (decimal)	Longitude (decimal)
Liver/Kidney/Heart	August 24, 1990	Tamiasciurus hudsonicus	MSB_66245	Museum of Southwest Biology	NK 20629	USA	Alaska		Chatanile River, 4 mi E	65.294	-146.337
Liver/Kidney/Heart	July 14, 1994	Tamiasciurus hudsonicus	MSB_70594	Museum of Southwest Biology	NK 62126	USA	Maine	Hancock County	ACADIA NATL PK, 44D2	44.375	-68.253
Liver/Kidney/Heart	July 13, 1994	Tamiasciurus hudsonicus	MSB_73178	Museum of Southwest Biology	NK 63048	USA	Ohio	Summit County	THE HOMESTEAD, 2 MI	41.233	-81.520
Liver/Kidney/Heart	August 8, 1994	Tamiasciurus hudsonicus	MSB_73420	Museum of Southwest Biology	NK 63189	USA	Minnesota	St Louis County	VOYAGEURS NATIONAL	48.260	-92.510
Liver/Kidney/Heart	July 21, 1994	Tamiasciurus hudsonicus	MSB_76659	Museum of Southwest Biology	NK 56591	USA	Colorado	Jackson County	40D27N 106D00W, Tra	40.450	-106.000
Liver/Kidney/Heart	August 16, 1991	Tamiasciurus hudsonicus	NMMNH_17677	New Mexico Museum of Natural History	DJH 3450	USA	New Mexico	Sandoval Co.	Cerro Grande, 7 mi. N,	36.003	-106.294
Liver/Kidney/Heart	August 16, 1991	Tamiasciurus hudsonicus	NMMNH_17678	New Mexico Museum of Natural History	DJH 3451	USA	New Mexico	Sandoval Co.	Cerro Grande, 7 mi. N,	36.003	-106.294
Skin	June 14, 1970	Tamiasciurus hudsonicus	PSM_13961	Slater Museum of Natural History at the University of Puget Sound	..	USA	Alaska	Denali	Mount McKinley National	63.571	-148.996
Skin	July 9, 1970	Tamiasciurus hudsonicus	PSM_13962	Slater Museum of Natural History at the University of Puget Sound	..	USA	Alaska	Denali	Mount McKinley National	63.333	-150.551
Skin	May 15, 1971	Tamiasciurus hudsonicus	PSM_13963	Slater Museum of Natural History at the University of Puget Sound	..	USA	Alaska	Denali	Mount McKinley National	63.722	-148.964
Skin	June 1, 1971	Tamiasciurus hudsonicus	PSM_13964	Slater Museum of Natural History at the University of Puget Sound	..	USA	Alaska	Denali	Mount McKinley National	63.722	-148.964
Skin	March 4, 1952	Tamiasciurus hudsonicus	PSM_4106	Slater Museum of Natural History at the University of Puget Sound	..	USA	Alaska	Yukon	Arctic Village, Brooks R	68.127	-145.538
Skin	February 9, 1951	Tamiasciurus hudsonicus	PSM_4107	Slater Museum of Natural History at the University of Puget Sound	..	USA	Alaska	Yukon	Upper Savioyuk River	67.973	-151.601
Skin	February 6, 1937	Tamiasciurus hudsonicus	RBCM_001938	Royal BC Museum	..	CANADA	British Columbia	Coast; Range 2	Calvert Island; Safety	51.559	-127.983
Skin	June 5, 1937	Tamiasciurus hudsonicus	RBCM_001939	Royal BC Museum	..	CANADA	British Columbia	Coast; Range 2	Calvert Island; Safety	51.536	-127.947
Skin	March 5, 1937	Tamiasciurus hudsonicus	RBCM_001941	Royal BC Museum	..	CANADA	British Columbia	Coast; Range 2	Calvert Island; Safety	51.536	-127.947
Skin	May 27, 1937	Tamiasciurus hudsonicus	RBCM_001943	Royal BC Museum	..	CANADA	British Columbia	Coast; Range 2	Calvert Island; Safety	51.536	-127.947
Skin	June 9, 1938	Tamiasciurus hudsonicus	RBCM_002900	Royal BC Museum	..	CANADA	British Columbia		Swindle Island; Meyers	52.601	-128.646
Skin	February 9, 1938	Tamiasciurus hudsonicus	RBCM_002901	Royal BC Museum	..	CANADA	British Columbia		Swindle Island; Meyers	52.601	-128.646
Skin	September 23, 1938	Tamiasciurus hudsonicus	RBCM_003176	Royal BC Museum	..	CANADA	British Columbia		Lowe Inlet	53.563	-129.544
Skin	September 23, 1938	Tamiasciurus hudsonicus	RBCM_003177	Royal BC Museum	..	CANADA	British Columbia		Lowe Inlet	53.563	-129.544
Skin	May 8, 1948	Tamiasciurus hudsonicus	RBCM_005433	Royal BC Museum	..	CANADA	British Columbia		Bardswell Islands Group	52.178	-128.503
Skin	June 8, 1948	Tamiasciurus hudsonicus	RBCM_005434	Royal BC Museum	..	CANADA	British Columbia		Bardswell Islands Group	52.178	-128.503
Skin	August 8, 1955	Tamiasciurus hudsonicus	RBCM_005853	Royal BC Museum	..	CANADA	British Columbia		Vancouver Island	50.098	-127.539
Skin	August 8, 1955	Tamiasciurus hudsonicus	RBCM_005854	Royal BC Museum	..	CANADA	British Columbia		Burnsby Island	50.098	-127.539
Skin	July 16, 1960	Tamiasciurus hudsonicus	RBCM_006660	Royal BC Museum	..	CANADA	British Columbia		Vancouver Island	49.152	-125.920
Skin	July 17, 1960	Tamiasciurus hudsonicus	RBCM_006661	Royal BC Museum	..	CANADA	British Columbia		Vancouver Island	49.152	-125.920
Skin	October 8, 1961	Tamiasciurus hudsonicus	RBCM_006793	Royal BC Museum	..	CANADA	British Columbia		Vancouver Island	49.156	-125.949
Skin	August 13, 1969	Tamiasciurus hudsonicus	RBCM_007330	Royal BC Museum	..	CANADA	British Columbia		Vancouver Island	48.914	-125.088
Skin	November 8, 1969	Tamiasciurus hudsonicus	RBCM_007331	Royal BC Museum	..	CANADA	British Columbia		Vancouver Island	48.914	-125.088
Skin	October 8, 1967	Tamiasciurus hudsonicus	RBCM_007332	Royal BC Museum	..	CANADA	British Columbia		Vancouver Island	48.868	-125.168
Skin	August 22, 1969	Tamiasciurus hudsonicus	RBCM_007334	Royal BC Museum	..	CANADA	British Columbia		Vancouver Island	48.909	-125.112
Skin	October 8, 1967	Tamiasciurus hudsonicus	RBCM_007624	Royal BC Museum	..	CANADA	British Columbia		Vancouver Island	48.886	-125.128
Skin	July 9, 1971	Tamiasciurus hudsonicus	RBCM_007680	Royal BC Museum	..	CANADA	British Columbia		Tatogga Lake	57.720	-130.007
Skin	August 16, 1977	Tamiasciurus hudsonicus	RBCM_009901	Royal BC Museum	..	CANADA	British Columbia		North; Cassiar	59.586	-133.690
Skin	00-Oct-80	Tamiasciurus hudsonicus	RBCM_010488	Royal BC Museum	..	CANADA	British Columbia		North; Cassiar	59.586	-133.690
Skin	May 22, 1982	Tamiasciurus hudsonicus	RBCM_010508	Royal BC Museum	..	CANADA	British Columbia		North; Peace	58.798	-121.979
Skin	May 23, 1982	Tamiasciurus hudsonicus	RBCM_010510	Royal BC Museum	..	CANADA	British Columbia		North; Peace	58.798	-121.979
