University of Nevada, Reno

Molecular and morphological variation in *Neotoma cinerea*

A thesis submitted in partial fulfillment of the requirements
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by

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ABSTRACT

Neotoma cinerea, the bushy-tailed woodrat, is a wide-ranging species displaying broad phenotypic variation cataloged by researchers through the last 200 years. However, all major taxonomic revisions and assessments of morphological patterns pre-date modern molecular and statistical techniques, which can help clarify evolutionary histories and relationships within taxa. The aim of this study is to assess broad-scale molecular (cytochrome *b*) and craniodental morphological variation in *N. cinerea*, and to infer biogeographic history from these data coupled with dated paleomidden records. Two major phylogenetic clades were identified, showing an average uncorrected sequence divergence of 6.5%. Morphology seems to be more strongly correlated with potential environmental variables than with phylogeny, supporting assertions that *N. cinerea* is sensitive to climate and evolves morphologically in response to it. Inferred biogeographic histories of the major clades suggest allopatry and independent evolution until relatively recently, and both molecular and morphological evidence suggest interbreeding between the major clades in regions of secondary contact.

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Taxonomic history of *Neotoma cinerea*, the bushy-tailed woodrat

GENUS AND SPECIES ESTABLISHMENT

Neotoma cinerea, the bushy-tailed woodrat, was among the first woodrat species to be described and named by Euro-American explorers and naturalists. The earliest scientific description is attributed to Meriwether Lewis of Lewis and Clark fame, who noted that a large rat with a furred tail had been caught among the baggage of the expedition near Great Falls, Montana (Lewis 1805). *Neotoma cinerea* was officially named in 1815 based on this description and others from the expedition journals; however, genus *Neotoma* had not yet been established, so this species was first dubbed *Mus cinereus*, the ash-colored rat (Ord 1815). Genus *Neotoma* was founded soon after based on dentition differences between New and Old World rats (Say and Ord 1825), and *Mus cinereus* was renamed *Neotoma cinerea*, the specific name still in use today (Baird 1858; Smith 1997).

TEONOMA SUBGENUS

As its common name suggests, the defining characteristic of *Neotoma cinerea* has been its bushy tail; all other *Neotoma* species lack such extensively furred tails and are collectively termed round-tailed woodrats. The importance of this single trait for classification has been questioned on the grounds that it may be merely superficial. Merriam advanced perhaps the most extreme opinion on this, partially or wholly disregarding the tail when he chose to classify groups of bushy-tailed woodrats under different subgenera (Merriam 1894b); prior to that, he had mulled over whether the groups even belonged under separate genera (Merriam 1893). However, other morphological traits of the pelage, cranium, and baculum coincide with the characteristic tail to support recognition of bushy-tailed woodrats as a distinct group (Baird 1858; Goldman 1910; Burt and Barkalow 1942). This evidence also suggests a relatively deep divergence from round-tailed woodrats, as does recent cytological and molecular work (Mascarello and Hsu 1974; Planz *et al.* 1996; Edwards and Bradley 2002). Thus from a practical standpoint, there is good evidence allowing use of the bushy tail as a convenient external diagnostic feature for this group.

Three subgenera of genus *Neotoma* are currently recognized: subgenus *Teonoma* containing only *Neotoma cinerea*, and subgenera *Neotoma* and *Teonopus* containing all other *Neotoma* species (Edwards and Bradley 2002). The divergence between *Neotoma cinerea* and other woodrat species is the basis for classification of bushy-tailed woodrats under subgenus *Teonoma*, although the use and rank of the name *Teonoma* have been disputed over time.

Teonoma was first proposed as a genus rank for bushy-tailed woodrats by Gray in 1843, though it was not generally accepted and for some time taxonomists relegated *Teonoma* to subgeneric status or chose not to recognize it at all (Merriam 1893; Goldman 1910). Indeed, Coues (1877), under the paradigm of taxonomic lumping, suggested that many of Gray's new genera including *Teonoma* could be disregarded. The push for use of *Teonoma* as a genus was revived in the early 1900's. The argument was based on the familiar bushy tail, but also the elongated rostrum, narrow interorbital constriction, and other cranial features of *Neotoma cinerea* which allowed easy identification compared to round-tailed *Neotoma* species (Elliot 1904). Numerous publications by Elliot in the early 1900's applied *Teonoma* as a genus rank; however, the attempt to establish a new genus was once again futile. In a sweeping taxonomic revision of genus *Neotoma* in 1910, Goldman returned to the use of *Teonoma* as a subgenus. He argued that although the bushy-tailed rats formed a well-defined group, the cranium and dentition confirmed their very close relationship to round-tailed *Neotoma* species; he deemed the bushy tail to be a superficial character that did not warrant more than subgeneric recognition (1910).

Goldman's treatment of *Teonoma* as a subgenus has been definitive through today, although new information is accumulating to help assess this standard. Recent molecular work suggests that *Neotoma cinerea* is fairly diverged from other *Neotoma* species, which could support arguments for raising *Teonoma* to genus level (Edwards and Bradley 2002). Alternatively, phylogenetic reconstructions with *Neotoma cinerea* nested in the same clade as the *Neotoma fuscipes* complex (subgenus *Homodontomys*) and *Neotoma lepida* complex (subgenus *Neotoma*) have begun to question the validity of *Teonoma* even as a subgenus (Longhofer and Bradley 2006; Matocq *et al.* 2007). Any proposals regarding the use and rank of *Teonoma* have been deferred until more complete information is available to resolve the deep relationships within *Neotoma*. In the meantime, recognition of *Teonoma* as a monotypic subgenus for *Neotoma cinerea* is considered sound (Edwards and Bradley 2002; Longhofer and Bradley 2006).

MAJOR GROUPS

Thirteen subspecies of *Neotoma cinerea* are currently recognized (Hall 1981; Smith 1997). Unfortunately, this scheme no longer reflects the two major intraspecific groups that were apparent based largely on morphology and pelage: the *occidentalis* group (True 1894) which will be referred to here as the Western group, and the *orolestes* group (Allen 1894) which will be referred to as the Eastern group. Following is an account of the formation of these groups, factors differentiating them, and subspecies classified under each; this information is summarized more completely in Appendices I-IV. Subspecies boundaries as most recently defined (Hall 1981) are shown in Figure 1.

Major Groups: Western

Not long after *Neotoma cinerea* was established, a new species called *Myoxus drummondii*, the Rocky Mountain dormouse, was described from southern British Columbia (Richardson 1828). With its general murine appearance and bushy tail, this species was initially assumed to be related to the familiar European dormouse of genus *Myoxus* (Coues 1874). However, it was soon recognized as akin to New World woodrats and was renamed accordingly as *Neotoma drummondii* (Richardson 1829). Another species, *Neotoma occidentalis*, was later proposed from coastal Washington (Baird 1855).

In 1877, Coues published a lucid monograph on North American rodents wherein he supported his previous assertion (1874) that *Neotoma cinerea*, *Neotoma drummondii*, and *Neotoma occidentalis* should be consolidated under the species name *Neotoma cinerea*, the bushy-tailed woodrat. This result was based on what Coues felt were gradations in size and pelage that made it impossible to delimit the 3 species from one another. Although Coues argued for only one species (*Neotoma cinerea*), he did recognize 3 forms (Arctic, Pacific Coast, United States prairie) which agreed only partially with the species that had been consolidated. He asserted that if more than one species were ultimately delineated, there must be 3 following his assessment; however, he did grant that the Arctic and Pacific coast forms were more similar to each other than to the United States prairie form (Coues 1877).

There may have been little controversy over this revision at the time; however, it was noted later that Coues' work was done at the height of the "wave of conservatism" when taxonomic lumping was popular and many species were reduced to varietal or subspecific status (Allen 1909). Even worse, Coues was primarily an ornithologist so his work in mammalogy may have been poorly received (Allen 1909), and at least his treatment of *Neotoma cinerea* was apparently ignored by some (*e.g.* True 1894, Elliot 1899). However, Coues' argument for a single species was and is generally accepted by mammalogists, who reclassified the previously described species as subspecies of *Neotoma cinerea* but apparently did not pursue Coues' 3 forms (Allen 1891; Merriam 1892).

Coues' (1877) consolidation, particularly his Arctic and Pacific coast forms, laid the basis for what can be recognized as the Western *Neotoma cinerea* group. Assignment of more taxa to this group has been based largely on general resemblance to and intergradations with recognized Western forms. Almost all new taxa were introduced as subspecies of *Neotoma cinerea* in keeping with Coues' treatment, and those that were not became quickly reclassified. In addition to *Neotoma cinerea cinerea*, *Neotoma cinerea drummondii*, and *Neotoma cinerea occidentalis*, Western group taxa still currently recognized include *Neotoma cinerea fusca* from coastal Oregon (True 1894), *Neotoma cinerea acraea* from southern California (Elliot 1903c), *Neotoma cinerea alticola* from northeastern California (Hooper 1940), and *Neotoma cinerea pulla* from northern California (Hooper 1940). *Neotoma cinerea lucida* from southern Nevada (Goldman 1917) is also recognized despite being synonymized under *Neotoma cinerea acraea* (Burt 1934; Hooper 1940); its retention to the present is not evidently explained and could represent an error, although it is retained here for consistency with the most recent authority (Hall 1981).

The irony of Coues' work was that although his 3 forms were never formally proposed or accepted, in them he had recognized perhaps the most fundamental morphological division within *Neotoma cinerea*. What's more, he identified this split based solely on pelage and external measurements, rather than on cranial morphology which seems to provide a much clearer sense of this division (see below). As noted, the species that Coues consolidated under *Neotoma cinerea* represented his closely-related Arctic and Pacific coast forms and established the basis for the Western group; however, there were no named taxa at that time to represent his quite different United States prairie form. That group, which could have been recognized based on Coues' work, had to be documented anew later.

Major Groups: Eastern

After the consolidation of *Neotoma cinerea* by Coues (1877), another group of bushy-tailed woodrats was recognized that did not seem to be so closely-related to the early described groups. Recognition of the Eastern group formally began when Merriam proposed a new species, *Neotoma arizonae* from northeast Arizona (1893). Although *Neotoma arizonae* displayed the characteristic bushy tail, he chose not to classify it under *Neotoma cinerea* or even under subgenus *Teonoma* (1894b). This decision was influenced by a relatively dramatic cranial difference: a pair of large gaps posterior to the hard palate between the sphenoid and palatine bones, which he termed sphenopalatine vacuities, here abbreviated SPV's (1893; Figure 2). These SPV's were open in all *Neotoma* (although variable in size; True 1894), except for taxa in Coues' *Neotoma* *cinerea* where they were instead usually fused closed by medial extensions of the palatines. Since the bushy tail was associated with *Neotoma cinerea*, but open SPV's were associated with round-tailed *Neotoma*, the co-occurrence of these traits was a peculiar find.

One year after establishing *Neotoma arizonae*, Merriam proposed another species, *Neotoma orolestes* from southern Colorado, which also showed this combination of bushy tail and open SPV's (1894a). He recognized that *Neotoma orolestes* was related to *Neotoma cinerea* and suggested they be classified together under subgenus *Teonoma*, using the SPV's distinguish between species: open SPV's in *Neotoma orolestes,* but closed SPV's in *Neotoma cinerea* and its subspecies (Merriam 1894). SPV morphology proved to be slightly more complicated than Merriam surmised, although it is quite consistent (Goldman 1910) and has become the primary character by which members of the Eastern (open SPV's) and Western (narrow or absent SPV's) groups have been distinguished.

Many groups of bushy-tailed woodrats were recognized in a flurry of descriptive activity from the late 1800's to early 1900's, such that development of the Western and Eastern groups occurred somewhat simultaneously. The early treatment by Coues (1877), however, impacted how new groups were classified. While taxonomy of the Western group generally proceeded by the addition of new *Neotoma cinerea* subspecies following Coues assessment, development of the Eastern group over the same time period proceeded by the addition of entirely new species. There may have been little interest at first in consolidating the new Eastern species that were clearly related, but in any case this was remedied by a broad revision of *Neotoma* by Goldman in 1910.

Goldman essentially extended Coues treatment; although he seems to have acknowledged a division between the major groups of *Neotoma cinerea*, his resulting classification does not reflect this. The Eastern group taxa were treated as subspecies and all classified under the species name *Neotoma cinerea*, equalizing the ranks of all Eastern and Western taxa (Goldman 1910).

In addition to *Neotoma cinerea arizonae* and *Neotoma cinerea orolestes*, eastern group subspecies still currently recognized include *Neotoma cinerea rupicola* from northwest South Dakota (Allen 1894), *Neotoma cinerea cinnamomea* from southwest Wyoming (Allen 1895), and *Neotoma cinerea macrodon* from eastern Utah (Kelson 1949). Several authors have suggested that *Neotoma cinerea cinnamomea* and perhaps *Neotoma cinerea macrodon* are not sufficiently diverged to warrant recognition, and should be synonymized under *Neotoma cinerea arizonae* (Finley 1958; Long 1965; Armstrong 1972).

CONCLUSIONS

While much of the current *Neotoma cinerea* classification scheme is attributable to accumulated minor revisions, probably the most notable or influential points came from the work of Coues (1877) and Goldman (1910). As noted, Coues' (1877) revision set the precedent for classification of all bushy-tailed woodrats under one species name, *Neotoma cinerea*, and his work foreshadowed the recognition of the major Eastern and Western groups despite not strongly asserting that division himself. Goldman's (1910) more recent revision had two major consequences. First, Goldman extended Coues' treatment and summarized the evidence that all groups of bushy-tailed woodrats are closely related by classifying them under the same subgenus and species names.

Subgenus *Teonoma* is currently monotypic; the names *Teonoma* and *Neotoma cinerea* are therefore essentially synonymous. Second, the equalization of all groups as subspecies obscured the intraspecific dichotomy (Eastern and Western groups) that could be reflective of actual hierarchical relationships within *Neotoma cinerea*. It is unclear whether the division of Western and Eastern groups is reasonable beyond SPV morphology, although Coues had essentially recognized this division based on external morphology alone.

The taxonomic classification of *Neotoma cinerea* has been reshaped by many authors, although nearly 5 decades have passed since any revision has been advanced and accepted, and nearly 3 decades have passed since the broad evolutionary relationships within this species have been summarized or examined at any length (Cowan and Guiguet 1960; Hall 1981). Taxonomy must be ever-evolving to update our hypotheses on evolutionary relationships with new information; however, this process results in classifications that are almost necessarily deceptively simple, masking their own complex development as it occurs. Reviews of past revisions and hypotheses help to put modern taxonomic schemes in perspective. It is evident that, insomuch as systematics aims to reflect evolutionary history through classification, some of the detail of intraspecific *Neotoma cinerea* relationships may have been lost in favor of the broader picture.

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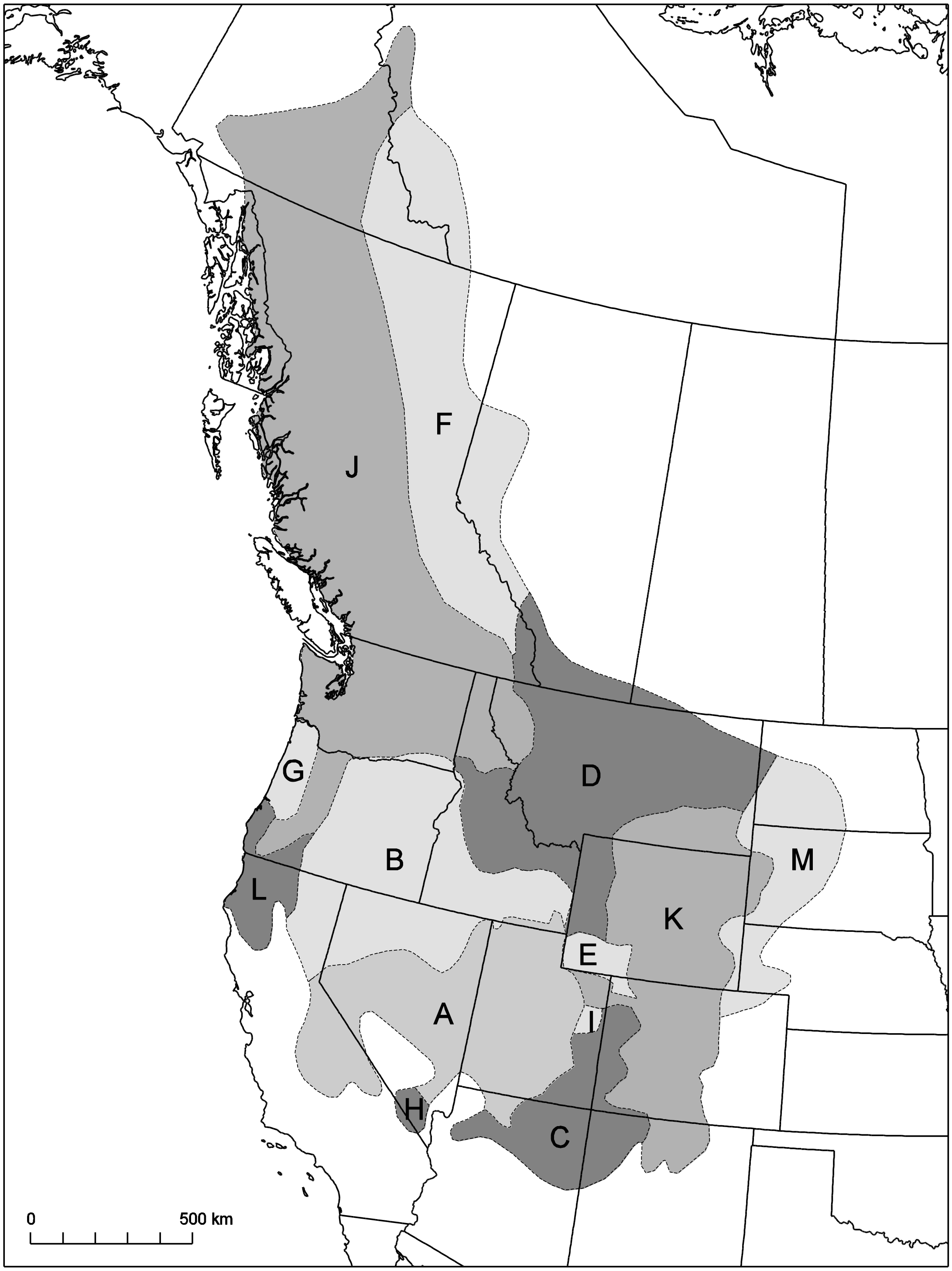

Figure 1.

Figure 1. Distribution of the 13 currently recognized subspecies of *Neotoma cinerea* (re-drawn from Hall 1981). Western group: (A) *acraea*; (B) *alticola*; (D) *cinerea*; (F) *drummondii*; (G) *fusca*; (H) *lucida*; (J) *occidentalis*; and (L) *pulla*. Eastern group: (C) *arizonae*; (E) *cinnamomea*; (I) *macrodon*; (K) *orolestes*; and (M) *rupicola.*

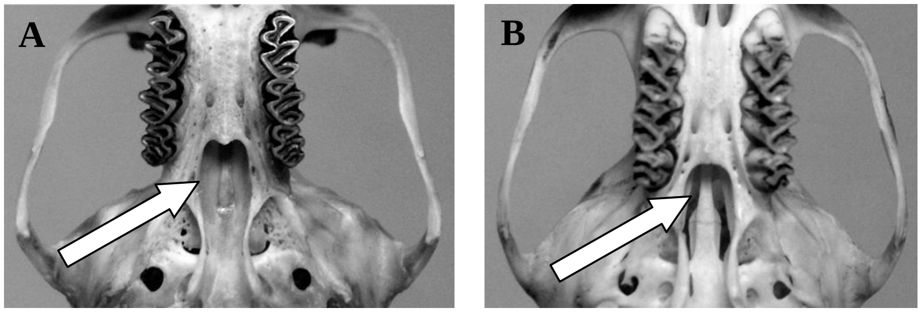

Figure 2.

Figure 2. Extremes of *Neotoma cinerea* sphenopalatine vacuity (SPV) morphology as seen on the ventral skull: (A) closed SPV's, MSB 108430, Western group *N. c. alticola* from southwest Idaho; (B) open SPV's, MSB 86004, Eastern group *N. c. orolestes* from northern New Mexico.

APPENDIX I: General taxonomic chronology of *Neotoma cinerea*

A note on spelling:
Two misspellings are pervasive in the historical *Neotoma cinerea* literature. The first is the spelling of "*acraea*" as "*acraia*", the latter being a typographical error in Elliot's (1903) original taxon account and noted by him the following year (1904) in attempt to correct it. The spelling "*acraea*" is used here in keeping with the author's original intention (*per* Smith 1997) regardless of which spelling was used by subsequent authors. The second common misspelling is of Richardson's (1828) "*drummondii*" as "*drummondi*", which began with Merriam (1892) for no clear reason and has continued through today (*e.g.* Smith 1997). This is assumed to be an error so use of the original spelling "*drummondii*" is revived here, again regardless of the spelling used by later authors. Both of these misspellings are so minor that they have certainly not confused intention or impacted communication between authors.

Neotoma cinerea cinerea (Hooper 1940)
Neotoma cinerea [*cinerea*] (Goldman 1910)
Teonoma cinerea (Elliot 1905)
Neotoma cinerea (Baird 1858)
Neotoma cinerea (*sensu lato* Say & Ord 1825)
***Mus cinereus* Ord (1815)**

Neotoma cinerea drummondii (Smith 1997)
Neotoma cinerea drummondii (Hooper 1940)
Neotoma cinerea drummondii (Goldman 1910)
Teonoma cinerea drummondii (Elliot 1905)
Neotoma drummondii (Osgood 1900)
Neotoma cinerea drummondii (Merriam 1892)
=Coues' (1877) "Arctic" form
=*Neotoma cinerea* (Coues 1874)
=*Neotoma cinerea* (Baird 1858)
Teonoma drummondii (Gray 1843)
Neotoma drummondii (Richardson 1829)
***Myoxus drummondii* Richardson (1828)**

Neotoma cinerea occidentalis (Goldman 1910)
Teonoma cinerea occidentalis (Elliot May 1903)
Neotoma occidentalis (Osgood 1900)
Neotoma occidentalis (Elliot 1899)
Neotoma occidentalis (True 1894)
Neotoma cinerea occidentalis (Allen 1891)
=*sensu* Coues' (1877) "Pacific coast" form
=*Neotoma cinerea* (Coues 1874)
***Neotoma occidentalis* Baird [often credited to Cooper, the collector] (1855)**

Neotoma cinerea arizonae (Goldman 1910)
Teonoma arizonae (Elliot 1905)
***Neotoma arizonae* Merriam (1893)**

Neotoma cinerea orolestes (Goldman 1910)
Teonoma oreolestes [=*orolestes*] (Elliot 1905)
***Neotoma orolestes* Merriam (1894)**

Neotoma cinerea rupicola (Goldman 1910)
Teonoma rupicola (Elliot 1905)
***Neotoma rupicola* Allen (1894)**
=*sensu* Coues' (1877) "United States prairie" form

=*Neotoma cinerea orolestes* (Goldman 1910)
***Neotoma grangeri* (Allen 1894)**

Neotoma cinerea fusca (Goldman 1910)
Teonoma fusca (Elliot May 1903)
Neotoma cinerea fusca (Trousessart 1897, from Goldman 1910)
***Neotoma occidentalis fusca* True (1894)**

Neotoma cinerea cinnamomea (Hall 1981)
=*Neotoma cinerea arizonae* (Armstrong 1972)
=*Neotoma cinerea arizonae* (Finley 1958)
Neotoma cinerea cinnamomea (Hooper 1944)
Neotoma cinerea cinnamomea (Warren 1942 *per* Finley 1958)
=*Neotoma cinerea orolestes* (Goldman 1910)
Teonoma cinnamomea (Elliot 1905)
***Neotoma cinnamomea* Allen (1895)**

=*Neotoma cinerea occidentalis* (Goldman 1910)
***Neotoma cinerea columbiana* Elliot (1899)**

=*Neotoma cinerea occidentalis* (Cowan and Guiguet 1960)
Neotoma cinerea saxamans (Hooper 1940)
Neotoma cinerea saxamans (Goldman 1910)
Teonoma saxamans (Elliot 1905)
Neotoma cinerea saxamans (Allen 1903)
***Neotoma saxamans* Osgood (1900)**

=*Neotoma cinerea fusca* (Goldman 1910)
Teonoma fusca apicalis (Elliot May 1903)
***Neotoma fuscus* [=*fusca*] *apicalis* Elliot (1903a)**

Neotoma cinerea acraea (Smith 1997)
Neotoma cinerea acraea (Burt 1934)
=*Neotoma cinerea* (Goldman 1910)
Teonoma acraea (Elliot 1905)
***Teonoma cinerea acraea* Elliot (1904)**
***Teonoma cinerea acraia* [=*acraea*] Elliot (1903c)**

Neotoma cinerea lucida (Hall 1981)
=*Neotoma cinerea acraea* (Burt 1934)
***Neotoma cinerea lucida* Goldman (1917)**

***Neotoma cinerea alticola* Hooper (1940)**

***Neotoma cinerea pulla* Hooper (1940)**

***Neotoma cinerea macrodon* Kelson (1949)**

APPENDIX II: Taxa implicated in major revisions of *Neotoma cinerea*

Gray (1843)

1. Proposed: genus *Teonoma*	Including: *sensu* all bushy-tailed woodrats
2. Proposed: *Teonoma drummondii*	Including: *Neotoma drummondii* Richardson

Baird (1858)

1. Supported: *Neotoma occidentalis*	Including: *Neotoma occidentalis* Baird
2. Proposed: *Neotoma cinerea*	Including: *Neotoma cinerea* Ord *Neotoma drummondii* Richardson

Coues (1974)

1. Proposed: *Neotoma cinerea*	Including: *Neotoma cinerea* Ord *Neotoma drummondii* Richardson *Neotoma occidentalis* Baird

Coues (1974, 1977)

1. Supported: *Neotoma cinerea*	Including: Arctic form [*Neotoma drummondii* Richardson] Pacific coast form [*sensu Neotoma occidentalis* Baird] United States prairie form [*sensu Neotoma rupicola* Allen, then un-named]

Merriam (1893)

1. Proposed: genus or subgenus *Teonoma*	Including: bushy-tailed woodrats with closed SPV's: *Neotoma cinerea* Ord *Neotoma drummondii* Richardson *Neotoma occidentalis* Baird Excluding: all round-tailed woodrats (open SPV's) bushy-tailed woodrats with open SPV's: *Neotoma arizonae* Merriam

Merriam (1894b)

1. Proposed: subgenus Teonoma	Including: bushy-tailed woodrats with closed SPV's: *Neotoma cinerea* Ord *Neotoma cinerea drummondii* Richardson *Neotoma cinerea occidentalis* Baird some bushy-tailed woodrats with open SPV's: *Neotoma orolestes* Merriam
2. Extended: subgenus *Neotoma*	To include: some bushy-tailed woodrats with open SPV's: *Neotoma arizonae* Merriam

Elliot (1903a; 1903b; 1905)

1.	Proposed:	Including:
	genus *Teonoma*	all bushy-tailed woodrats
2.	Proposed:	Including:
	Teonoma cinerea	*Neotoma cinerea* Ord
	Teonoma cinerea columbiana	*Neotoma cinerea columbiana* Elliot
	Teonoma cinerea drummondii	*Neotoma drummondii* Richardson
	Teonoma cinerea occidentalis	*Neotoma occidentalis* Baird
3.	Proposed:	Including:
	Teonoma acraea	*Teonoma cinerea acraea* Elliot
4.	Proposed:	Including:
	Teonoma arizonae	*Neotoma arizonae* Merriam
5.	Proposed:	Including:
	Teonoma cinnamomea	*Neotoma cinnamomea* Allen
6.	Proposed:	Including:
	Teonoma fusca	*Neotoma occidentalis fusca* True
	Teonoma fusca apicalis	*Neotoma fusca apicalis* Elliot
7.	Proposed:	Including:
	Teonoma grangeri	*Neotoma grangeri* Allen
8.	Proposed:	Including:
	Teonoma orolestes	*Neotoma orolestes* Merriam
9.	Proposed:	Including:
	Teonoma rupicola	*Neotoma rupicola* Allen
10.	Proposed:	Including:
	Teonoma saxamans	*Neotoma saxamans* Osgood

Goldman (1910)

1.	Supported:	Including:
	subgenus *Teonoma*	all bushy-tailed woodrats:
		Neotoma cinerea and subspecies
2.	Proposed:	Including:
	Neotoma cinerea [*cinerea*]	*Neotoma cinerea* Ord
		Teonoma cinerea acraea Elliot
	Neotoma cinerea arizonae	*Neotoma arizonae* Merriam
	Neotoma cinerea drummondii	*Neotoma drummondii* Richardson
	Neotoma cinerea fusca	*Neotoma occidentalis fusca* True
		Neotoma fusca apicalis Elliot
	Neotoma cinerea occidentalis	*Neotoma occidentalis* Baird
		Neotoma cinerea columbiana Elliot
	Neotoma cinerea orolestes	*Neotoma orolestes* Merriam
		Neotoma cinnamomea Allen
		Neotoma grangeri Allen
	Neotoma cinerea rupicola	*Neotoma rupicola* Allen
	Neotoma cinerea saxamans	*Neotoma saxamans* Osgood

Burt (1934)

1. Proposed:	Including:
Neotoma cinerea acraea	*Teonoma cinerea acraea* Elliot
	Neotoma cinerea lucida Goldman

Cowan and Guiguet (1960)

1. Proposed:	Including:
Neotoma cinerea occidentalis	*Neotoma occidentalis* Baird
	Neotoma saxamans Osgood

APPENDIX III: *Neotoma cinerea* type localities

Neotoma cinerea cinerea Ord
Great Falls, Cascade County, Montana

Neotoma cinerea acraea Elliot
Hot Springs, Long Canyon, Mount Whitney, Inyo County, California

Neotoma cinerea alticola Hooper
Parker Creek [=Shields Creek], Warner Mountains, Modoc County, California

Neotoma cinerea arizonae Merriam
Keams Canyon, Apache [=Navajo] County, Arizona

Neotoma cinerea cinnamomea Allen
Kinney Ranch, Bitter Creek, Sweetwater County, Wyoming

Neotoma cinerea drummondii Richardson
near Jasper House, Alberta (Goldman 1910)

Neotoma cinerea fusca True
U.S.N.M Ft. Umpqua, Douglas County, Oregon

Neotoma fuscus apicalis Elliot [=*Neotoma cinerea fusca*]
Gardiner, Coos County, Oregon

Neotoma cinerea lucida Goldman
Charleston Peak, Charleston Mountains, Clark County, Nevada

Neotoma cinerea macrodon Kelson
Northern edge of the East Tavaputs Plateau, Uintah County, Utah

Neotoma cinerea occidentalis Baird
Shoalwater [=Willapa] Bay, Pacific County, Washington