Skin	May 24, 1982	Tamiasciurus hudsonicus	RBCM_010511	Royal BC Museum	..	CANADA	British Columbia		North; Peace	58.798	-121.979
Skin	January 10, 1980	Tamiasciurus hudsonicus	RBCM_010800	Royal BC Museum	..	CANADA	British Columbia		North; Cassiar	59.636	-133.368
Skin	January 10, 1980	Tamiasciurus hudsonicus	RBCM_010801	Royal BC Museum	..	CANADA	British Columbia		North; Cassiar	59.636	-133.368
Liver/Kidney/Heart	August 7, 1996	Tamiasciurus hudsonicus	UAM_43102	University of Alaska Museum of the North	AF 17873	USA	Alaska		9 miles NW of Chicagof	57.750	-136.283
Liver/Kidney/Heart	September 30, 1996	Tamiasciurus hudsonicus	UAM_51395	University of Alaska Museum of the North	AF 17840	USA	Alaska		Smith Lake, Fairbanks	64.866	-147.867
Skin	June 15, 1948	Tamiasciurus hudsonicus	UBC_2482	Beaty Biodiversity Museum at the University of British Columbia	..	CANADA	British Columbia		Anahim L.	52.494	-125.318
Skin	May 31, 1948	Tamiasciurus hudsonicus	UBC_2483	Beaty Biodiversity Museum at the University of British Columbia	..	CANADA	British Columbia		Anahim L.	52.494	-125.318
Liver/Kidney/Heart	September 27, 1984	Tamiasciurus hudsonicus	UMMZ_162427	University of Michigan Museum of Zoology	LRH 2801	USA	Michigan	Mackinac	12MI N ST. IGNACE	45.855	-84.708
Skin	October 16, 1971	Tamiasciurus hudsonicus	UWBM_30055	Burke Museum, University of Washington	..	USA	Montana	Gallatin	S of Bozeman	45.556	-111.055
Skin	June 29, 1973	Tamiasciurus hudsonicus	UWBM_30058	Burke Museum, University of Washington	..	USA	Alaska		Skagway-Hoonah-Angoon	58.707	-137.671
Skin	June 29, 1973	Tamiasciurus hudsonicus	UWBM_30061	Burke Museum, University of Washington	..	USA	Alaska		Skagway-Hoonah-Angoon	58.637	-137.573
Skin	July 6, 1973	Tamiasciurus hudsonicus	UWBM_30062	Burke Museum, University of Washington	..	USA	Alaska		Skagway-Hoonah-Angoon	58.367	-136.883
Skin	July 29, 1980	Tamiasciurus hudsonicus	UWBM_32082	Burke Museum, University of Washington	..	USA	Alaska		Fairbanks North Star	64.944	-147.988
Skin	September 13, 1980	Tamiasciurus hudsonicus	UWBM_32083	Burke Museum, University of Washington	..	USA	Alaska		Fairbanks North Star	64.944	-147.988
Skin	July 19, 1985	Tamiasciurus hudsonicus	UWBM_35237	Burke Museum, University of Washington	..	USA	Michigan		Kalamazoo	42.354	-85.580
Skin	April 14, 1992	Tamiasciurus hudsonicus	UWBM_38330	Burke Museum, University of Washington	..	USA	New York		Otsego	42.635	-74.965
Skin	July 22, 1963	Tamiasciurus hudsonicus	UWBM_43180	Burke Museum, University of Washington	..	CANADA	Nova Scotia		Victoria	46.700	-60.367
Skin	August 13, 1963	Tamiasciurus hudsonicus	UWBM_43185	Burke Museum, University of Washington	..	CANADA	Alberta		Kananaskis District	50.742	-115.058
Skin	August 20, 1963	Tamiasciurus hudsonicus	UWBM_43186	Burke Museum, University of Washington	..	CANADA	British Columbia		Revelstoke	50.983	-118.315
Skin	July 7, 1965	Tamiasciurus hudsonicus	UWBM_43188	Burke Museum, University of Washington	..	CANADA	British Columbia		Helmcken Falls, Wells	51.950	-120.183
Skin	July 7, 1965	Tamiasciurus hudsonicus	UWBM_43189	Burke Museum, University of Washington	..	CANADA	British Columbia		Helmcken Falls, Wells	51.950	-120.183
Skin	August 16, 1971	Tamiasciurus hudsonicus	UWBM_43200	Burke Museum, University of Washington	..	USA	Montana	Glacier	St. Mary	48.657	-113.426
Skin	November 5, 1972	Tamiasciurus hudsonicus	UWBM_43204	Burke Museum, University of Washington	..	USA	Utah	San Juan	La Sal Mountains	38.421	-109.249

Tissue Source	Date	Genus species	Museum Number	Museum	Prep ID:	Country	StateOrProv	County	Locality	Latitude (decimal)	Longitude (decimal)
Skin	September 15, 1972	Tamiasciurus hudsonicus	UWBM_43225	Burke Museum, University of Washington	..	USA	Utah	Cache	Logan Canyon	41.835	-111.592
Skin	September 15, 1972	Tamiasciurus hudsonicus	UWBM_43226	Burke Museum, University of Washington	..	USA	Utah	Cache	Logan Canyon	41.835	-111.592
Skin	September 2, 1976	Tamiasciurus hudsonicus	UWBM_43245	Burke Museum, University of Washington	..	USA	Utah	Summit	Kamas	40.643	-111.280
Skin	September 2, 1976	Tamiasciurus hudsonicus	UWBM_43246	Burke Museum, University of Washington	..	USA	Utah	Summit	Kamas	40.643	-111.280
Skin	July 1, 1970	Tamiasciurus hudsonicus	UWBM_43254	Burke Museum, University of Washington	..	CANADA	Yukon		Alcan Highway, mile 99	60.833	-136.950
Skin	July 1, 1970	Tamiasciurus hudsonicus	UWBM_43255	Burke Museum, University of Washington	..	CANADA	Yukon		Alcan Highway, mile 99	60.833	-136.950
Skin	July 1, 1970	Tamiasciurus hudsonicus	UWBM_43256	Burke Museum, University of Washington	..	CANADA	Yukon		Alcan Highway, mile 99	60.833	-136.950
Skin	June 27, 1974	Tamiasciurus hudsonicus	UWBM_43257	Burke Museum, University of Washington	..	USA	Montana	Missoula	Missoula, 6 mi SE	46.828	-113.960
Skin	July 1, 1970	Tamiasciurus hudsonicus	UWBM_43263	Burke Museum, University of Washington	..	CANADA	Yukon		Alcan Highway, mile 99	60.833	-136.950
Skin	August 4, 1955	Tamiasciurus hudsonicus	UWBM_43276	Burke Museum, University of Washington	..	USA	Wyoming	Park	Lamar District	44.624	-110.085
Skin	September 15, 1986	Tamiasciurus hudsonicus	UWBM_44442	Burke Museum, University of Washington	..	USA	Alaska		Glacier Bay Lodge	58.454	-135.883
Skin	February 17, 1970	Tamiasciurus hudsonicus	UWBM_44943	Burke Museum, University of Washington	..	USA	Indiana	Tippecanoe	West Lafayette	40.434	-86.957
Liver/Kidney/Heart	June 1, 1997	Tamiasciurus hudsonicus	UWBM_74113	Burke Museum, University of Washington	EEM 305	USA	West Virginia	Randolf	Elkins	38.984	-79.847
Liver/Kidney/Heart	October 1, 2000	Tamiasciurus hudsonicus	UWBM_75493	Burke Museum, University of Washington	XGZ 379	CANADA	British Columbia	Vancouver Island	Lantzville	49.143	-124.057