Neotoma cinerea columbiana Elliot [=*Neotoma cinerea occidentalis*]
Campbell's Ranch, Elwah River, Olympic Mountains, Washington
Boulder Creek, Olympic Mountains, Washington
Johnson's Ranch, Elwah River, Olympic Mountains, Washington
Happy Lake, Olympic Mountains, Washington

Neotoma cinerea saxamans Osgood [=*Neotoma cinerea occidentalis*]
Bennett City, head of Lake Bennett, British Columbia [northern British Columbia]

Neotoma cinerea orolestes Merriam
Saguache Valley (20 miles west of Saguache), Saguache County, Colorado

Neotoma grangeri Allen [=*Neotoma cinerea orolestes*]
Custer, Black Hills, South Dakota

Neotoma cinerea pulla Hooper
Kohenberger's Ranch, South Fork Mountains, Trinity County, California

Neotoma cinerea rupicola Allen
Corral Draw (southeastern base of the Black Hills), Pine River Indian Reservation, South Dakota

APPENDIX IV: Pertinent morphological features of *Neotoma cinerea* subspecies

Neotoma cinerea cinerea Ord

- SPV's absent or very small (Goldman 1910); wider (0.3-0.6 mm) than in other Western group subspecies (*N. c. alticola*, *acraea*, *fusca*, *occidentalis*, *pulla*; Hooper 1940)
- Comparing *N. c. cinerea* (grouped with *drummondii*), molars comparable length but broader compared to *N. c. occidentalis* (Baird 1858)
- Bullae moderately sized (Hooper 1940); Bullae large (Cowan and Guiguet 1960)
- Zygomatics spread wide posteriorly (Hooper 1940)
- *N. c. cinerea* intergrades with *acraea* very gradually (Burt 1934) [zone of intergradation later named *N. c. alticola* Hooper]

Neotoma cinerea acraea Elliot

- SPV's absent (Goldman 1910); SPV's closed (Hooper 1940)
- Specimens from southern Utah and Northern Arizona have enlarged bullae (Goldman 1910)
- Zygomatic spread relatively large (Hooper 1940)
- Molar row short, molars smaller than in *N. c. alticola* (Hooper 1940)
- *N. c. cinerea* intergrades with *acraea* very gradually (Burt 1934) [zone of intergradation later named *N. c. alticola* Hooper]
- Intergrades with *N. c. alticola* (Hooper 1940)
- May intergrade with *N. c. cinnamomea* (Finley 1958)

Neotoma cinerea alticola Hooper

- SPV's absent or very small (Hooper 1940)
- Bullae large, zygomatics spread moderately wide, molar row long and molars massive, rostrum narrow and deep (Hooper 1940)
- *N. c. cinerea* intergrades with *acraea* very gradually (Burt 1934) [zone of intergradation later named *N. c. alticola* Hooper]

Neotoma cinerea arizonae Merriam

- SPV's large (Goldman 1910)
- Inflated bullae compared with *N. cinerea* [*cinerea, drummondii, occidentalis*] (Merriam 1893); larger bullae compared to *orolestes* (Goldman 1910)
- Shorter nasals compared with *N. cinerea* [*cinerea, drummondii, occidentalis*] (Merriam 1893)
- Larger molars compared with *N. cinerea* [*cinerea, drummondii, occidentalis*] (Merriam 1893)
- Intergrades with *N. c. orolestes* (Finley 1958)

Neotoma cinerea cinnamomea Allen

- SPV's large, 0.6-1.0mm wide (Hooper 1944); Belongs in *N. c. orolestes* [Eastern] group, although it's much smaller than *orolestes* (Allen 1895)
- Bullae larger than in *N. c. orolestes* (Hooper 1944)
- Rostrum longer and narrower than *N. c. rupicola* (Hooper 1944)
- May intergrade with *N. c. acraea* (Finley 1958)

Neotoma cinerea drummondii Richardson

- SPV's absent or very small (Goldman 1910); SPV's absent or small (Cowan and Guiguet 1960)
- Comparing *N. c. drummondii* (grouped with *cinerea*), molars comparable length but broader compared to *N. c. occidentalis* (Baird 1858)
- Slightly larger than *N. c. cinerea* and with heavier dentition (Goldman 1910)

Neotoma cinerea fusca True

- SPV's absent (*sensu* True 1894); SPV's absent, otherwise similar to *N. c. cinerea* (Goldman 1910); SPV's thin slits (about 0.2mm wide; Hooper 1940)
- Bullae small, skull large, molar row long and molars moderately massive (Hooper 1940)
- Indistinguishable from *N. c. occidentalis* based on skull (Hooper 1940)
- Intergradation with *N. c. pulla* is not known (Hooper 1940)

Neotoma cinerea lucida Goldman

- SPV's absent (Goldman 1917)
- Zygomatics roughly parallel with median line (narrow posteriorly) (Goldman 1917)
- Among the smallest forms of *N. cinerea* (Goldman 1917)

Neotoma cinerea macrodon Kelson

- SPV's large, indicating it belongs in the *N. c. orolestes* [Eastern] group (Kelson 1949)
- Most closely resembles *N. c. arizonae* (Kelson 1949)
- Bullae moderately large, molar row long (Kelson 1949)

Neotoma cinerea occidentalis Baird

- SPV's absent or very small (Goldman 1910); SPV's narrow (about 0.2 mm wide; Hooper 1940)
- Bullae small (Hooper 1940); smaller bullae compared to *N. c. cinerea* (Cowan and Guiguet 1960)
- Skull long and narrow (Hooper 1940)
- Molar row "actually and relatively short" (Hooper 1940)
- Longer palatal bridge than *N. c. cinerea* (Hooper 1940)
- Shorter nasals and narrower zygomatic spread than *N. c. pulla* (Hooper 1940)

Neotoma cinerea orolestes Merriam

- SPV's open (Merriam 1894); SPV's large, otherwise similar to *N. c. cinerea* (Goldman 1910)
- Quite variable in cranial characteristics, with only weak geographic signal (Finley 1958)
- Intergrades with *N. c. arizonae*, likely intergrades with *N. c. rupicola* (Finley 1958)

Neotoma cinerea pulla Hooper

- SPV's narrow (less than 0.2 mm wide; Hopper 1940)
- Bullae moderately large, zygomatics spread relatively wide, molar row short and narrow, rostrum shallow, long, and broad, (Hooper 1940)
- Intergrades with *N. c. alticola*, *occidentalis*, and probably *fusca* (Hooper 1940)

Neotoma cinerea rupicola Allen

- SPV's large (Goldman 1910); belongs in the *N. c. orolestes* [Eastern] group based on large SPV's, but otherwise resembles the Western groups [*N. c. cinerea*, *drummondii*, *occidentalis*] (Allen 1894)
- Dentition heavy (Goldman 1910)
- Likely intergrades with *N. c. orolestes* (Finley 1958)

Neotoma cinerea saxamans Osgood [=*Neotoma cinerea occidentalis*]

- SPV's open (Osgood 1900); SPV's "present, but short and somewhat triangular" (Goldman 1910)
- Closely related to *N. c drummondii* (Goldman 1910); similar to *N. c. drummondii* (Osgood 1900)
- Nasals narrower than *N. c. drummondii* (Osgood 1900)
- Narrower interorbital constriction than *N. c. cinerea* (Goldman 1910) and *N. c. drummondii* (Osgood 1900)

CHAPTER 2:
Historical biogeography of *Neotoma cinerea*

INTRODUCTION

Understanding the phylogeographic structure of a taxon can be a complex task, requiring knowledge of the numerous biotic and abiotic factors that influence how genetic structure develops and is maintained through time. As it relates to climate, understanding is aided by our increasing knowledge of Pleistocene and Holocene environmental conditions and improving techniques for modeling paleoclimate (Bartlein and Hostetler 2004). Concurrent with these advances, fossil and subfossil records are becoming increasingly important for understanding the biological impacts of climate change (Hadly *et al.* 2004; Chan *et al.* 2005; Lyman and O'Brien 2005; Riddle *et al.* 2008). Detailed historical distribution records that could allow in-depth understanding of temporal responses to climate change are uncommon for most mammalian species, with notable exceptions in the North American genus *Neotoma*.

The bushy-tailed woodrat, *Neotoma cinerea*, is the largest of the woodrats and a common inhabitant of the American West. On the basis of morphology, this species has been divided into 13 subspecies (Hall 1981; Figure 1); however, nearly nothing is known of its evolutionary history and intraspecific phylogeographic relationships. Molecular work in other *Neotoma* species indicates that evolutionary divisions in this genus are often deeper than previously recognized, prompting the elevation of several groups to species status in recent years (*N. magister*, Hayes and Harrison 1992; *N. leucodon*, Edwards *et al.* 2001; *N. macrotis*, Matocq 2002; *N. insularis*, Patton *et al.* 2008). Given the wide range of *N. cinerea* habitats and morphological differences, it is plausible that the boundaries of one or more of these subspecies may similarly represent more substantial divisions than are currently reflected by taxonomy.

Neotoma cinerea is a dietary generalist, and its range appears to be dictated largely by reliance on rocky shelters and sensitivity to extreme temperatures (Brown and Lee 1969; Smith *et al.* 1995; Smith 1997; King 2008). The effect of temperature has likely allowed direct reaction to climate change rather than secondary reaction to plant community shifts or other relatively slowly-changing biotic components (Smith and Betancourt 1998; Smith and Betancourt 2006). It is presumed that *N. cinerea* shifted to its current range in concert with the well-documented environmental changes associated with the Pleistocene-Holocene transition (Smith 1997). In particular, the northern range boundary was likely restricted by Pleistocene glaciation as recently as *ca*. 15,000 years before present (YBP; Ray and Adams 2001). This necessitates that the modern ranges of at least two northernmost subspecies, *N. c. occidentalis* and *N. c. drummondii*, were mostly or completely covered at the height of glaciation, and that these populations have presumably resulted from relatively recent re-colonization.

The apparently more consistent occupation history south of the Pleistocene glacial limit makes *N. cinerea* of notable importance in paleoecological research of the Great Basin, home to possibly the world's most detailed record of small mammals from the late Pleistocene and Holocene (Grayson 2006). This distinction is due in large part to paleomiddens, layered piles of debris including bones, plant materials, and fecal pellets collected and deposited by *Neotoma* species. These collections form chronological strata of debris that can reach several meters deep and persist tens of thousands of years, providing an essentially unparalleled opportunity for detailed analyses of the reaction of a small mammal to climate changes. While paleomiddens have been used extensively to track vegetation changes over time, their full utility in cases such as this is likely still left to be appreciated.

To begin investigating the effects of environment on *N. cinerea* evolution, this study focuses on describing the current, broad-scale phylogeographic patterns in this species. Though phylogeography only captures the modern distribution of variation, it provides a starting point for an historical biogeographic understanding of how these patterns have developed and been maintained. The two major questions and associated predictions are as follows:

1. What are the phylogenetic relationships within *N. cinerea*? From a practical standpoint, how do the intraspecific relationships in this species relate to its morphology-based taxonomic classification?

   Morphological evidence suggests there are two major groups of *N. cinerea*, here called the Eastern and Western groups (see Chapter 1), which are expected to be evident through reciprocal monophyly in phylogenetic reconstructions. Subspecies predicted for the Eastern group include *N. c. arizonae*, *cinnamomea*, *macrodon*, *orolestes*, and *rupicola*; and for the Western group *N. c. acraea*, *alticola*, *cinerea*, *drummondii*, *fusca*, *lucida*, *occidentalis*, and *pulla* (Figure 1).

2. How do the patterns of molecular variation compare with the distribution of *N. cinerea* inferred from paleomidden records, and can we use concordance between these sources to infer historical processes that led to the spatial and temporal distribution of this species?

Neotoma cinerea occupies a wide range of habitats, including regions covered or bordered by glaciers in the late Pleistocene (Ray and Adams 2001) which could have impacted both occupancy and dispersal. Specifically, northern groups that gained much of their current distribution by migration into de-glaciated areas are expected to show evidence of recent population expansion (significant negative values of Tajima's D and Fu's F_S statistics; unimodal pairwise sequence mismatch distributions) compared to groups largely south of the last glacial maximum. Dated paleomidden records may help support molecular evidence of recent colonization or long-term occupancy by providing spatial and temporal records of *N. cinerea* habitation.

METHODS

Sampling

Tissue samples for genetic analysis came from both museum and field collections. To begin identifying samples, I first performed multi-institution searches for *Neotoma cinerea* through the Mammal Networked Information System (MaNIS) and Arctos databases (queried July-August 2007), supplemented by searches in the individual databases of several other museums not networked through MaNIS or Arctos. I identified *N. cinerea* specimens for which tissues were available and requested samples from nearly all, avoiding redundant sampling of individuals for which DNA sequence information was already available (Matocq *et al.* 2007; M. Matocq unpub. data; J. Patton unpub. data). A total of 112 previously-collected specimens were used in analyses (Appendix V). I plotted the trapping locations of these according to each specimen's geographic coordinates or locality, producing a preliminary map which highlighted regions of the *N. cinerea* range that were poorly sampled and thus good focal areas in which to conduct collections.

I performed field collections between July-November 2008, sampling primarily from localities where *N. cinerea* had previously been collected but tissues not retained. Trapping was performed using 16x5x5" collapsible Tomahawk live-traps baited with peanut butter and oats, which I set in the evening and collected early the following morning. All *N. cinerea* recovered were euthanized via chest compression or isoflurane exposure, frozen on dry ice, and prepared after returning from the field. A total of 70 new specimens were collected, including 65 specimens from my collections and 5 from other collectors (Appendix V). All fieldwork was conducted under standards approved by Institutional Animal Care and Use Committees at Idaho State University and the University of Nevada-Reno, and allowed under state-specific collection permits. The distribution of all tissues used in analyses, including those from museums, field collections, and previous molecular work, can be seen in Figure 3.

Data Collection

I extracted DNA from all specimens using Qiagen DNeasy Blood & Tissue Kits according to manufacturer's instructions. The complete cytochrome *b* gene (cyt *b*, 1143 bp) was amplified using universal primers MVZ05 (Irwin *et al.* 1991) and MVZ14 (Smith and Patton 1993) in 15 μL reactions consisting of 1x AccuPrime Buffer II (Invitrogen), 0.2 mM $MgCl_2$ (Invitrogen), 0.4 μM of each primer, and 0.3 uL of AccuPrime *Taq* DNA polymerase (Invitrogen). After an initial denaturation at 94°C for 2 min, PCR was conducted via 35 cycles of 94°C for 30 sec, 50°C for 30 sec, and 68°C for 1 min 30 sec. I visualized templates by gel electrophoresis, and treated successful reactions at a ratio of 5 μL template : 2 μL ExoSAP-IT (USB Corporation) incubated at 37°C for 15 min and 80°C for 15 min.

I submitted treated templates to the Nevada Genomics Center for further processing, including cycle sequencing with ABI BigDye Terminator v3.1 kits (Applied Biosystems, Inc.), gel-filtration clean-up (Edge Biosystems), and analysis on ABI Prism 3730 DNA analyzer (Applied Biosystems, Inc.). All templates were sequenced in both directions using external universal primers MVZ05 and MVZ14, and as needed with internal primers MVZ16 (Smith and Patton 1993) and cytb2a (Matocq *et al.* 2007) to resolve ambiguous areas.