Liver/Kidney/Heart	October 1, 2000	Tamiasciurus hudsonicus	UWBM_75494	Burke Museum, University of Washington	XGZ 380	CANADA	British Columbia	Vancouver Island	Lantzville	49.143	-124.057
Liver/Kidney/Heart	June 24, 2002	Tamiasciurus hudsonicus	UWBM_76425	Burke Museum, University of Washington	GJK 708	USA	Alaska	Wrangell-Petersburg	Mitkof Island	56.407	-132.560
Liver/Kidney/Heart	March 13, 2001	Tamiasciurus hudsonicus	UWBM_76565	Burke Museum, University of Washington	EEM 363	CANADA	British Columbia	Vancouver Island	Koegh	50.501	-127.167
Liver/Kidney/Heart	August 14, 2003	Tamiasciurus hudsonicus	UWBM_78088	Burke Museum, University of Washington	CMH 099	USA	Washington	Ferry	Colville NF	48.425	-118.265
Liver/Kidney/Heart	August 14, 2003	Tamiasciurus hudsonicus	UWBM_78101	Burke Museum, University of Washington	CMH 113	USA	Washington	Ferry	Colville NF	48.337	-118.426
Liver/Kidney/Heart	August 26, 2003	Tamiasciurus hudsonicus	UWBM_78125	Burke Museum, University of Washington	CMH 138	USA	Washington	Pend Oreille	Selkirk Mts	48.500	-117.106
Liver/Kidney/Heart	August 27, 2003	Tamiasciurus hudsonicus	UWBM_78150	Burke Museum, University of Washington	CMH 163	USA	Washington	Pend Oreille	Selkirk Mts	48.500	-117.106
Liver/Kidney/Heart	September 2, 2008	Tamiasciurus hudsonicus	UWBM_81513	Burke Museum, University of Washington	ASC 118	USA	Oregon	Grant	Blue Mts. - Granite	44.796	-118.531
Liver/Kidney/Heart	September 2, 2008	Tamiasciurus hudsonicus	UWBM_81514	Burke Museum, University of Washington	ASC 119	USA	Oregon	Grant	Blue Mts. - Granite	44.796	-118.531
Liver/Kidney/Heart	September 3, 2008	Tamiasciurus hudsonicus	UWBM_81519	Burke Museum, University of Washington	ASC 124	USA	Oregon	Union	Wallowa Mts.	45.290	-117.692
Liver/Kidney/Heart	September 3, 2008	Tamiasciurus hudsonicus	UWBM_81524	Burke Museum, University of Washington	ASC 129	USA	Oregon	Union	Wallowa Mts.	45.290	-117.692
Liver/Kidney/Heart	July 28, 2009	Tamiasciurus hudsonicus	UWBM_81891	Burke Museum, University of Washington	ASC 169	USA	Washington	Okanogan	Loup Loup Pass	48.391	-119.877
Liver/Kidney/Heart	July 28, 2009	Tamiasciurus hudsonicus	UWBM_81892	Burke Museum, University of Washington	ASC 170	USA	Washington	Okanogan	Loup Loup Pass	48.435	-119.890
Liver/Kidney/Heart	August 4, 2009	Tamiasciurus hudsonicus	UWBM_81919	Burke Museum, University of Washington	ASC 197	CANADA	British Columbia	Vancouver Island	Nimpkish Lake	50.485	-126.990
Liver/Kidney/Heart	August 4, 2009	Tamiasciurus hudsonicus	UWBM_81920	Burke Museum, University of Washington	ASC 198	CANADA	British Columbia	Vancouver Island	Nimpkish Lake	50.485	-126.990
Liver/Kidney/Heart	August 5, 2009	Tamiasciurus hudsonicus	UWBM_81921	Burke Museum, University of Washington	ASC 199	CANADA	British Columbia	Vancouver Island	Rooney Lake	50.350	-126.160
Liver/Kidney/Heart	August 7, 2009	Tamiasciurus hudsonicus	UWBM_81922	Burke Museum, University of Washington	ASC 200	CANADA	British Columbia	Vancouver Island	Mt. Washington	49.738	-125.200
Liver/Kidney/Heart	August 5, 2009	Tamiasciurus hudsonicus	UWBM_81923	Burke Museum, University of Washington	ASC 201	CANADA	British Columbia	Vancouver Island	Mt. Washington	49.738	-125.200
Liver/Kidney/Heart	August 6, 2009	Tamiasciurus hudsonicus	UWBM_81924	Burke Museum, University of Washington	ASC 202	CANADA	British Columbia	Vancouver Island	Mt. Washington	49.738	-125.200
Liver/Kidney/Heart	August 7, 2009	Tamiasciurus hudsonicus	UWBM_81925	Burke Museum, University of Washington	ASC 203	CANADA	British Columbia	Vancouver Island	Mt. Washington	49.738	-125.200
Liver/Kidney/Heart	August 6, 2009	Tamiasciurus hudsonicus	UWBM_81926	Burke Museum, University of Washington	ASC 204	CANADA	British Columbia	Vancouver Island	Mt. Washington	49.738	-125.200
Liver/Kidney/Heart	August 11, 2009	Tamiasciurus hudsonicus	UWBM_81927	Burke Museum, University of Washington	ASC 205	CANADA	British Columbia	Vancouver Island	Mt. Schofield	49.412	-124.751
Liver/Kidney/Heart	August 11, 2009	Tamiasciurus hudsonicus	UWBM_81928	Burke Museum, University of Washington	ASC 206	CANADA	British Columbia	Vancouver Island	Mt. Schofield	49.412	-124.751
Liver/Kidney/Heart	August 11, 2009	Tamiasciurus hudsonicus	UWBM_81929	Burke Museum, University of Washington	ASC 207	CANADA	British Columbia	Vancouver Island	Mt. Schofield	49.412	-124.751
Liver/Kidney/Heart	August 8, 2009	Tamiasciurus hudsonicus	UWBM_81930	Burke Museum, University of Washington	ASC 208	CANADA	British Columbia	Vancouver Island	Mt. Schofield	49.412	-124.751
Liver/Kidney/Heart	August 7, 2009	Tamiasciurus hudsonicus	UWBM_81931	Burke Museum, University of Washington	ASC 209	CANADA	British Columbia	Vancouver Island	Mt. Schofield	49.412	-124.751
Liver/Kidney/Heart	August 13, 2009	Tamiasciurus hudsonicus	UWBM_81932	Burke Museum, University of Washington	ASC 210	CANADA	British Columbia	Vancouver Island	Cowichan River	48.755	-123.913
Liver/Kidney/Heart	August 13, 2009	Tamiasciurus hudsonicus	UWBM_81933	Burke Museum, University of Washington	ASC 211	CANADA	British Columbia	Vancouver Island	Cowichan River	48.755	-123.913
Liver/Kidney/Heart	August 13, 2009	Tamiasciurus hudsonicus	UWBM_81934	Burke Museum, University of Washington	ASC 212	CANADA	British Columbia	Vancouver Island	Cowichan River	48.755	-123.913
Liver/Kidney/Heart	August 13, 2009	Tamiasciurus hudsonicus	UWBM_81935	Burke Museum, University of Washington	ASC 213	CANADA	British Columbia	Vancouver Island	Cowichan River	48.755	-123.913
Liver/Kidney/Heart	June 19, 2009	Tamiasciurus hudsonicus	UWBM_81936	Burke Museum, University of Washington	ASC 214	CANADA	British Columbia	Vancouver Island	Nanaimo	49.157	-123.978
Liver/Kidney/Heart	August 16, 2008	Tamiasciurus hudsonicus	UWBM_81937	Burke Museum, University of Washington	ASC 215	CANADA	British Columbia	Vancouver Island	Sooke	48.396	-123.983