I checked the chromatograms visually and assembled fragments in Sequencher v4.2 (Gene Codes Corporation) to form complete sequences. I then imported each sequence to MacClade v4.08 (Maddison and Maddison 2004) where I aligned them by eye against other sequences. This helped to highlight polymorphisms as the data accumulated, each of which I confirmed by double-checking against the original chromatograms. When all sequences were aligned and checked, I merged redundant haplotypes to create the final dataset. I calculated standard molecular diversity indices using Arlequin 3.1.1 (Excoffier *et al.* 2005) and MEGA v4.1 (Tamura *et al.* 2007), and p-distances using PAUP* v4.0b10 (Swofford 2002)

Phylogenetic analyses

Phylogenetic reconstructions (neighbor-joining, maximum parsimony, and Bayesian inference) were based on complete cyt *b* sequences from *N. cinerea* and nine outgroups (Matocq *et al.* 2007). For those methods implementing an explicit model of molecular evolution, I used Modeltest v3.7 (Posada and Crandall 1998) to identify the most appropriate parameters. A general time-reversible model GTR+I+Γ (I=0.5331, α=1.2124) was favored under the hierarchical likelihood ratio test, an outcome corroborated by a close second-best AIC value for the same model.

I performed two neighbor-joining analyses using PAUP* v4.0b10. One analysis was based on simple uncorrected p-distances, while the other implemented the GTR+I+Γ model using I and α values returned by Modeltest. Majority-rule consensus trees were built from each analysis after 10,000 bootstraps.

I performed maximum parsimony analysis using MEGA v4.1 using all sites with equal weighting. For each of 1,000 bootstraps, I chose to build 10 preliminary trees by random sequence addition to help avoid settling at local optima under the parsimony criterion. Preliminary trees were then subjected to heuristic searches via level 3 close neighbor interchange (CNI) rearrangements in search of the most parsimonious topologies, and I summarized equally-parsimonious outcomes in a single majority-rule consensus tree.

I performed Bayesian phylogenetic inference using MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001) through the Idaho State University Evolutionary, Ecological, and Environmental Genomics Group (EGG) biocomputing cluster. I applied the GTR+I+Γ model and decreased the chain-heating temperature from the default 0.2 to 0.05 to aid in mobility of the cold chain identity; all other defaults including flat priors for I and α were maintained. Two independent runs of 4 chains each were performed simultaneously for 5,000,000 generations, and in each independent run the log likelihood of the current tree was sampled from the cold chain every 1,000 generations. Because early samples in each run represented sub-optimal trees, I chose an appropriate number of burn-in samples to omit from the final analyses based on two methods. First, I plotted the log likelihoods of all samples using Tracer v1.4 (Rambaut and Drummond 2007) and identified the number of generations after which the log likelihood failed to improve dramatically. Asymptote was easily achieved in both runs within 100,000 generations (100 samples). Second, I tracked the level of convergence between the 2 independent runs by noting the average standard deviation of split frequencies in each sampling bout; as this number decreased, the 2 runs presumably converged on the same set of highly likely trees. As a rule of thumb, burn-in may be considered complete when this value is <0.05 (Hall 2008), which was achieved within 650,000 generations (650 samples). Based on these two methods, I chose to discard the first 1,000,000 generations (1,000 samples) of each run, thus building a consensus tree based on the remaining samples.

Spatial and demographic analyses

I performed four analyses to explore the geographic partitioning of variation and to test for demographic evidence of recent population expansion. The data were partitioned for each analysis in one of two ways, either by geographic location or phylogenetic clade. First, I defined 71 populations based on location, grouping haplotypes within 15 miles of each other into populations irrespective of phylogeny (one sample was omitted because its locality resulted from accidental human transport; RBCM R0207, N. Panter, pers. comm.). This readied the data for SAMOVA v1.0 (Spatial Analysis of MOlecular VAriance; Dupanloup *et al.* 2002), a program which partitions populations into larger groups based on location and molecular variation. The goal of SAMOVA is to assemble groups that show the highest level of differentiation (F_{CT}) and thus lowest presumable levels of gene flow among groups, which may provide some indication of where barriers to gene flow occur geographically. Because the number of groups (*K*) in SAMOVA is user-defined, I performed 9 separate analyses from *K*=2 to *K*=10. Each analysis was based on pairwise sequence difference with 100 initial conditions, which are preliminary random partitions of the populations that the SAMOVA algorithm attempts to improve upon. As in other heuristic methods, the use of several preliminary conditions helps to avoid local optima and minimize the effects of any given starting condition on the final outcome (Dupanloup 2002).

I performed three tests to assess evidence of recent population expansion using Arlequin 3.1.1: Tajima's *D* test, Fu's F_S test, and mismatch distribution analyses. For these tests, the haplotypes were grouped based on phylogenetic clade instead of geographic location, and I defined 8 clades and subclades based on monophyly, population size, and overall support across all three phylogenetic reconstructions (as described in Results). Tajima's *D* test compares two estimates of θ, based on the number of segregating sites (θ_S) and the average number of mismatches between sequences (θ_Π), which would be equal under the assumptions of neutral evolution. Negative values of *D* suggest an excess of rare alleles and may evidence recent population expansion, although interpretation should be tentative as other forces such as selection can create similar patterns (Tajima 1989a, Tajima 1989b; Excoffier *et al.* 2005). Fu's F_S is a similar test of neutrality based on θ, although it simulates data according to neutral assumptions and compares the number of alleles observed to that expected; here, I based the Fu's F_S tests on 1,000 simulated samples. A negative value of F_S may indicate recent population expansion similar to Tajima's *D*, although Fu's F_S is considered to be particularly sensitive to population expansion (Fu 1997; Excoffier *et al.* 2005).

Analysis of mismatch distributions may also provide evidence of recent expansion based on the modality of the frequency of pairwise differences between samples. A ragged or multimodal distribution may indicate the influence of population stability and lineage sorting, while a unimodal distribution may indicate expansion according to the stepping-stone model (SSM; Rogers and Harpending 1992; Schneider and Excoffier 1999). The observed mismatch distributions were compared to simulated SSM distributions based on 500 bootstraps, and statistical tests of conformity to the SSM (null) model were performed in Arlequin 3.1.1.

RESULTS

I identified 120 unique cyt *b* haplotypes representing 182 *N. cinerea* specimens. Average nucleotide composition across all sites was (A) 32.10%, (C) 26.85%, (G) 13.35%, (T) 27.70%; this notable deficit of guanine is typical for cyt *b* sequences across mammals (Irwin *et al*. 1991). Two hundred sixty-six of 1143 sites were variable, including 79 singletons, and the transition : transversion ratio was 4.2 : 1. In the translated sequence, 57 of 381 amino acid positions showed variability due to non-synonymous nucleotide sequence substitutions. Thirteen of these 57 sites showed rare amino acid substitutions based on the empirically-derived BLOSUM62 substitution matrix, which could reflect changes in protein functionality (Henikoff and Henikoff 1992; Eddy 2004); however, 10 of those 13 sites are known to be variable in mammals and are located in protein domains presumed to be of lower functional importance (Irwin *et al.* 1991). The remaining 3 sites showed amino acid substitutions in only n = 1, 1, and 3 specimens respectively, confirming the rarity of these polymorphisms. Thus, *N.*

cinerea cyt *b* sequences appear highly conservative with respect to functionality, and consistent with our understanding of the evolutionary constraints on this crucial gene.

Phylogenetic analyses

Trees constructed by all three phylogenetic methods were nearly identical in topology and largely comparable in nodal support (neighbor-joining, not shown; maximum parsimony, Figure 4; Bayesian inference, Figure 5). Two major clades with generally strong parsimony bootstrap (BS) and Bayesian posterior probability (PP) support are evident: the Eastern clade (BS = 99, PP = 1.00) and the Western clade (BS = 99, PP = 0.68). There is moderate haplotype sequence divergence between these clades, with an average uncorrected p-distance of 6.5% (max = 7.6%, min = 5.4%) while distances within clades average 1.7% (max = 3.5%, min = 0.1%) in the Eastern clade and 2.6% (max = 4.6%, min < 0.0%) in the Western clade. Divergence is expectedly higher when estimated using the GTR+I+Γ model and parameters, showing a corrected average distance of 8.8% (max = 10.8%, min = 6.9%) between the Eastern and Western clades. None of the 13 *N. cinerea* subspecies within these major clades were monophyletic.

Spatial and demographic analyses

The Eastern clade is confined to regions east of the Colorado and Green Rivers, while the Western clade is found across a broader area encompassing the majority of the species' range. These clades are almost exclusively allopatric based on these data, showing only one locality of sympatry (Figure 6).

The geographic separation evident between the two clades was echoed by the SAMOVA analyses, which at $K = 2$ partitioned the populations according to the major Eastern and Western clades (with the point of sympatry grouped with the Eastern clade).

Partitions at higher levels of K largely continued to follow hierarchical divisions seen in the phylogeny as mapped in Figure 7, and were all supported at $P < 0.00000$. Generally, at $K = 3$ the Great Basin populations (including disjunct Northern haplotypes) were split from the remainder of the Western clade, and at $K = 4$ the exclusively Pacific Northwest populations were likewise partitioned off. At $K = 5$, the remaining 3 populations of the Great Basin disjunct were split from the Great Basin group. Finally, at $K = 6$ the Eastern clade was partitioned into its two major groups, Middle Rockies and Southern Rockies. F_{CT} values began to asymptote at $K = 6$, suggesting that groupings at higher levels of K would be less informative.

Following the phylogenies and SAMOVA results, groups defined for demographic expansion tests included the 5 major monophyletic clades noted (Southern Rockies, Middle Rockies, Pacific Northwest, Northern, and Great Basin) and other monophyletic groups of $n \geq 10$, including 3 subclades of the Middle Rockies (MR1, MR2, and MR3; Figure 4). The results of all expansion tests are summarized in Table 1. Tajima's D and Fu's F_S outcomes were largely in agreement, though only the Northern ($P_D = 0.010$, $P_F = 0.015$) and Great Basin ($P_D = 0.004$, $P_F < 0.000$) subclades showed statistically significant values. The mismatch distributions evidenced recent expansion for all subclades based on conformity to the SSM, with the exception of the Middle Rockies (P = 0.026; Figure 8).

DISCUSSION

The most profound result of the phylogenetic analyses is recognition of two major clades, consistent with the hypothesis of two *N. cinerea* groups based on historical morphological data. The subspecies hypothesized for each group (Eastern: *arizonae*, *cinnamomea*, *macrodon*, *orolestes*, *rupicola*; Western: *acraea*, *alticola*, *cinerea*, *drummondii*, *fusca*, *lucida*, *occidentalis*, *pulla*) were highly consistent with the resulting phylogeny, with the exception of four haplotypes that associated with the Western clade but occurred within presumed Eastern subspecies boundaries (Figure 4). All of these haplotypes were found at the interface between the two major clades (Figure 6), so their unexpected phylogenetic classifications can be explained either by imprecise subspecies boundary estimates or by genetic introgression between the clades in contact areas (see below). Overall, the phylogenetic reconstructions are in agreement with the broad historical morphological divisions and lend strong support to the distinction of two major *N. cinerea* groups.

Historical biogeography

The phylogeographic pattern of *N. cinerea* provides just a snapshot in time; incorporation of expansion test results and paleomidden data allow numerous hypotheses on the historical biogeography of this species. Following are historical accounts and hypotheses for the major Eastern and Western clades. Paleomidden data (Table 2) have been used to help evidence past distributions, but it should be well-noted that the inherent sampling variability of paleomiddens both spatially and temporally means that lack of *N. cinerea* samples cannot be interpreted as absolute evidence of their absence. Only unusually detailed paleomidden profiles (*e.g.* Grayson and Madsen 2000) are used here to infer local extinction. Ages referenced are uncalibrated ^{14}C years before present (YBP).

Eastern clade

The Eastern clade appears to have spread from a point of origin in the Rockies Mountains. The paleomidden record shows that *N. cinerea* ranged further south during the late Pleistocene, at least to the southern border of New Mexico (Harris 1984; Grayson 2006). As the climate shifted from the relatively cool and wet Pleistocene to the warm and dry Holocene, suitable habitat was likely lost at this southern edge. Dated paleomidden materials confirm that *N. cinerea* occurred in southern New Mexico between *ca.* 20,000-13,000 YBP (Harris 1993; Figure 9A), but it has since disappeared from that area (Hall 1981). At the northern boundary, *N. cinerea* apparently occupied northern Wyoming in the Pleistocene by 27,050 YBP (Lyford 2001) and perhaps as early as *ca.* 40,000 YBP (Wells 1983b; Figure 9A). It may have been restricted from moving further north by uninhabitable polar desert during Pleistocene glacial periods, as was seen across parts of southern Montana and northern Wyoming during the last glacial maximum *ca.* 15,000 YBP (Péwé 1983; Ray and Adams 2001). Records indicate that *N. cinerea* ranged further into southern Montana by 10,650 YBP (Mead 1982; Figure 9B) and into central Montana by 7,039 YBP (Smith and Betancourt 2006; Figure 9C); however, it may be more parsimonious to attribute these records to members of the Western clade given the current phylogeographic pattern.

Outcomes of the expansion tests for the Eastern subclades are consistent with the inference of population stability. Insignificant values of Tajima's D and Fu's F_S suggest no evidence of recent expansion, and significant and marginal SSM deviations in mismatch distributions also suggest stability of these populations over time. Additionally, the Eastern clade appears to have occupied much of its current range for tens of thousands of years based on paleomidden records (Figure 9A-D), allowing for minor range shifts in response to warmer Pleistocene interglacial periods and southern habitat loss during the Pleistocene-Holocene transition. Overall, the Eastern clade shows a signature of long-term population stability.

Western clade

The apparent history of the Western clade contrasts sharply with that of the Eastern. The best working hypothesis for the Western clade origin may be the northwestern United States, for two main reasons. First, the Pacific Northwest subclade is basal to the other Western subclades in both the parsimony and Bayesian trees, although the support for this is quite low (BS = 56, PP = 0.65) and the relationship is even collapsed (BS < 50%) in both neighbor-joining trees (not shown). Building on that weak support, directionality of the Pacific Northwest subclade under Bayesian and neighbor-joining reconstructions suggests dispersal from the Olympic peninsula in Washington (occidentalis19 and 20), through middle Washington (occidentalis5, 6, 13, 15), and into northern British Columbia and Yukon (occidentalis1, 2, 9, 12; Figure 5); the parsimony tree also supports the derived nature of northernmost haplotypes (occidentalis1, 9, 12; Figure 4B). Second, all three of the Western subclades overlap or occur in Washington state. The nominal evidence for basal position of the Pacific Northwest subclade allows the phylogeny to be interpreted as simultaneous divergence of all 3 subclades, so the region where all three subclades are found could be assumed ancestral. Though lacking in strong support, Western clade origins in the northwestern United States seems to be the strongest hypothesis at this time.

Because most of the Pacific Northwest and Northern subclade distributions were previously glaciated, the expectation was that recolonization would result in marked expansion signatures in those regions. While neither subclade rejected the null SSM expansion model, Tajima's D and Fu's F_S statistics did not suggest recent population growth of the Pacific Northwest subclade. It is unclear why this group shows equivocal evidence of expansion, particularly because it seems to have expanded solely from the northwestern United States and not from additional high-latitude glacial refugia utilized by other species (*e.g.* Conroy and Cook 2000; Demboski and Cook 2001; Aubry *et al.* 2009), which could have negated expansion signatures by inadvertent admixture of multiple groups for statistical purposes. What is known of the paleomidden record in Canada is consistent with recent colonization, with the oldest dated record merely 1,150 YBP (Hebda *et al.* 1990; Figure 9D).