Liver/Kidney/Heart	August 16, 2008	Tamiasciurus hudsonicus	UWBM_81938	Burke Museum, University of Washington	ASC 216	CANADA	British Columbia	Vancouver Island	Nanaimo	48.396	-123.983

Both <i>Tamiasciurus douglasii</i> (TD) and <i>Tamiasciurus hudsonicus</i> (TH) STRUCTURE results. Values show the proportion of each individual's genome that originated from each population. Numbers in parentheses with labels are the same as those in Fig. 1												
Museum Number	TD-Pacific Coastal (1)	TD-Baja California (2)	TH-North (3)	TH-Mainland BC Coast (4)	TH-Vancouver Island (5)	TH-Interior Northwest (6)	TH-Northern Rockies (7)	TH-Southern Rockies (8)	TH-Eastern (9)	Population Assignment of Samples Used in the *BEAST Species Tree	Clade Designation of Samples Used in the mtDNA Phylogeny	Population Assignment of Samples Used in the IMA2 Analysis
HSUVM_8218	0.99	0.01								TD-PACIFIC COASTAL	<i>T. douglasii</i> Clade	TD
HSUVM_8220	1.00	0.00										
HSUVM_8235	0.99	0.01								TD-PACIFIC COASTAL	<i>T. douglasii</i> Clade	TD
HSUVM_8237	0.99	0.01										
MSB_47459	0.06	0.94								TD-BAJA CALIFORNIA	<i>T. douglasii</i> Clade	TD
MSB_47460	0.07	0.93								TD-BAJA CALIFORNIA	<i>T. douglasii</i> Clade	
MSB_47461	0.02	0.98								TD-BAJA CALIFORNIA	<i>T. douglasii</i> Clade	
MVZ_201566	1.00	0.01										TD
MVZ_201567	0.99	0.01								TD-PACIFIC COASTAL	<i>T. douglasii</i> Clade	
MVZ_222808	0.99	0.01								TD-PACIFIC COASTAL	<i>T. douglasii</i> Clade	
MVZ_222809	1.00	0.00										
MVZ_223974	1.00	0.00										TD
MVZ_223975	1.00	0.00										
MVZ_224506	1.00	0.00								TD-PACIFIC COASTAL	<i>T. douglasii</i> Clade	TD
MVZ_224507	0.99	0.01										
MVZ_224633	1.00	0.00										TD
MVZ_224634	0.99	0.01										
RBCM_013116	0.98	0.02										
RBCM_013117	1.00	0.00										
RBCM_016992	1.00	0.00										
UWBM_41850	0.99	0.01										
UWBM_49091	0.99	0.01										TD
UWBM_49092	1.00	0.00										
UWBM_49093	1.00	0.00										TD
UWBM_74107	1.00	0.00										
UWBM_74110	1.00	0.00								TD-PACIFIC COASTAL	<i>T. douglasii</i> Clade	TD
UWBM_74114	1.00	0.00										
UWBM_74139	1.00	0.00										TD
UWBM_75142	1.00	0.00								TD-PACIFIC COASTAL	<i>T. douglasii</i> Clade	TD
UWBM_75455	1.00	0.00										
UWBM_75461	1.00	0.00										
UWBM_75828	1.00	0.00										
UWBM_78345	1.00	0.00										
UWBM_78685	1.00	0.00										
UWBM_80404	0.99	0.01										TD
UWBM_80630	1.00	0.00										TD
UWBM_80685	1.00	0.01								TD-PACIFIC COASTAL	<i>T. douglasii</i> Clade	TD
UWBM_81939	1.00	0.00								TD-PACIFIC COASTAL	<i>T. douglasii</i> Clade	
UWBM_81940	1.00	0.00										TD
UWBM_81941	0.99	0.01										TD
UWBM_81942	1.00	0.01										
UWBM_82026	1.00	0.00										
UWBM_82029	0.99	0.01								TD-PACIFIC COASTAL	<i>T. douglasii</i> Clade	
UWBM_82030	1.00	0.00										TD
UWBM_82048	0.99	0.01										TD
UWBM_82049	0.98	0.02								TD-PACIFIC COASTAL	<i>T. douglasii</i> Clade	
UWBM_82058	1.00	0.00										
UWBM_82059	1.00	0.00										
UWBM_82091	0.99	0.01										TD
UWBM_82092	0.98	0.02										
UWBM_82110	0.98	0.02										
BYU_13761			0.00	0.00	0.00	0.00	0.00	0.99	0.01			TH
FHSM-M_35931			0.01	0.00	0.00	0.00	0.92	0.02	0.06	TH-NORTHERN ROCKIES	<i>T. hudsonicus</i> Clade	TH
KU_120015			0.97	0.00	0.00	0.00	0.00	0.01	0.02			
MSB_62078			0.00	0.00	0.00	0.01	0.00	0.99	0.00	TH-SOUTHERN ROCKIES		TH
MSB_62079			0.00	0.00	0.00	0.00	0.00	1.00	0.00	TH-SOUTHERN ROCKIES		
MSB_66244			1.00	0.00	0.00	0.00	0.00	0.00	0.00	TH-NORTH	<i>T. hudsonicus</i> Clade	

Museum Number	TD-Pacific Coastal (1)	TD-Baja California (2)	TH-North (3)	TH-Mainland BC Coast (4)	TH-Vancouver Island (5)	TH-Interior Northwest (6)	TH-Northern Rockies (7)	TH-Southern Rockies (8)	TH-Eastern (9)	Population Assignment of Samples Used in the *BEAST Species Tree	Clade Designation of Samples Used in the mtDNA Phylogeny	Population Assignment of Samples Used in the IMA2 Analysis
MSB_66245			0.99	0.01	0.00	0.00	0.00	0.00	0.00			
MSB_70594			0.00	0.00	0.00	0.00	0.01	0.00	0.98	TH-EASTERN	<i>T. hudsonicus</i> Clade	TH
MSB_73178			0.00	0.00	0.00	0.00	0.00	0.01	0.99	TH-EASTERN	<i>T. hudsonicus</i> Clade	TH
MSB_73420			0.02	0.00	0.00	0.00	0.00	0.01	0.98			
MSB_76659			0.00	0.00	0.00	0.01	0.00	0.99	0.00	TH-SOUTHERN ROCKIES	<i>T. hudsonicus</i> Clade	TH
NMMNH_17677			0.00	0.00	0.00	0.00	0.00	0.99	0.01	TH-SOUTHERN ROCKIES	<i>T. hudsonicus</i> Clade	TH
NMMNH_17678			0.00	0.00	0.00	0.00	0.00	0.99	0.00	TH-SOUTHERN ROCKIES		TH
PSM_13961			1.00	0.00	0.00	0.00	0.00	0.00	0.00			
PSM_13962			0.98	0.00	0.00	0.00	0.00	0.00	0.02			
PSM_13963			0.99	0.01	0.00	0.00	0.00	0.00	0.00	TH-NORTH	<i>T. hudsonicus</i> Clade	
PSM_13964			0.98	0.01	0.00	0.00	0.00	0.00	0.01			
PSM_4106			1.00	0.00	0.00	0.00	0.00	0.00	0.00	TH-NORTH	<i>T. hudsonicus</i> Clade	
PSM_4107			0.99	0.00	0.00	0.00	0.00	0.00	0.00			
RBCM_001938			0.01	0.97	0.03	0.00	0.00	0.00	0.00	TH-MAINLAND BC COAST		
RBCM_001939			0.00	0.96	0.00	0.03	0.00	0.00	0.00			
RBCM_001941			0.00	0.39	0.61	0.00	0.00	0.00	0.00			
RBCM_001943			0.01	0.56	0.42	0.00	0.00	0.00	0.00			
RBCM_002900			0.01	0.00	0.95	0.03	0.00	0.00	0.00	TH-VANCOUVER ISLAND	<i>T. hudsonicus</i> Clade	
RBCM_002901			0.02	0.90	0.08	0.00	0.00	0.00	0.00	TH-MAINLAND BC COAST		
RBCM_003176			0.26	0.73	0.01	0.00	0.00	0.00	0.00			
RBCM_003177			0.05	0.93	0.00	0.00	0.00	0.01	0.00	TH-MAINLAND BC COAST	<i>T. hudsonicus</i> Clade	
RBCM_005433			0.00	1.00	0.00	0.00	0.00	0.00	0.00	TH-MAINLAND BC COAST	<i>T. hudsonicus</i> Clade	
RBCM_005434			0.02	0.94	0.00	0.00	0.02	0.00	0.02	TH-MAINLAND BC COAST	<i>T. hudsonicus</i> Clade	
RBCM_005853			0.00	0.00	1.00	0.00	0.00	0.00	0.00			
RBCM_005854			0.00	0.00	0.96	0.00	0.02	0.00	0.02			
RBCM_006660			0.00	0.00	1.00	0.00	0.00	0.00	0.00		<i>T. douglasii</i> Clade	VI
RBCM_006661			0.00	0.00	0.99	0.00	0.00	0.00	0.00		<i>T. douglasii</i> Clade	VI
RBCM_006793			0.00	0.00	1.00	0.00	0.00	0.00	0.00			
RBCM_007330			0.00	0.01	0.99	0.00	0.00	0.00	0.00	TH-VANCOUVER ISLAND	<i>T. douglasii</i> Clade	
RBCM_007331			0.00	0.00	1.00	0.00	0.00	0.00	0.00		<i>T. douglasii</i> Clade	VI
RBCM_007332			0.00	0.00	0.98	0.01	0.00	0.00	0.01		<i>T. douglasii</i> Clade	VI
RBCM_007334			0.00	0.00	1.00	0.00	0.00	0.00	0.00		<i>T. douglasii</i> Clade	VI
RBCM_007624			0.00	0.00	0.99	0.01	0.00	0.00	0.00		<i>T. douglasii</i> Clade	
RBCM_007680			0.52	0.10	0.00	0.00	0.00	0.00	0.38			
RBCM_009901			1.00	0.00	0.00	0.00	0.00	0.00	0.00			
RBCM_010488			0.91	0.00	0.00	0.00	0.00	0.00	0.09	TH-NORTH	<i>T. hudsonicus</i> Clade	
RBCM_010508			0.98	0.00	0.00	0.01	0.01	0.00	0.00	TH-NORTH	<i>T. hudsonicus</i> Clade	
RBCM_010510			1.00	0.00	0.00	0.00	0.00	0.00	0.00			
RBCM_010511			1.00	0.00	0.00	0.00	0.00	0.00	0.00			
RBCM_010800			0.97	0.03	0.00	0.00	0.00	0.00	0.00			
RBCM_010801			0.97	0.02	0.00	0.00	0.00	0.00	0.01			
UAM_43102			0.98	0.00	0.01	0.00	0.00	0.01	0.00	TH-NORTH	<i>T. hudsonicus</i> Clade	
UAM_51395			1.00	0.00	0.00	0.00	0.00	0.00	0.00	TH-NORTH	<i>T. hudsonicus</i> Clade	
UBC_2482			0.99	0.01	0.00	0.00	0.00	0.00	0.00			
UBC_2483			0.79	0.20	0.00	0.00	0.00	0.00	0.00			
UMMZ_162427			0.02	0.00	0.00	0.00	0.00	0.00	0.98	TH-EASTERN	<i>T. hudsonicus</i> Clade	TH
UWBM_30055			0.06	0.01	0.00	0.00	0.92	0.00	0.00	TH-NORTHERN ROCKIES	<i>T. hudsonicus</i> Clade	TH
UWBM_30058			0.99	0.00	0.00	0.00	0.00	0.01	0.00			
UWBM_30061			0.99	0.00	0.00	0.01	0.00	0.00	0.00			
UWBM_30062			0.99	0.00	0.00	0.00	0.00	0.00	0.01	TH-NORTH	<i>T. hudsonicus</i> Clade	
UWBM_32082			0.99	0.00	0.01	0.00	0.00	0.00	0.00	TH-NORTH	<i>T. hudsonicus</i> Clade	
UWBM_32083			0.97	0.03	0.00	0.00	0.00	0.00	0.00	TH-NORTH	<i>T. hudsonicus</i> Clade	
UWBM_35237			0.01	0.01	0.00	0.00	0.00	0.00	0.98	TH-EASTERN	<i>T. hudsonicus</i> Clade	TH
UWBM_38330			0.02	0.00	0.01	0.00	0.00	0.00	0.97	TH-EASTERN	<i>T. hudsonicus</i> Clade	TH
UWBM_43180			0.00	0.00	0.00	0.00	0.00	0.00	0.99	TH-EASTERN	<i>T. hudsonicus</i> Clade	TH
UWBM_43185			0.00	0.00	0.00	0.75	0.00	0.01	0.24			
UWBM_43186			0.00	0.00	0.00	0.65	0.35	0.00	0.00			
UWBM_43188			0.91	0.00	0.00	0.00	0.00	0.00	0.09	TH-NORTH	<i>T. hudsonicus</i> Clade	
UWBM_43189			0.00	0.00	0.00	0.00	0.98	0.00	0.01			
UWBM_43200			0.05	0.20	0.00	0.75	0.00	0.00	0.00			
UWBM_43204			0.01	0.00	0.00	0.00	0.00	0.99	0.01	TH-SOUTHERN ROCKIES	<i>T. hudsonicus</i> Clade	TH

Museum Number	GenBank Accession CAHSP1	GenBank Accession CLCN6	GenBank Accession CSE11	GenBank Accession GABRP	GenBank Accession GAD2	GenBank Accession GDAP1	GenBank Accession METTL1.1A	GenBank Accession P4HA2	GenBank Accession PPOX	GenBank Accession PNPO	GenBank Accession PPAN	GenBank Accession SLC17A9	GenBank Accession TBC1D21	GenBank Accession THOC1	GenBank Accession TTR	GenBank Accession MTDNA
HSUVM_8218	KF882738	KF882891	KF883055	KF883217	KF883371	KF883533	KF883688	KF883840	KF884004	KF884162	KF884327	KF884492	KF884657	KF884822	KF884982	KF885145
HSUVM_8220	KF882739	KF882892	KF883056	KF883218	KF883372	KF883534	KF883689	KF883841	KF884005	KF884163	KF884328	KF884493	KF884658	KF884823	KF884983	
HSUVM_8235	KF882740	KF882893	KF883057	KF883219	KF883373	KF883535	KF883690	KF883842	KF884006	KF884164	KF884329	KF884494	KF884659	KF884824	KF884984	KF885146
HSUVM_8237	KF882741	KF882894	KF883058	KF883220	KF883374	KF883536	KF883691	KF883843	KF884007	KF884165	KF884330	KF884495	KF884660	KF884825	KF884985	
MSB_47459	KF882743	KF882896	KF883060	KF883222	KF883376	KF883538	KF883693	KF883845	KF884009	KF884167	KF884332	KF884497	KF884662	KF884827	KF884987	KF885147
MSB_47460	KF882744	KF882897	KF883061	KF883223	KF883377	KF883539	KF883694	KF883846	KF884010	KF884168	KF884333	KF884498	KF884663	KF884828	KF884988	KF885148
MSB_47461	KF882745	KF882898	KF883062	KF883224	KF883378	KF883540	KF883695	KF883847	KF884011	KF884169	KF884334	KF884499	KF884664	KF884829	KF884989	KF885149
MVZ_201566	KF882754	KF882907	KF883071	KF883230	KF883386	KF883548	KF883704	KF883856	KF884020	KF884178	KF884343	KF884508	KF884673	KF884838	KF884998	
MVZ_201567	KF882755	KF882908	KF883072	KF883231	KF883387	KF883549	KF883705	KF883857	KF884021	KF884179	KF884344	KF884509	KF884674	KF884839	KF884999	KF885154
MVZ_222808	KF882756	KF882909	KF883073	KF883232	KF883388	KF883550	KF883706	KF883858	KF884022	KF884180	KF884345	KF884510	KF884675	KF884840	KF885000	KF885155
MVZ_222809	KF882757	KF882910	KF883074	KF883233	KF883389	KF883551	KF883707	KF883859	KF884023	KF884181	KF884346	KF884511	KF884676	KF884841	KF885001	
MVZ_223974	KF882758	KF882911	KF883075	KF883234	KF883390	KF883552	KF883708	KF883860	KF884024	KF884182	KF884347	KF884512	KF884677	KF884842	KF885002	
MVZ_223975	KF882759	KF882912	KF883076	KF883235	KF883391	KF883553	KF883709	KF883861	KF884025	KF884183	KF884348	KF884513	KF884678	KF884843	KF885003	
MVZ_224506	KF882760	KF882913	KF883077	KF883236	KF883392	KF883554	KF883710	KF883862	KF884026	KF884184	KF884349	KF884514	KF884679	KF884844	KF885004	KF885156
MVZ_224507	KF882761	KF882914	KF883078	KF883237	KF883393	KF883555	KF883711	KF883863	KF884027	KF884185	KF884350	KF884515	KF884680	KF884845	KF885005	
MVZ_224633	KF882762	KF882915	KF883079	KF883238	KF883394	KF883556	KF883712	KF883864	KF884028	KF884186	KF884351	KF884516	KF884681	KF884846	KF885006	
MVZ_224634	KF882763	KF882916	KF883080	KF883239	KF883395	KF883557	KF883713	KF883865	KF884029	KF884187	KF884352	KF884517	KF884682	KF884847	KF885007	
RBCM_013116	KF882798	KF882953	KF883117	KF883275	KF883432	KF883591	KF883748	KF883902	KF884066	KF884224	KF884389	KF884554	KF884719	KF884884	KF885044	