In contrast, the Northern subclade shows evidence of expansion in all 3 tests, consistent with expected population growth during glacial retreat. As noted earlier, records of *N. cinerea* occupancy in southern Montana by 10,650 YBP (Mead 1982; Figure 9B) and central Montana by 7,039 YBP (Smith and Betancourt 2006; Figure 9C) are presumably attributable to the Western clade, and specifically the Northern or Great Basin subclades. These areas may have been largely uninhabitable by *N. cinerea* in the late Pleistocene due to widespread permafrost and tundra (Péwé 1983; Ray and Adams 2001), thus restricting occupancy to relatively recent times. These records are attributed to the Western clade based solely on the modern phylogeographic pattern; from an historical geographic perspective, a more sound hypothesis may be that the Eastern clade was first to spread into central Montana but was displaced by the Western clade as passage from the west across alpine environments of Montana and central Idaho became easier in the Pleistocene-Holocene transition. Molecular information from paleomiddens could potentially be used to distinguish between occupancy of different lineages over time, allowing an eventual test of these alternative hypotheses.

Although the vast majority of the Great Basin subclade range was not recently glaciated, that group shows the strongest evidence of population growth. This was unexpected, but may indicate a response to Pleistocene climate fluctuations. Much of the Great Basin was riddled with pluvial lakes reaching their height *ca.* 17,000-14,000 YBP (Benson 2004), so expansion into this region may have occurred during aridification in the Pleistocene-Holocene transition. For example, as Lake Lahontan receded sharply *ca.* 14,000 YBP to form the modern Pyramid Lake, elevations previously under water were quickly colonized by *Neotoma* (potentially *N. cinerea*) within 1,000 years of drying (Benson *et al.* 1995). This pattern could have occurred across the Great Basin as pluvial lakes receded and disappeared (Figure 9A-B). Another wide-scale colonization could have occurred even more recently as the Great Basin rebounded from the arid middle Holocene. Paleomidden records at Homestead Cave near Great Salt Lake suggest that *N. cinerea* was very common there during the Pleistocene-Holocene transition (Figure 9B), but essentially disappeared by the middle Holocene *ca.* 8,000 YBP due to the increasingly warm or arid conditions (Grayson and Madsen 2000; Grayson 2006; Figure 9C). Because *N. cinerea* is found across the Great Basin today, including at Homestead Cave, re-colonization may have occurred quite recently in the late Holocene (Grayson and Madsen 2000; Figure 9D). Though few paleomidden records show comparable detail to make such an inference, this general pattern of *N. cinerea* Holocene extinction appears to have occurred simultaneously at several locations in the Great Basin (see Grayson 2006 for summary).

Paleomidden records show that *N. cinerea* was present in southern Nevada and southeastern California before the Holocene, as early as 31,899 YBP (Hockett 2000; Figure 9A), which suggests a long history of occupancy; however, the molecular evidence suggests a history of instability and recent population expansion. Perhaps extinctions and recolonizations similar to those inferred from Holocene records occurred serially through Pleistocene glacial and interglacial periods. These demographic cycles in the Great Basin could be attributed to the Great Basin clade, although that assumption is not necessary; in fact, the Northern clade may have staged a relatively early wave of colonization in that region. Two Northern clade haplotypes (acraea9, 13) are found in central California, curiously disjunct from the remainder of the clade (Figure 4; Figure 7). These may be remnants of a once-broader Northern clade distribution that spanned the Great Basin but suffered broad extinction due to climate change, taking refuge in the Sierra Nevada mountains and thus opening the way for one or more later colonization events by the Great Basin clade.

The Great Basin clade also has an unusual distribution that could indicate a complex history of population expansion and contraction. The basal haplotypes are geographically disjunct in Montana and South Dakota (cinerea2; orolestes1-3; rupicola1); the next-basal haplotypes are found in the Sierra Nevada mountains (acraea14, 15; alticola14); and the star-like derived clade is scattered across the Great Basin (Figure 4B; Figure 7). Despite the apparently recent colonization by this subclade, there are higher levels of allozyme heterozygosity across the Great Basin than in either the western Carson Range (Nevada) or the eastern Tushar Range (Utah; Mewaldt and Jenkins 1986). The most recent Great Basin colonization could have been staged from several points, thus mixing alleles from source populations at the edges of the Basin; alternatively, incomplete extinctions in the Great Basin could have allowed mixing of alleles from descendents of more than one colonization event.

Although the numerous Great Basin paleomiddens could be used to confirm the temporal presence of *N. cinerea* and make many of these ideas testable, the presence of desert-adapted *Neotoma* species such as *N. lepida* throughout the Holocene (Patton *et al.* 2008) means we cannot assume midden strata were built by *N. cinerea*. Positive species identification by pellet size or morphology remains precarious or prohibitively difficult; at very least, it is a rare undertaking (but see Grayson and Madsen 2000; Smith and Betancourt 2006, Smith *et al.* 2009). We may be able to recover molecular information from paleomiddens in the future, potentially allowing both species and clade identification to help clarify this seemingly complicated history of *N. cinerea* in the Great Basin. Even without these data, it seems the Western clade, and particularly the Northern and Great Basin subclades, show relative population instability and potentially strong demographic reactions to past climate change.

Secondary contact

Although some uncertainty of the Eastern and Western geographic epicenters remains, it is apparent that the clades arose most recently from geographically disparate locations. This pattern of deep intraspecific divergence and allopatry is very common in small mammals, and it likely indicates long-term isolation and independent evolution resulting in part from limited dispersal abilities (Avise 2000). The deep division between Rocky Mountain and coastal populations seen in *N. cinerea* is similar to patterns seen in other widespread small mammals (Conroy and Cook 2000; Demboski and Cook 2001), and the cause of this division may similarly reflect a vicariant or dispersal event thousands or even millions of years in the past that has been reinforced by cyclic Pleistocene climate changes (Demboski and Cook 2001). Glaciation and extreme climates such as polar and alpine tundra (Péwé 1983; Ray and Adams 2001) could have restricted contact in Montana and Wyoming during Pleistocene glacial periods. In the south, the Green River and upper Colorado River appear to have been effective barriers as seen in some other small animals (Findley and Anderson 1956; Conroy and Cook 2000; Patton *et al.* 2008; Wilson *et al.* 2005), and contact of the major *N. cinerea* clades does not seem to have occurred despite Pleistocene avulsions of the lower Colorado River (e.g. Jezkova *et al.* 2009).

Given the divergence and independent histories of the Eastern and Western clades, it is reasonable to consider whether these clades would be better recognized as separate species. The corrected average distance of 8.8% is around the middle of the range for corrected distances used to help delineate species in other *Neotoma* groups (Hayes and Harrison 1992; Matocq 2002); however, the question of species would be better addressed with additional data from morphological and nuclear genetic variation to avoid the potential vagaries of single-gene phylogenetic inference. It may be particularly helpful to augment sampling in the apparent zones of secondary contact between these clades, including western South Dakota and potentially southern Montana and northern Wyoming, to understand if or how the once-separate evolutionary histories of these groups affect their modern molecular, morphological, and ultimately reproductive compatibility.

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Table 1. Summary and expansion test statistics for major *N. cinerea* clades and subclades of $n \geq 10$. Significant outcomes are marked with asterisks.

Table 1.

A. Eastern clade	Southern Rockies	Middle Rockies	Subclade MR1	Subclade MR2	Subclade MR3
Sample size (*n*)	10	61	21	26	11
No. haplotypes	9	33	13	11	6
No. segregating sites (*S*) in 1143 bp	38	79	26	21	11
Tajima's *D* statistic	0.221	-0.535	-1.193	0.295	0.030
Tajima's *D* P-value (α = 0.05)	0.641	0.309	0.115	0.667	0.547
Fu's F_S statistic	-0.871	-4.720	-3.465	-0.082	0.032
Fu's F_S P-value (α = 0.02)	0.259	0.112	0.065	0.508	0.497
Mismatch SSM P-value (α = 0.05)	0.120	0.026*	0.564	0.066	0.154

B. Western clade	Pacific Northwest	Northern	Great Basin
Sample size (*n*)	11	37	63
No. haplotypes	10	23	45
No. segregating sites (*S*) in 1143 bp	32	69	129
Tajima's *D* statistic	-0.517	-1.870*	-1.836*
Tajima's *D* P-value (α = 0.05)	0.325	0.010*	0.008*
Fu's F_S statistic	-2.313	-6.558*	-19.847*
Fu's F_S P-value (α = 0.02)	0.093	0.015*	0.000*
Mismatch SSM P-value (α = 0.05)	0.676	0.454	0.344

Table 2. Paleomidden samples representing *N. cinerea* through the late Pleistocene and Holocene. Samples included were those that had been verified to species based on skeletal morphology, pellet size (as a proxy for body size), or origin from sites highly likely to exclude all other *Neotoma* species. Information was taken directly from primary literature (source A), from secondary-source summaries of *N. cinerea* midden materials (source B), and from the USGS-NOAA Packrat Midden Database queried June, 2009 (source C). Ages are uncalibrated ^{14}C years before present.

Table 2.

Age (^{14}C YBP)	Region	Reference	Source
490	northern Wyoming / southern Montana	Lyford *et al.* 2002	A
700	southern British Columbia	Hebda *et al.* 1990	A
1000	northwest Utah	Grayson and Madsen 2000	A
1150	southern British Columbia	Hebda *et al.* 1990	A
1930	eastern Utah	Smith and Betancourt 1998	A
2223	middle Montana	Smith and Betancourt 2006	A
2840	northern Wyoming / southern Montana	Lyford *et al.* 2002	A
3240	northern Wyoming / southern Montana	Lyford *et al.* 2002	A
3713	eastern California	Smith *et al.* 2009	A
3880	middle Idaho	Smith and Betancourt 2003	A
3925	middle Idaho	Smith and Betancourt 2003	A
3970	middle Idaho	Smith and Betancourt 2003	A
4050	middle Idaho	Smith and Betancourt 2003	A
4677	eastern California	Smith *et al.* 2009	A
5105	middle Montana	Smith and Betancourt 2006	A
5575	northern Wyoming / southern Montana	Lyford *et al.* 2002	A
6100	southeast Utah	Smith and Betancourt 1998	A
6310	eastern Arizona	Smith and Betancourt 1998	A
7039	middle Montana	Smith and Betancourt 2006	A
7160	northern Wyoming / southern Montana	Mead 1982	C
7615	northern Wyoming / southern Montana	Lyford *et al.* 2002	A
8200	northwest Utah	Grayson and Madsen 2000	A
8312	southern Nevada	Hockett 2000	A
8350	northwest Utah	Grayson and Madsen 2000	A
8700	northwest Utah	Grayson and Madsen 2000	A
8810	northwest Utah	Schmitt *et al.* 2002	A
8861	eastern California	Smith *et al.* 2009	A
9042	southern Nevada	Hockett 2000	A
9460	northern New Mexico	Smith and Betancourt 1998	A
9560	northwest Utah	Schmitt *et al.* 2002	A
9751	eastern California	Smith *et al.* 2009	A
9980	northern Wyoming / southern Montana	Lyford *et al.* 2002	A
10000	southern Nevada	Goodwin and Reynolds 1989, from Grayson 2006	B
10000	southern Nevada	Jefferson 1991, from Grayson 2006	B
10000	southern Nevada	Mead and Murray 1991, from Grayson 2006	B
10063	southern Nevada	Hockett 2000	A

Table 2. Continued.

Age (^{14}C YBP)	Region	Reference	Source
10105	northern Wyoming / southern Montana	Lyford *et al.* 2002	A
10260	northern Wyoming / southern Montana	Mead 1982	C
10650	northern Wyoming / southern Montana	Mead 1982	C
10750	northwest Utah	Grayson and Madsen 2000	A
10757	northwest Utah	Grayson 1988	A
11168	northwest Utah	Smith and Betancourt 2003	A
11310	southeast Utah	Smith and Betancourt 1998	A
12090	eastern Arizona	Smith and Betancourt 1998	A
12420	eastern Utah	Smith and Betancourt 1998	A
12697	eastern California	Smith *et al.* 2009	A
13000	southern New Mexico	Harris 1993	A
13800	southeast Utah	Smith and Betancourt 1998	A
14684	southern Nevada	Hockett 2000	A
15000	southern New Mexico	Harris 1993	A
16460	eastern Arizona	Smith and Betancourt 1998	A
17261	eastern California	Smith *et al.* 2009	A
18000	southern New Mexico	Harris 1993	A
18000	southern New Mexico	Harris 1993	A
18190	middle Wyoming	Lyford 2001	C
18300	middle Wyoming	Smith and Betancourt 2006	A
19991	eastern California	Smith *et al.* 2009	A
20000	southern New Mexico	Harris 1993	A
20000	southern New Mexico	Harris 1993	A
20050	eastern Utah	Smith and Betancourt 1998	A
22018	eastern California	Smith *et al.* 2009	A
23860	northern Wyoming / southern Montana	Lyford 2001	C
23860	northern Wyoming / southern Montana	Smith and Betancourt 2006	A
26720	northern Wyoming / southern Montana	Lyford 2001	C
27000+	northern Wyoming / southern Montana	Wells 1983	C
27050	northern Wyoming / southern Montana	Lyford 2001	C
30000+	northern Wyoming / southern Montana	Wells 1983	C
31899	southern Nevada	Hockett 2000	A
40000+	northern Wyoming / southern Montana	Wells 1983	C

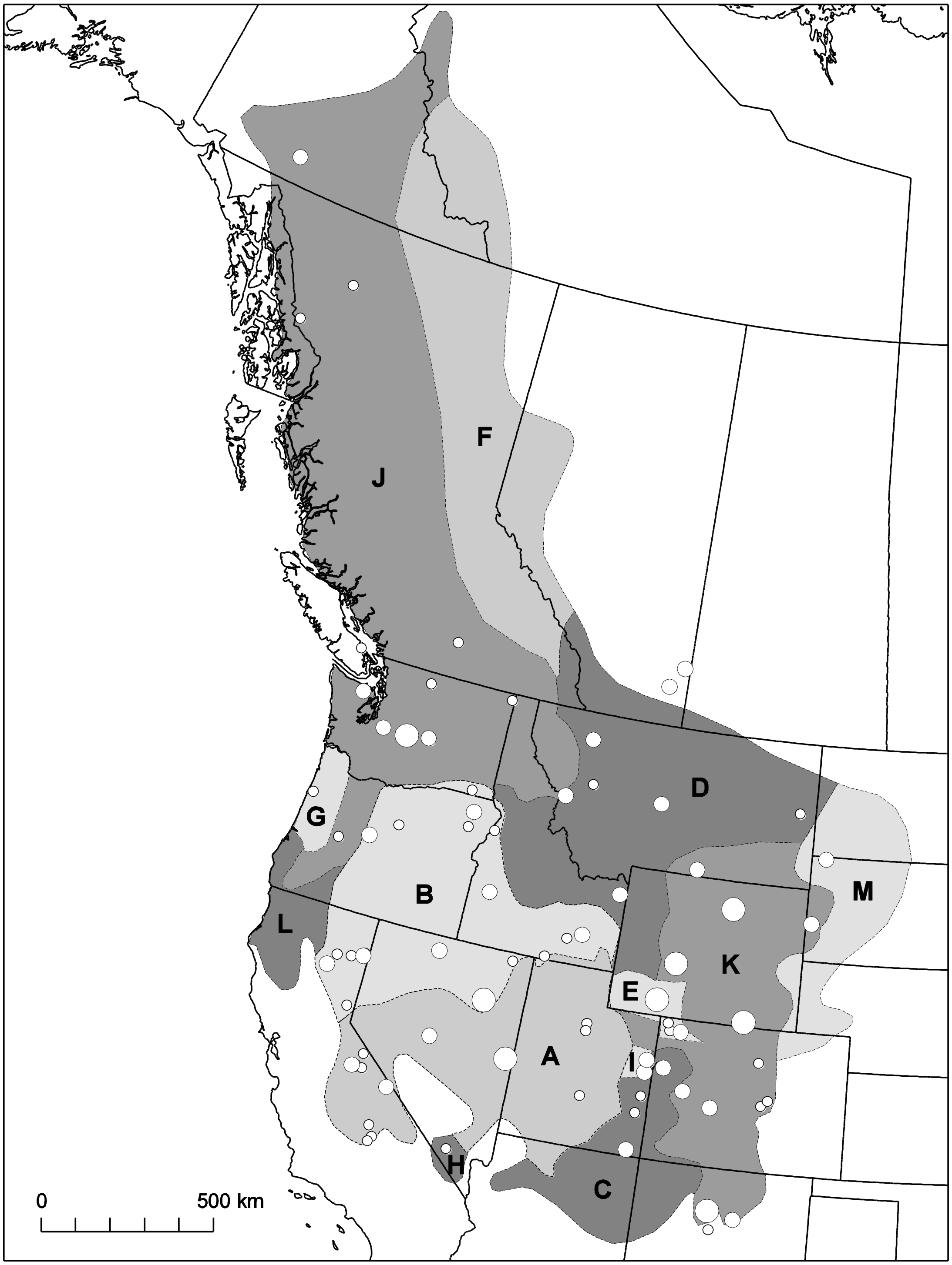
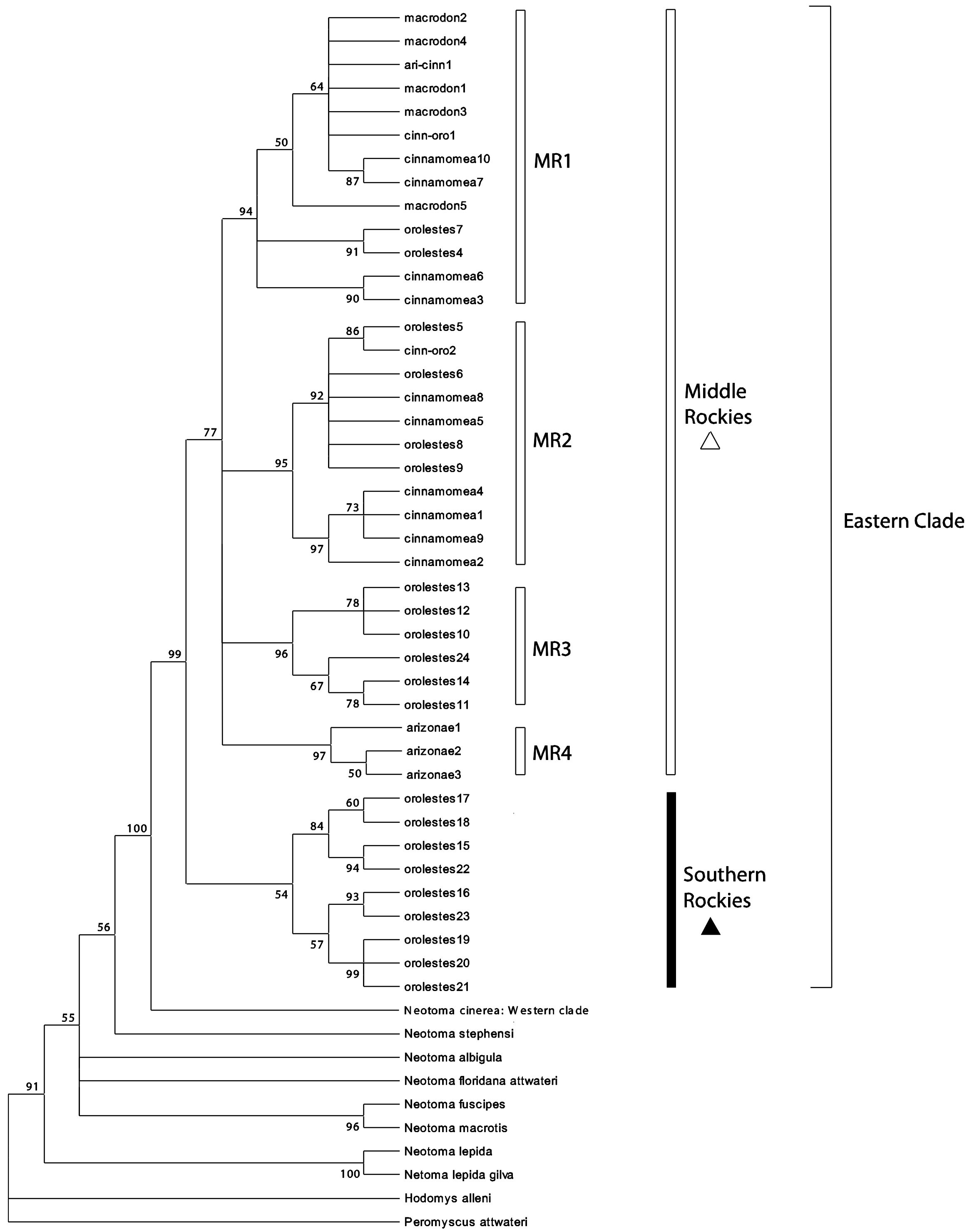


Figure 3.

Figure 3. *Neotoma cinerea* subspecies and distribution of samples used in molecular analyses. Circle size corresponds to sample size: small circles, n = 1; medium circles, n = 2-5; large circles, n = 6-10. Subspecies (re-drawn from Hall 1981) are as follows: (A) *N. c. acraea*; (B) *alticola*; (C) *arizonae*; (D) *cinerea*; (E) *cinnamomea*; (F) *drummondii*; (G) *fusca*; (H) *lucida*; (I) *macrodon*; (J) *occidentalis*; (K) *orolestes*; (L) *pulla*; (M) *rupicola*.



macrodon2
macrodon4
ari-cinn1
macrodon1
macrodon3
cinn-oro1
cinnamomea10
cinnamomea7
macrodon5
orolestes7
orolestes4
cinnamomea6
cinnamomea3
orolestes5
cinn-oro2
orolestes6
cinnamomea8
cinnamomea5
orolestes8
orolestes9
cinnamomea4
cinnamomea1
cinnamomea9
cinnamomea2
orolestes13
orolestes12
orolestes10
orolestes24
orolestes14
orolestes11
arizonae1
arizonae2
arizonae3
orolestes17
orolestes18
orolestes15
orolestes22
orolestes16
orolestes23
orolestes19
orolestes20
orolestes21
Neotoma cinerea: Western clade
Neotoma stephensi
Neotoma albigula
Neotoma floridana attwateri
Neotoma fuscipes
Neotoma macrotis
Neotoma lepida
Netoma lepida gilva
Hodomys alleni
Peromyscus attwateri
MR1
MR2
MR3
MR4
Middle
Rockies
Southern
Rockies
Eastern Clade
64
87
50
94
91
90
86
92
95
77
73
97
78
96
67
78
99
97
50
60
84
94
100
54
93
57
99
56
55
96
91
100

Figure 4A.

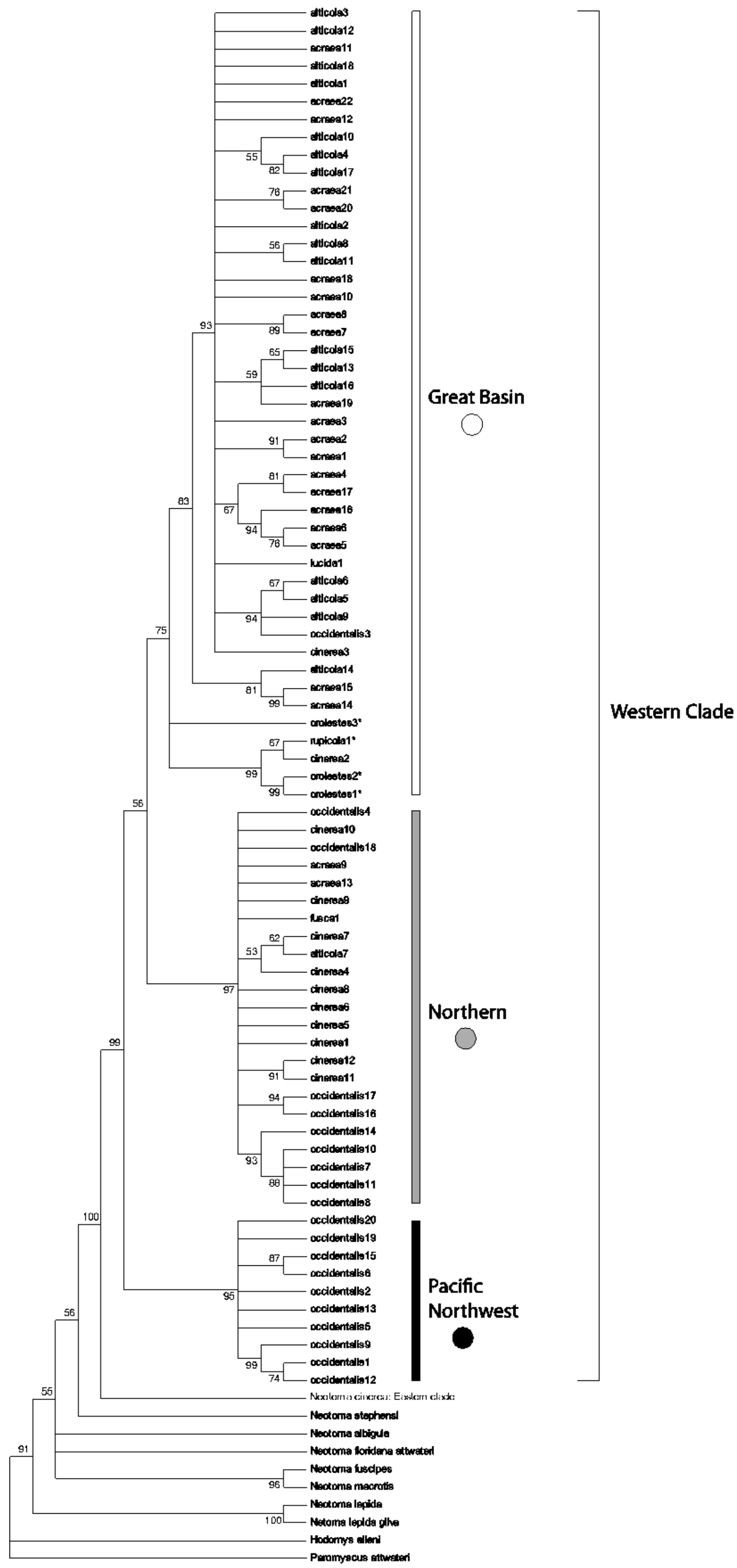

Great Basin
Northern
Pacific Northwest
Western Clade
alticola3
alticola12
acraea11
alticola18
alticola1
acraea22
acraea12
alticola10
alticola4
alticola17
acraea21
acraea20
alticola2
alticola8
alticola11
acraea18
acraea10
acraea8
acraea7
alticola15
alticola13
alticola16
acraea19
acraea3
acraea2
acraea1
acraea4
acraea17
acraea16
acraea6
acraea5
lucida1
alticola6
alticola5
alticola9
occidentalis3
cinerea3
alticola14
acraea15
acraea14
orolestes3*
rupicola1*
cinerea2
orolestes2*
orolestes1*
occidentalis4
cinerea10
occidentalis18
acraea9
acraea13
cinerea9
fusca1
cinerea7
alticola7
cinerea4
cinerea8
cinerea6
cinerea5
cinerea1
cinerea12
cinerea11
occidentalis17
occidentalis16
occidentalis14
occidentalis10
occidentalis7
occidentalis11
occidentalis8
occidentalis20
occidentalis19
occidentalis15
occidentalis6
occidentalis2
occidentalis13
occidentalis5
occidentalis9
occidentalis1
occidentalis12
Neotoma cinerea: Eastern clade
Neotoma stephensi
Neotoma albigula
Neotoma floridana attwateri
Neotoma fuscipes
Neotoma macrotis
Neotoma lepida
Netoma lepida gilva
Hodomys alleni
Peromyscus attwateri

Figure 4B.

Figure 4. (A) Maximum parsimony consensus tree with the *N. cinerea* Eastern clade expanded. Haplotypes are labeled by the subspecies from which they were collected. Hyphenated names represent haplotypes collected from within more than one subspecies range (“ari-cinn,” *arizonae* and *cinnamomea*; “cinn-oro,” *cinnamomea* and *orolestes*). Nodes are labeled with bootstrap support; those with < 50% support are collapsed. (B) Maximum parsimony consensus tree with the *N. cinerea* Western clade expanded. Haplotypes are labeled by the subspecies from which they were collected. Asterisks mark samples collected within Eastern group subspecies boundaries. Nodes are labeled with bootstrap support; those with <50% support are collapsed.

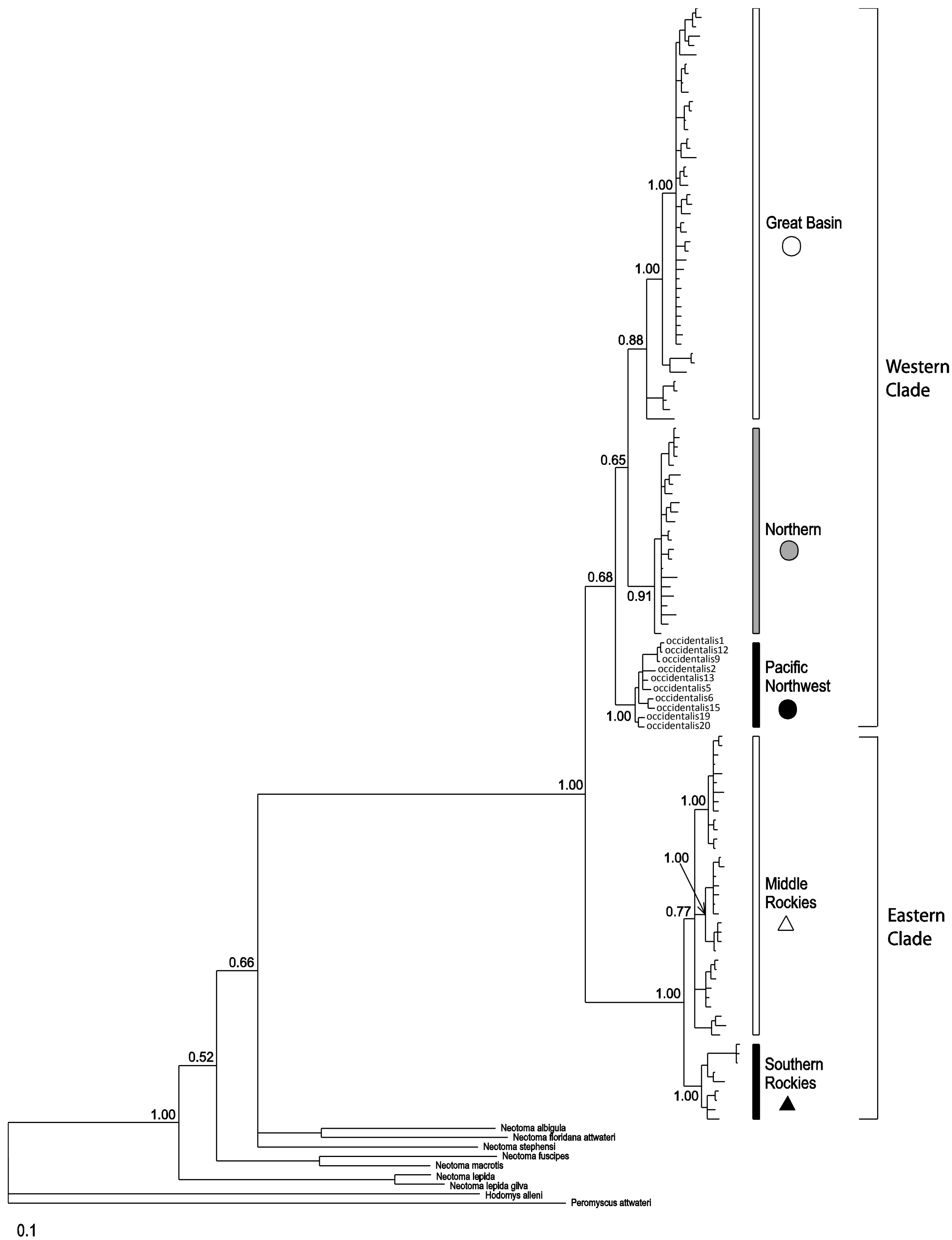

1.00
1.00
0.88
0.65
0.68
0.91
1.00
1.00
1.00
1.00
0.77
1.00
1.00
0.66
0.52
1.00
occidentalis1
occidentalis12
occidentalis9
occidentalis2
occidentalis13
occidentalis5
occidentalis6
occidentalis15
occidentalis19
occidentalis20
Great Basin
Northern
Pacific Northwest
Middle Rockies
Southern Rockies
Western Clade
Eastern Clade
Neotoma albigula
Neotoma floridana attwateri
Neotoma stephensi
Neotoma fuscipes
Neotoma macrotis
Neotoma lepida
Neotoma lepida gilva
Hodomys alleni
Peromyscus attwateri
0.1

Figure 5.