RBCM_013117	KF882799	KF882954	KF883118	KF883276	KF883433	KF883592	KF883749	KF883903	KF884067	KF884225	KF884390	KF884555	KF884720	KF884885	KF885045	
RBCM_016992	KF882800	KF882955	KF883119	KF883277	KF883434	KF883593		KF883904	KF884068	KF884226	KF884391	KF884556	KF884721	KF884886	KF885046	
UWBM_41850	KF882807	KF882968	KF883132	KF883286	KF883448	KF883603	KF883757	KF883917	KF884078	KF884240	KF884405	KF884570	KF884735	KF884896	KF885059	
UWBM_49091	KF882824	KF882988	KF883152	KF883305	KF883467	KF883622	KF883775	KF883937	KF884095	KF884260	KF884425	KF884590	KF884755	KF884915	KF885079	
UWBM_49092	KF882825	KF882989	KF883153	KF883306	KF883468	KF883623	KF883776	KF883938	KF884096	KF884261	KF884426	KF884591	KF884756	KF884916	KF885080	
UWBM_49093	KF882826	KF882990	KF883154	KF883307	KF883469	KF883624	KF883777	KF883939	KF884097	KF884262	KF884427	KF884592	KF884757	KF884917	KF885081	
UWBM_74107	KF882827	KF882991	KF883155	KF883308	KF883470	KF883625	KF883778	KF883940	KF884098	KF884263	KF884428	KF884593	KF884758	KF884918	KF885082	
UWBM_74110	KF882828	KF882992	KF883156	KF883309	KF883471	KF883626	KF883779	KF883941	KF884099	KF884264	KF884429	KF884594	KF884759	KF884919	KF885083	KF885190
UWBM_74114	KF882830	KF882994	KF883158	KF883310	KF883472	KF883628	KF883781	KF883943	KF884101	KF884266	KF884431	KF884596	KF884761	KF884921	KF885085	
UWBM_74139	KF882831	KF882995	KF883159	KF883311	KF883473	KF883629	KF883782	KF883944	KF884102	KF884267	KF884432	KF884597	KF884762	KF884922	KF885086	
UWBM_75142	KF882832	KF882996	KF883160	KF883312	KF883474	KF883630	KF883783	KF883945	KF884103	KF884268	KF884433	KF884598	KF884763	KF884923	KF885087	KF885191
UWBM_75455	KF882833	KF882997	KF883161	KF883313	KF883475	KF883631	KF883784	KF883946	KF884104	KF884269	KF884434	KF884599	KF884764	KF884924	KF885088	
UWBM_75461	KF882834	KF882998	KF883162	KF883314	KF883476	KF883632	KF883785	KF883947	KF884105	KF884270	KF884435	KF884600	KF884765	KF884925	KF885089	
UWBM_75828	KF882837	KF883001	KF883165	KF883317	KF883479	KF883635	KF883788	KF883950	KF884108	KF884273	KF884438	KF884603	KF884768	KF884928	KF885092	
UWBM_78345	KF882844	KF883008	KF883172	KF883324	KF883486	KF883642	KF883795	KF883957	KF884115	KF884280	KF884445	KF884610	KF884775	KF884935	KF885099	
UWBM_78685	KF882845	KF883009	KF883173	KF883325	KF883487	KF883643	KF883796	KF883958	KF884116	KF884281	KF884446	KF884611	KF884776	KF884936	KF885100	
UWBM_80404	KF882846	KF883010	KF883174	KF883326	KF883488	KF883644	KF883797	KF883959	KF884117	KF884282	KF884447	KF884612	KF884777	KF884937	KF885101	
UWBM_80630	KF882847	KF883011	KF883175	KF883327	KF883489	KF883645	KF883798	KF883960	KF884118	KF884283	KF884448	KF884613	KF884778	KF884938	KF885102	
UWBM_80685	KF882848	KF883012	KF883176	KF883328	KF883490	KF883646	KF883799	KF883961	KF884119	KF884284	KF884449	KF884614	KF884779	KF884939	KF885103	KF885194
UWBM_81939	KF882875	KF883039	KF883203	KF883355	KF883517	KF883672	KF883824	KF883988	KF884146	KF884311	KF884476	KF884641	KF884806	KF884966	KF885130	KF885214
UWBM_81940	KF882876	KF883040	KF883204	KF883356	KF883518	KF883673	KF883825	KF883989	KF884147	KF884312	KF884477	KF884642	KF884807	KF884967	KF885131	
UWBM_81941	KF882877	KF883041	KF883205	KF883357	KF883519	KF883674	KF883826	KF883990	KF884148	KF884313	KF884478	KF884643	KF884808	KF884968	KF885132	
UWBM_81942	KF882878	KF883042	KF883206	KF883358	KF883520	KF883675	KF883827	KF883991	KF884149	KF884314	KF884479	KF884644	KF884809	KF884969	KF885133	
UWBM_82026	KF882879	KF883043	KF883207	KF883359	KF883521	KF883676	KF883828	KF883992	KF884150	KF884315	KF884480	KF884645	KF884810	KF884970	KF885134	
UWBM_82029	KF882880	KF883044	KF883208	KF883360	KF883522	KF883677	KF883829	KF883993	KF884151	KF884316	KF884481	KF884646	KF884811	KF884971	KF885135	KF885215
UWBM_82030	KF882881	KF883045	KF883209	KF883361	KF883523	KF883678	KF883830	KF883994	KF884152	KF884317	KF884482	KF884647	KF884812	KF884972	KF885136	
UWBM_82048	KF882882	KF883046	KF883210	KF883362	KF883524	KF883679	KF883831	KF883995	KF884153	KF884318	KF884483	KF884648	KF884813	KF884973	KF885137	
UWBM_82049	KF882883	KF883047	KF883211	KF883363	KF883525	KF883680	KF883832	KF883996	KF884154	KF884319	KF884484	KF884649	KF884814	KF884974	KF885138	KF885216
UWBM_82058	KF882884	KF883048	KF883212	KF883364	KF883526	KF883681	KF883833	KF883997	KF884155	KF884320	KF884485	KF884650	KF884815	KF884975	KF885139	
UWBM_82059	KF882885	KF883049	KF883213	KF883365	KF883527	KF883682	KF883834	KF883998	KF884156	KF884321	KF884486	KF884651	KF884816	KF884976	KF885140	
UWBM_82091	KF882886	KF883050	KF883214	KF883366	KF883528	KF883683	KF883835	KF883999	KF884157	KF884322	KF884487	KF884652	KF884817	KF884977	KF885141	
UWBM_82092	KF882887	KF883051	KF883215	KF883367	KF883529	KF883684	KF883836	KF884000	KF884158	KF884323	KF884488	KF884653	KF884818	KF884978	KF885142	
UWBM_82110	KF882888	KF883052	KF883216	KF883368	KF883530	KF883685	KF883837	KF884001	KF884159	KF884324	KF884489	KF884654	KF884819	KF884979	KF885143	
BYU_13761	KF882736	KF882889	KF883053		KF883369	KF883681	KF883833	KF883997	KF884155	KF884320	KF884485	KF884650	KF884815	KF884975	KF885139	
FHSM-M_35931	KF882737	KF882890	KF883054		KF883370	KF883682	KF883834	KF883998	KF884003	KF884161	KF884326	KF884491	KF884656	KF884821	KF884981	KF885144
KU_120015	KF882742	KF882895	KF883059	KF883221	KF883375	KF883537	KF883692	KF883849	KF884008	KF884166	KF884331	KF884496	KF884661	KF884826	KF884986	
MSB_62078	KF882746	KF882899	KF883063		KF883379	KF883541	KF883696	KF883848	KF884012	KF884170	KF884335	KF884500	KF884665	KF884830	KF884990	
MSB_62079	KF882747	KF882900	KF883064		KF883380	KF883542	KF883697	KF883849	KF884013	KF884171	KF884336	KF884501	KF884666	KF884831	KF884991	
MSB_62244	KF882748	KF882901	KF883065	KF883225	KF883381	KF883543	KF883698	KF883850	KF884014	KF884172	KF884337	KF884502	KF884667	KF884832	KF884992	KF885150