Figure 5. Bayesian phylogram showing major clades of *N. cinerea*, constructed using the GTR+I+Γ model. Major nodes are labeled with posterior probabilities, though all nodes shown have support ≥ 0.50.

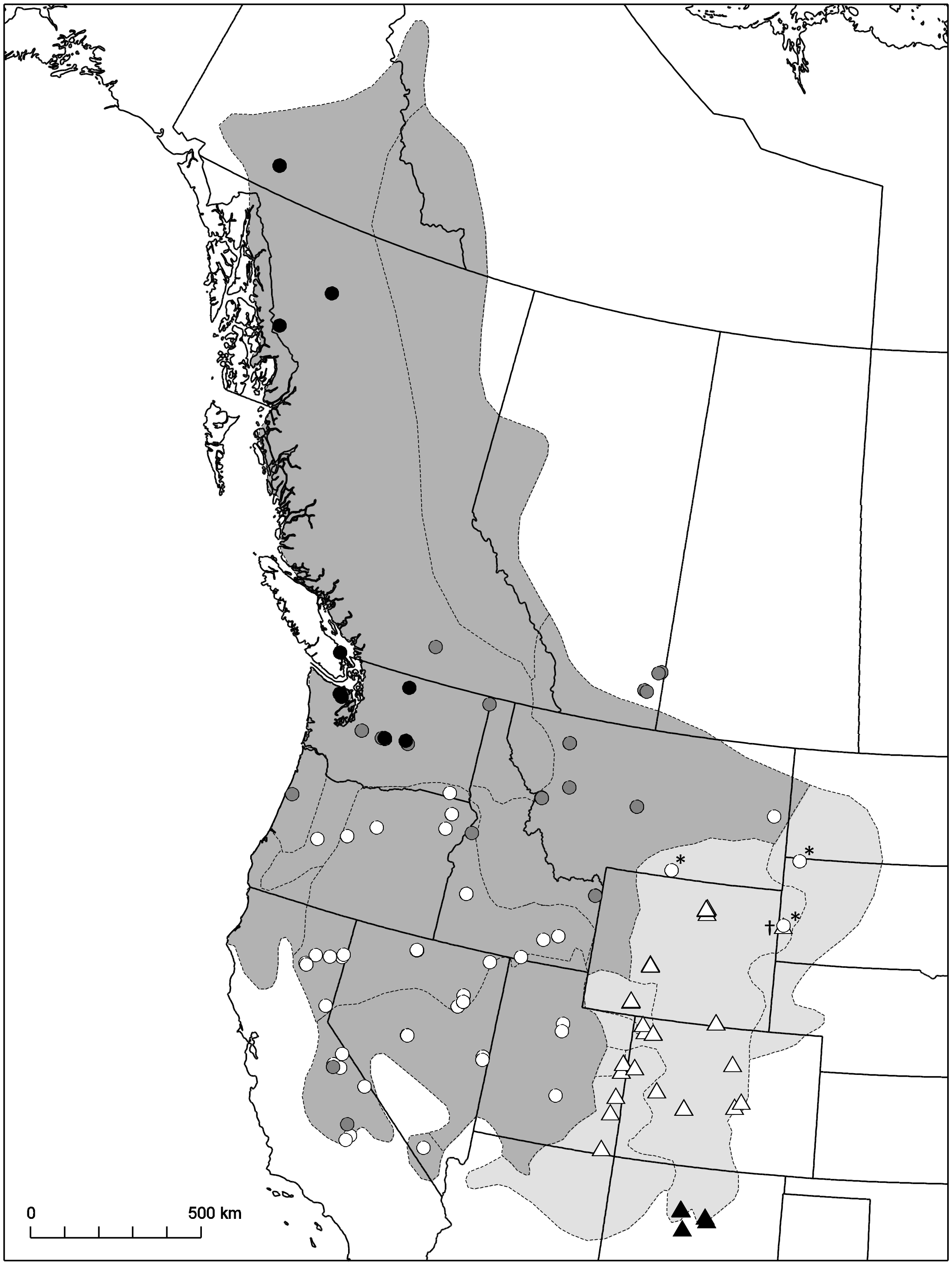
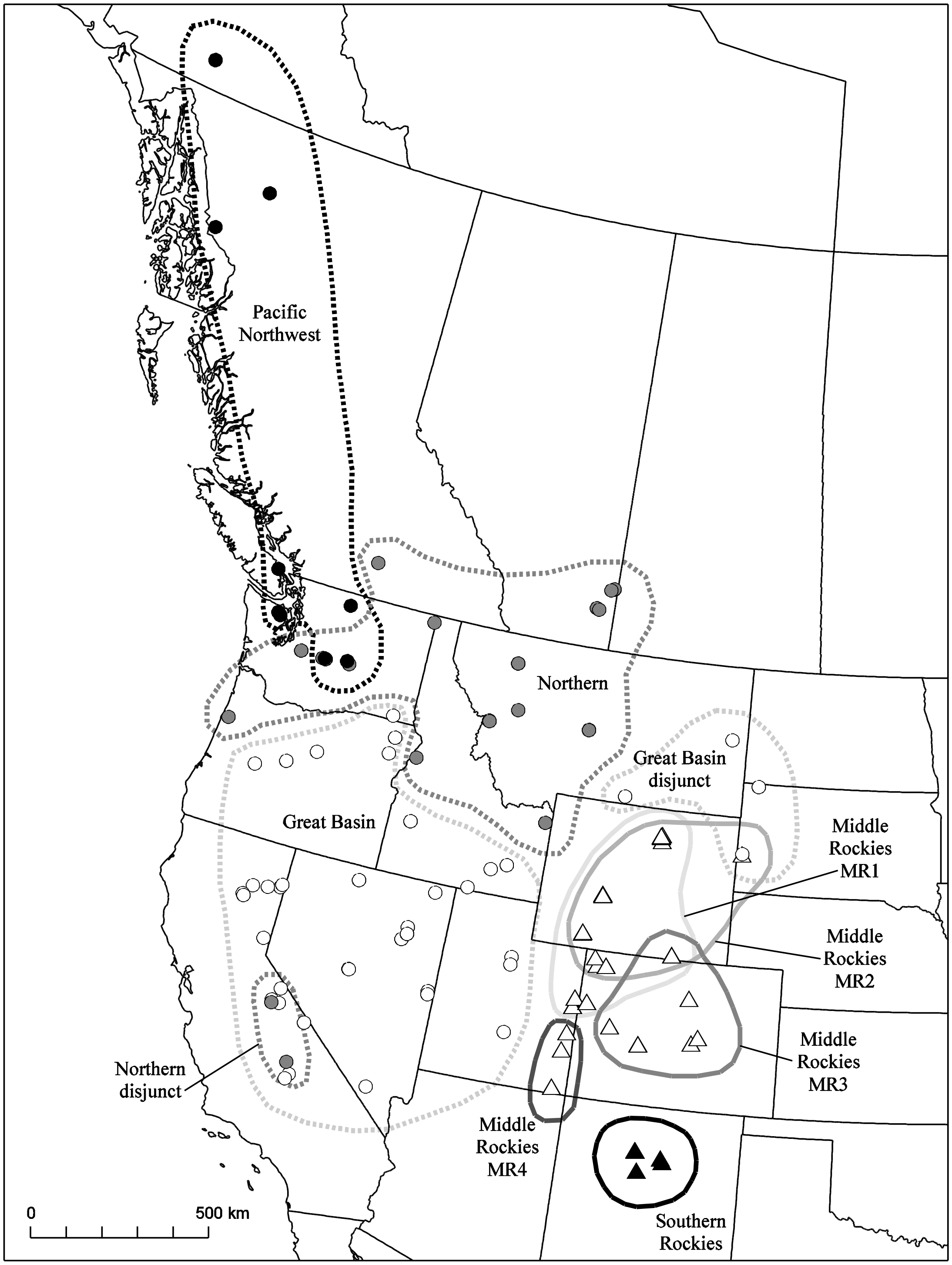


Figure 6.

Figure 6. Distribution of major *N. cinerea* clades against subspecies boundaries. Eastern subclades are represented by triangles as follows: Southern Rockies, black triangles; Middle Rockies, white triangles. Western subclades are represented by circles as follows: Pacific Northwest, black circles; Northern, gray circles; Great Basin, white circles. Shaded light gray areas show the ranges of Eastern group subspecies, while dark gray areas show the ranges of Western group subspecies (re-drawn from Hall 1981; for subspecies identifications see Figure 1). Asterisks mark samples that were collected within Eastern group boundaries but associated with the Western clade in phylogenetic analyses (Figure 4B; see text), and the dagger marks the only point of sympatry between the Eastern and Western clades (Black Hills, South Dakota).



Pacific
Northwest
Northern
Great Basin
disjunct
Great Basin
Middle
Rockies
MR1
Middle
Rockies
MR2
Middle
Rockies
MR3
Northern
disjunct
Middle
Rockies
MR4
Southern
Rockies
0
500 km

Figure 7.

Figure 7. Extent and overlap of major *N. cinerea* clades. Eastern clade points are marked with triangles, and boundaries with solid lines. Western clade points are marked with circles, and boundaries with dotted lines. Groups are named according to phylogenetic clades in Figure 4 and Figure 5, and are also generally concordant with SAMOVA partitions (see text).

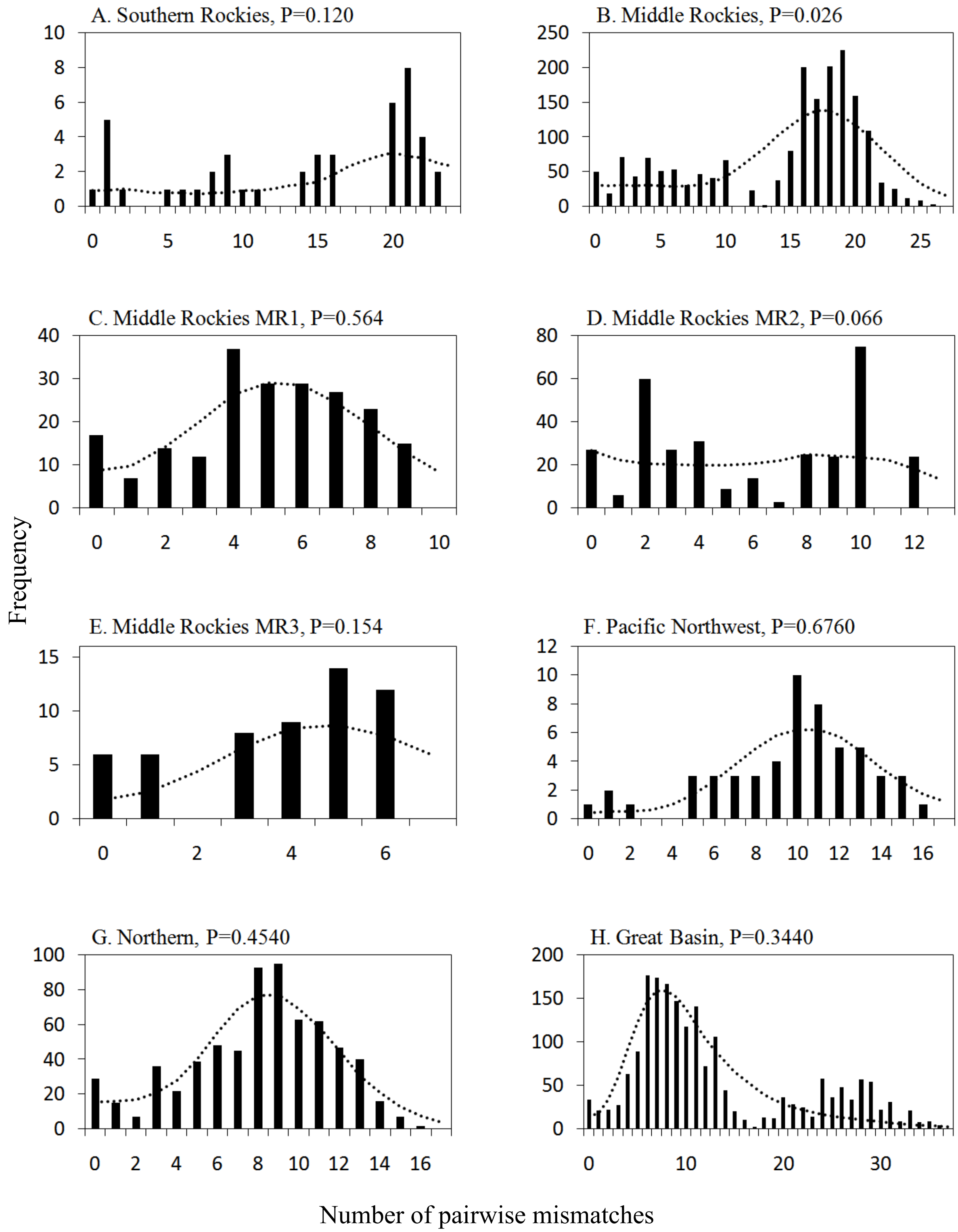

A. Southern Rockies, P=0.120
B. Middle Rockies, P=0.026
C. Middle Rockies MR1, P=0.564
D. Middle Rockies MR2, P=0.066
E. Middle Rockies MR3, P=0.154
F. Pacific Northwest, P=0.6760
G. Northern, P=0.4540
H. Great Basin, P=0.3440
Frequency
Number of pairwise mismatches

Figure 8.

Figure 8. Mismatch distributions for major *N. cinerea* clades and subclades of $n \geq 10$. Observed data are shown as bars. Simulated data representing the null stepping-stone model (SSM) of population expansion are shown as dotted lines, and P-values ($\alpha = 0.05$) indicate degree of departure from this model by the observed data.