Museum Number	GenBank Accession CARHSP1	GenBank Accession CLCNG	GenBank Accession CSE11	GenBank Accession GABRP	GenBank Accession GAD2	GenBank Accession GDAP1	GenBank Accession METT1.11A	GenBank Accession P4HA2	GenBank Accession P1POX	GenBank Accession PNPO	GenBank Accession PPAN	GenBank Accession SLC1.7A9	GenBank Accession TBC1D21	GenBank Accession THOC1	GenBank Accession TTR	GenBank Accession MTDNA
MSB_66245	KF882749	KF882902	KF883066	KF883226	KF883382	KF883544	KF883699	KF883851	KF884015	KF884173	KF884338	KF884503	KF884668	KF884833	KF884993	
MSB_70594	KF882750	KF882903	KF883067	KF883227			KF883700	KF883852	KF884016	KF884174	KF884339	KF884504	KF884669	KF884834	KF884994	KF885151
MSB_73178	KF882751	KF882904	KF883068	KF883228	KF883383	KF883545	KF883701	KF883853	KF884017	KF884175	KF884340	KF884505	KF884670	KF884835	KF884995	KF885152
MSB_73420	KF882752	KF882905	KF883069	KF883229	KF883384	KF883546	KF883702	KF883854	KF884018	KF884176	KF884341	KF884506	KF884671	KF884836	KF884996	
MSB_76659	KF882753	KF882906	KF883070		KF883385	KF883547	KF883703	KF883855	KF884019	KF884177	KF884342	KF884507	KF884672	KF884837	KF884997	KF885153
NMMNH_17677	KF882764	KF882917	KF883081	KF883240	KF883396	KF883558	KF883714	KF883866	KF884030	KF884188	KF884353	KF884518	KF884683	KF884848	KF885008	KF885157
NMMNH_17678	KF882765	KF882918	KF883082		KF883397	KF883559	KF883715	KF883867	KF884031	KF884189	KF884354	KF884519	KF884684	KF884849	KF885009	
PSM_13961	KF882766	KF882919	KF883083	KF883241	KF883398		KF883716	KF883868	KF884032	KF884190	KF884355	KF884520	KF884685	KF884850	KF885010	
PSM_13962	KF882767	KF882920	KF883084	KF883242	KF883399	KF883560		KF883869	KF884033	KF884191	KF884356	KF884521	KF884686	KF884851	KF885011	
PSM_13963	KF882768	KF882921	KF883085	KF883243	KF883400			KF883870	KF884034	KF884192	KF884357	KF884522	KF884687	KF884852	KF885012	KF885158
PSM_13964	KF882769	KF882922	KF883086	KF883244	KF883401		KF883717	KF883871	KF884035	KF884193	KF884358	KF884523	KF884688	KF884853	KF885013	
PSM_4106	KF882770	KF882923	KF883087	KF883245	KF883402	KF883561	KF883718	KF883872	KF884036	KF884194	KF884359	KF884524	KF884689	KF884854	KF885014	KF885159
PSM_4107	KF882771	KF882924	KF883088	KF883246	KF883403	KF883562	KF883719	KF883873	KF884037	KF884195	KF884360	KF884525	KF884690	KF884855	KF885015	
RBCM_001938	KF882772	KF882925	KF883089	KF883247	KF883404	KF883563	KF883720	KF883874	KF884038	KF884196	KF884361	KF884526	KF884691	KF884856	KF885016	
RBCM_001939		KF882926	KF883090	KF883248	KF883405	KF883564	KF883721	KF883875	KF884039	KF884197	KF884362	KF884527	KF884692	KF884857	KF885017	
RBCM_001941	KF882773	KF882927	KF883091	KF883249	KF883406	KF883565	KF883722	KF883876	KF884040	KF884198	KF884363	KF884528	KF884693	KF884858	KF885018	
RBCM_001943	KF882774	KF882928	KF883092	KF883250	KF883407	KF883566	KF883723	KF883877	KF884041	KF884199	KF884364	KF884529	KF884694	KF884859	KF885019	
RBCM_002900	KF882775	KF882929	KF883093	KF883251	KF883408	KF883567	KF883724	KF883878	KF884042	KF884200	KF884365	KF884530	KF884695	KF884860	KF885020	KF885160
RBCM_002901	KF882776	KF882930	KF883094	KF883252	KF883409	KF883568	KF883725	KF883879	KF884043	KF884201	KF884366	KF884531	KF884696	KF884861	KF885021	
RBCM_003176	KF882777	KF882931	KF883095	KF883253	KF883410	KF883569	KF883726	KF883880	KF884044	KF884202	KF884367	KF884532	KF884697	KF884862	KF885022	
RBCM_003177	KF882778	KF882932	KF883096	KF883254	KF883411	KF883570	KF883727	KF883881	KF884045	KF884203	KF884368	KF884533	KF884698	KF884863	KF885023	KF885161
RBCM_005433	KF882779	KF882933	KF883097	KF883255	KF883412	KF883571	KF883728	KF883882	KF884046	KF884204	KF884369	KF884534	KF884699	KF884864	KF885024	KF885162
RBCM_005434	KF882780	KF882934	KF883098	KF883256	KF883413	KF883572	KF883729	KF883883	KF884047	KF884205	KF884370	KF884535	KF884700	KF884865	KF885025	KF885163
RBCM_005853	KF882781	KF882935	KF883099	KF883257	KF883414	KF883573	KF883730	KF883884	KF884048	KF884206	KF884371	KF884536	KF884701	KF884866	KF885026	
RBCM_005854		KF882936	KF883100	KF883258	KF883415	KF883574	KF883731	KF883885	KF884049	KF884207	KF884372	KF884537	KF884702	KF884867	KF885027	
RBCM_006660	KF882782	KF882937	KF883101	KF883259	KF883416	KF883575	KF883732	KF883886	KF884050	KF884208	KF884373	KF884538	KF884703	KF884868	KF885028	KF885164
RBCM_006661	KF882783	KF882938	KF883102	KF883260	KF883417	KF883576	KF883733	KF883887	KF884051	KF884209	KF884374	KF884539	KF884704	KF884869	KF885029	KF885165
RBCM_006793	KF882784	KF882939	KF883103	KF883261	KF883418	KF883577	KF883734	KF883888	KF884052	KF884210	KF884375	KF884540	KF884705	KF884870	KF885030	
RBCM_007330	KF882785	KF882940	KF883104	KF883262	KF883419	KF883578	KF883735	KF883889	KF884053	KF884211	KF884376	KF884541	KF884706	KF884871	KF885031	KF885166
RBCM_007331	KF882786	KF882941	KF883105	KF883263	KF883420	KF883579	KF883736	KF883890	KF884054	KF884212	KF884377	KF884542	KF884707	KF884872	KF885032	KF885167
RBCM_007332	KF882787	KF882942	KF883106	KF883264	KF883421	KF883580	KF883737	KF883891	KF884055	KF884213	KF884378	KF884543	KF884708	KF884873	KF885033	KF885168
RBCM_007334	KF882788	KF882943	KF883107	KF883265	KF883422	KF883581	KF883738	KF883892	KF884056	KF884214	KF884379	KF884544	KF884709	KF884874	KF885034	KF885169
RBCM_007624	KF882789	KF882944	KF883108	KF883266	KF883423	KF883582	KF883739	KF883893	KF884057	KF884215	KF884380	KF884545	KF884710	KF884875	KF885035	KF885170
RBCM_007680	KF882790	KF882945	KF883109	KF883267	KF883424	KF883583	KF883740	KF883894	KF884058	KF884216	KF884381	KF884546	KF884711	KF884876	KF885036	
RBCM_009901	KF882791	KF882946	KF883110	KF883268	KF883425	KF883584	KF883741	KF883895	KF884059	KF884217	KF884382	KF884547	KF884712	KF884877	KF885037	
RBCM_010488	KF882792	KF882947	KF883111	KF883269	KF883426	KF883585	KF883742	KF883896	KF884060	KF884218	KF884383	KF884548	KF884713	KF884878	KF885038	KF885171
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RBCM_010510	KF882794	KF882949	KF883113	KF883271	KF883428	KF883587	KF883744	KF883898	KF884062	KF884220	KF884385	KF884550	KF884715	KF884880	KF885040	
RBCM_010511	KF882795	KF882950	KF883114	KF883272	KF883429	KF883588	KF883745	KF883899	KF884063	KF884221	KF884386	KF884551	KF884716	KF884881	KF885041	
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UAM_51395	KF882801	KF882957	KF883121		KF883436	KF883595	KF883751	KF883906	KF884070	KF884228	KF884393	KF884558	KF884723	KF884888	KF885048	KF885174
UBC_2482	KF882802	KF882958	KF883122	KF883279	KF883437	KF883596		KF883907	KF884071	KF884229	KF884394	KF884559	KF884724	KF884889	KF885049	
UBC_2483	KF882803	KF882959	KF883123	KF883280	KF883438	KF883597			KF884072	KF884230	KF884395	KF884560	KF884725	KF884890	KF885050	
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UWBM_30055	KF882804	KF882961	KF883125		KF883440		KF883753	KF883909	KF884074	KF884232	KF884397	KF884562	KF884727	KF884892	KF885052	KF885176
UWBM_30058	KF882805	KF882962	KF883126	KF883282	KF883441	KF883599	KF883754	KF883910	KF884075	KF884233	KF884398	KF884563	KF884728	KF884893	KF885053	
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UWBM_32082		KF882965	KF883129		KF883444			KF883913		KF884236	KF884401	KF884566	KF884731		KF885056	KF885178
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UWBM_43180		KF882969	KF883133					KF883918		KF884241	KF884406	KF884571	KF884736		KF885059	KF885182
UWBM_43185	KF882808	KF882970	KF883134	KF883287	KF883449	KF883604	KF883758	KF883919	KF884079	KF884242	KF884407	KF884572	KF884737	KF884897	KF885061	
UWBM_43186	KF882809	KF882971	KF883135	KF883288	KF883450	KF883605	KF883759	KF883920	KF884080	KF884243	KF884408	KF884573	KF884738	KF884898	KF885062	
UWBM_43188	KF882810	KF882972	KF883136	KF883289	KF883451	KF883606	KF883760	KF883921	KF884081	KF884244	KF884409	KF884574	KF884739	KF884899	KF885063	KF885183
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UWBM_43200		KF882974	KF883138	KF883291	KF883453	KF883608	KF883762	KF883923		KF884246	KF884411	KF884576	KF884741	KF884901	KF885065	
UWBM_43204	KF882812	KF882975	KF883139	KF883292	KF883454	KF883609	KF883763	KF883924	KF884083	KF884247	KF884412	KF884577	KF884742			

Museum Number	GenBank Accession CARHSP1	GenBank Accession CLCNG	GenBank Accession CSE11	GenBank Accession GABRP	GenBank Accession GAD2	GenBank Accession GDAP1	GenBank Accession METT.L11A	GenBank Accession P4HA2	GenBank Accession P1POX	GenBank Accession PNPO	GenBank Accession PPAN	GenBank Accession SLC17A9	GenBank Accession TBC1D21	GenBank Accession THOC1	GenBank Accession TTR	GenBank Accession MTDNA
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UWBM_43226	KF882814	KF882977	KF883141	KF883294	KF883456	KF883611	KF883765	KF883926	KF884085	KF884249	KF884414	KF884579	KF884744	KF884904	KF885068	KF885186
UWBM_43245	KF882815	KF882978	KF883142	KF883295	KF883457	KF883612	KF883766	KF883927	KF884086	KF884250	KF884415	KF884580	KF884745	KF884905	KF885069	
UWBM_43246	KF882816	KF882979	KF883143	KF883296	KF883458	KF883613	KF883767	KF883928	KF884087	KF884251	KF884416	KF884581	KF884746	KF884906	KF885070	
UWBM_43254	KF882817	KF882980	KF883144	KF883297	KF883459	KF883614	KF883768	KF883929	KF884088	KF884252	KF884417	KF884582	KF884747	KF884907	KF885071	
UWBM_43255	KF882818	KF882981	KF883145	KF883298	KF883460	KF883615	KF883769	KF883930	KF884089	KF884253	KF884418	KF884583	KF884748	KF884908	KF885072	KF885187
UWBM_43256	KF882819	KF882982	KF883146	KF883299	KF883461	KF883616	KF883770	KF883931	KF884090	KF884254	KF884419	KF884584	KF884749	KF884909	KF885073	
UWBM_43257	KF882820	KF882983	KF883147	KF883300	KF883462	KF883617	KF883771	KF883932	KF884091	KF884255	KF884420	KF884585	KF884750	KF884910	KF885074	
UWBM_43263	KF882821	KF882984	KF883148	KF883301	KF883463	KF883618	KF883772	KF883933	KF884092	KF884256	KF884421	KF884586	KF884751	KF884911	KF885075	
UWBM_43276		KF882985	KF883149	KF883302	KF883464	KF883619		KF883934		KF884257	KF884422	KF884587	KF884752	KF884912	KF885076	KF885188
UWBM_44442	KF882822	KF882986	KF883150	KF883303	KF883465	KF883620	KF883773	KF883935	KF884093	KF884258	KF884423	KF884588	KF884753	KF884913	KF885077	
UWBM_44943	KF882823	KF882987	KF883151	KF883304	KF883466	KF883621	KF883774	KF883936	KF884094	KF884259	KF884424	KF884589	KF884754	KF884914	KF885078	KF885189
UWBM_74113	KF882829	KF882993	KF883157			KF883627	KF883780	KF883942	KF884100	KF884265	KF884430	KF884595	KF884760	KF884920	KF885084	
UWBM_75493	KF882835	KF882999	KF883163	KF883315	KF883477	KF883633	KF883786	KF883948	KF884106	KF884271	KF884436	KF884601	KF884766	KF884926	KF885090	KF885192
UWBM_75494	KF882836	KF883000	KF883164	KF883316	KF883478	KF883634	KF883787	KF883949	KF884107	KF884272	KF884437	KF884602	KF884767	KF884927	KF885091	KF885193
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UWBM_78125	KF882842	KF883006	KF883170	KF883322	KF883484	KF883640	KF883793	KF883955	KF884113	KF884278	KF884443	KF884608	KF884773	KF884933	KF885097	
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UWBM_81513	KF882849	KF883013	KF883177	KF883329	KF883491	KF883647	KF883800	KF883962	KF884120	KF884285	KF884450	KF884615	KF884780	KF884940	KF885104	
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UWBM_81519	KF882851	KF883015	KF883179	KF883331	KF883493	KF883649	KF883801	KF883964	KF884122	KF884287	KF884452	KF884617	KF884782	KF884942	KF885106	
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UWBM_81925	KF882861	KF883025	KF883189	KF883341	KF883503	KF883659	KF883810	KF883974	KF884132	KF884297	KF884462	KF884627	KF884792	KF884952	KF885116	KF885202
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