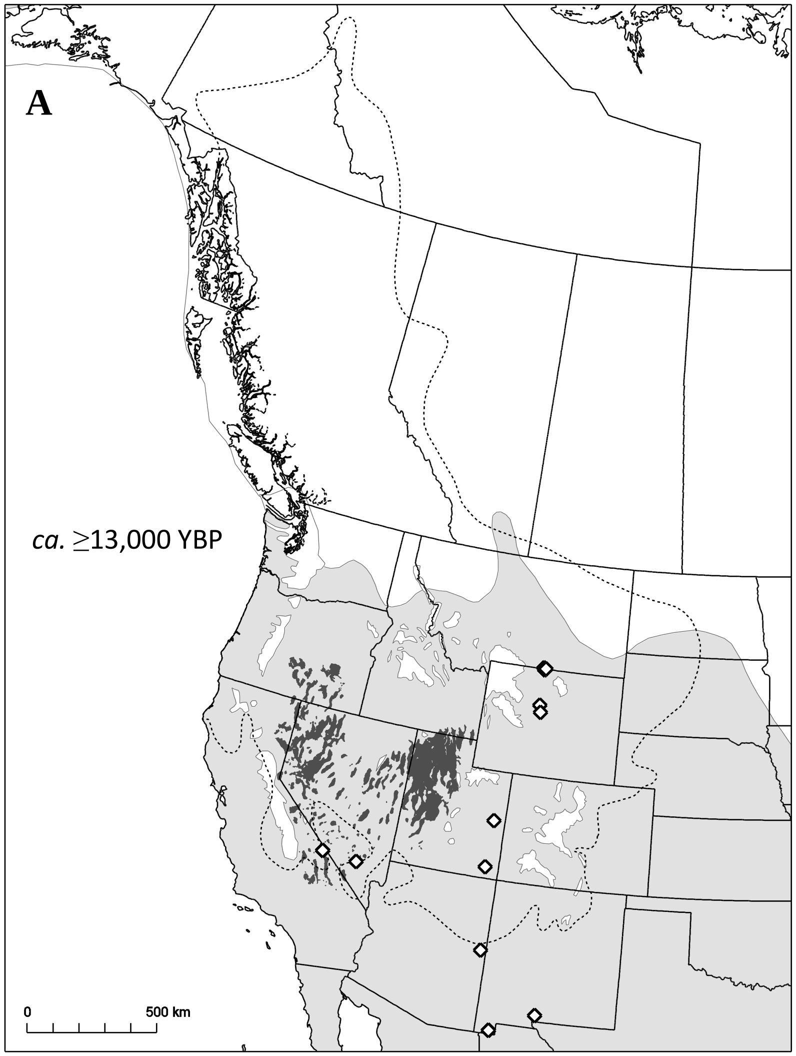


Figure 9A.

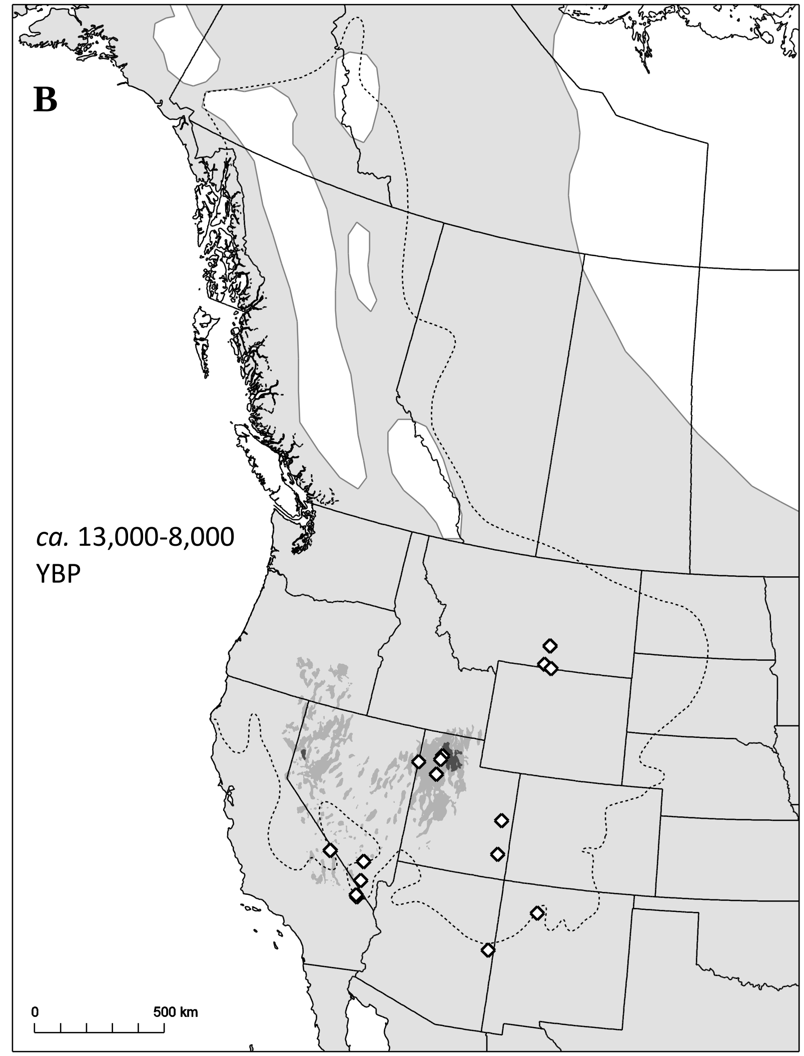


Figure 9B.

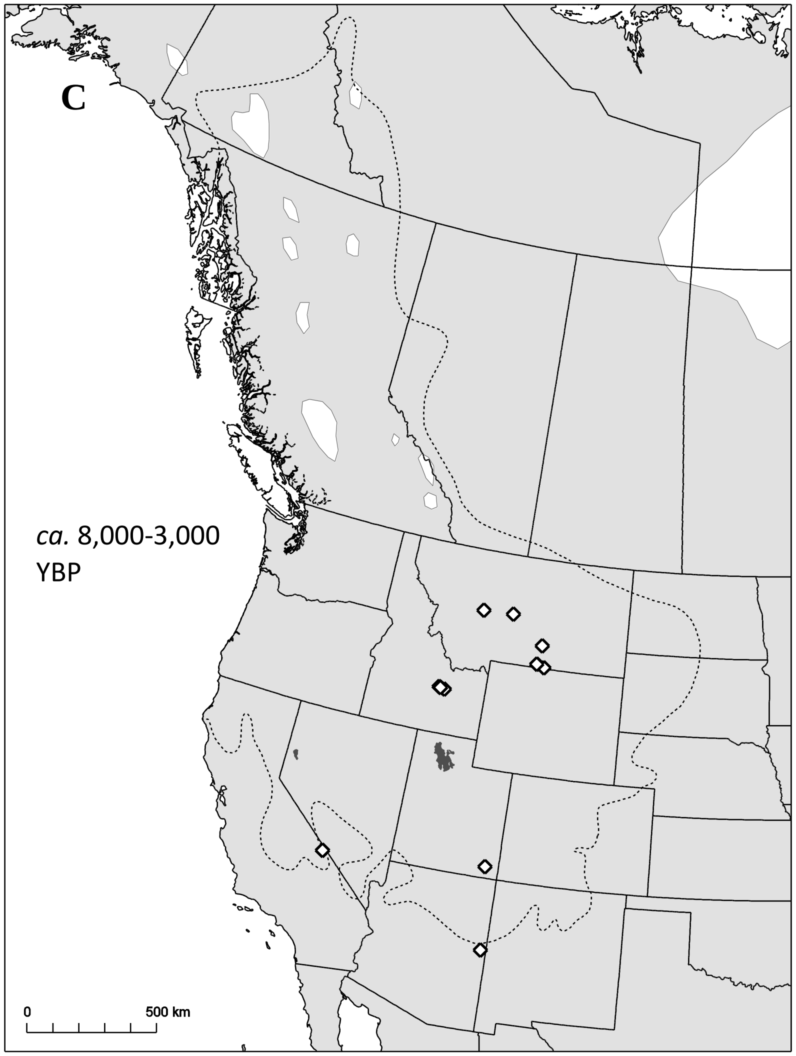


Figure 9C.

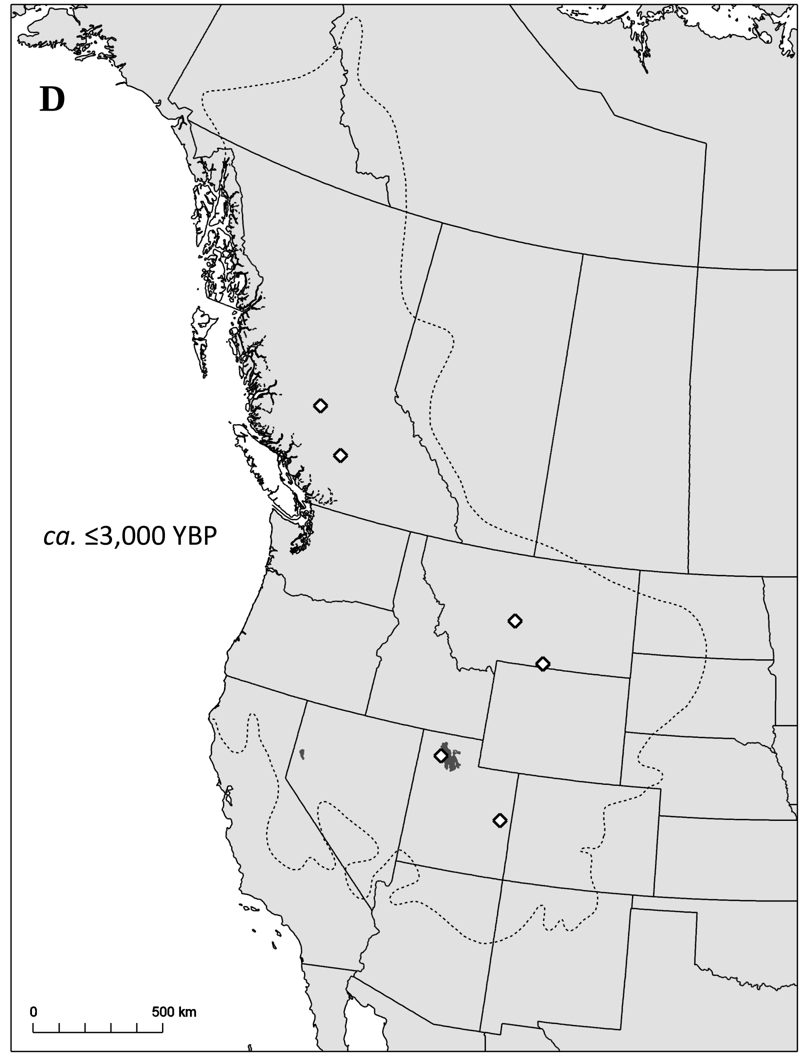


Figure 9D.

Figure 9. (A) *Neotoma cinerea* evidence and potential barriers at the end of the Pleistocene last glacial maximum *ca.* 15,000 YBP. White diamonds show localities of subfossil evidence dating 13,000 YBP or older, while the dotted line shows the modern *N. cinerea* range. White areas are glaciers, dark gray areas are pluvial lakes, and the dark gray line represents the Green and Colorado Rivers. Glaciers are redrawn from Pielou (2001), Ray and Adams (2001), and Pierce (2004). (B) *Neotoma cinerea* evidence and potential barriers during the Pleistocene-Holocene transition 13,000-8,000 YBP, including glaciers *ca.* 10,000 YBP. Medium gray areas show the pluvial lakes that declined in size sharply *ca.* 14,000 YBP (Benson 2004); remaining dark grey areas show modern remnants of the pluvial lakes (notably Pyramid Lake in northwest Nevada and Great Salt Lake in northwest Utah). All other features are as in Figure 9A. (C) *Neotoma cinerea* evidence and potential barriers during the middle Holocene 8,000-3,000 YBP, including glaciers at *ca.* 7,000 YBP. All other features are as in Figure 9B. (D) *Neotoma cinerea* evidence and potential barriers during the later Holocene up to 3,000 YBP. All other features are as in Figure 9B.

APPENDIX V: *Neotoma cinerea* tissues used in analyses

Specimen ID codes:

[none]	Obtained from Dr. Marjorie Matocq, University of Nevada, Reno
ADH	Collected by Angela D. Hornsby
BYU	Brigham Young University Monte L. Bean Life Science Museum
CUMV	Cornell University Museum of Vertebrates
DMNS ZM	Denver Museum of Nature and Science
FMNH	Field Museum of Natural History
JHB	Collected by Johnny H. Bender
LSUMZ	Louisiana State University Museum of Natural Science
MDM	Obtained from Dr. Marjorie Matocq, University of Nevada, Reno
MSB	University of New Mexico Museum of Southwestern Biology
MVZ	University of California Museum of Vertebrate Zoology
NMMNH	New Mexico Museum of Natural History and Science
OSU	Obtained from Dr. Clinton Epps, Oregon State University
PSM	University of Puget Sound Slater Museum
RAM	Royal Alberta Museum
RBCM	Royal British Columbia Museum
ROM	Royal Ontario Museum
UAM	University of Alaska Museum of the North
UCM	University of Colorado Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
UMNH	University of Utah Museum of Natural History

Specimen ID	Latitude	Longitude	Clade	Subclade	Haplotype
137	42.8685	-112.4404	Western	Great Basin	alticola1
182	42.8685	-112.4404	Western	Great Basin	alticola2
ADH 10	46.83469	-110.2774	Western	Northern	cinerea1
ADH 11	46.83244	-110.2806	Western	Northern	cinerea1
ADH 12	46.83244	-110.2806	Western	Northern	cinerea1
ADH 13	45.21292	-108.51588	Western	Great Basin	orolestes1
ADH 14	45.21292	-108.51588	Western	Great Basin	orolestes2
ADH 15	47.06244	-104.67522	Western	Great Basin	cinerea2
ADH 16	45.87466	-103.48643	Western	Great Basin	rupicola1
ADH 17	45.87466	-103.48643	Western	Great Basin	rupicola1
ADH 18	44.04304	-103.88467	Eastern	Middle Rockies 2	orolestes8
ADH 19	44.04304	-103.88467	Western	Great Basin	orolestes3
ADH 2	42.68404	-112.97845	Western	Great Basin	cinerea3
ADH 20	44.3018	-106.94785	Eastern	Middle Rockies 1	orolestes4
ADH 21	44.3018	-106.94785	Eastern	Middle Rockies 2	orolestes5
ADH 22	44.3238	-106.91302	Eastern	Middle Rockies 2	orolestes5
ADH 23	44.28702	-106.9648	Eastern	Middle Rockies 2	orolestes6

Specimen ID	Latitude	Longitude	Clade	Subclade	Haplotype
ADH 24	44.28463	-106.94404	Eastern	Middle Rockies 1	orolestes7
ADH 25	44.30178	-106.95128	Eastern	Middle Rockies 2	orolestes5
ADH 26	44.30178	-106.95128	Eastern	Middle Rockies 1	orolestes7
ADH 27	44.16916	-106.89883	Eastern	Middle Rockies 2	orolestes8
ADH 28	44.27757	-106.94853	Eastern	Middle Rockies 2	orolestes6
ADH 29	44.27757	-106.94853	Eastern	Middle Rockies 2	orolestes6
ADH 3	46.59677	-114.16418	Western	Northern	cinerea4
ADH 30	41.14354	-106.05341	Eastern	Middle Rockies 1	cinn-oro1
ADH 31	41.14354	-106.05341	Eastern	Middle Rockies 1	cinn-oro1
ADH 32	41.14354	-106.05341	Eastern	Middle Rockies 1	cinn-oro1
ADH 33	41.14354	-106.05341	Eastern	Middle Rockies 2	orolestes9
ADH 34	41.14354	-106.05341	Eastern	Middle Rockies 3	orolestes10
ADH 35	41.14354	-106.05341	Eastern	Middle Rockies 1	cinn-oro1
ADH 36	38.65583	-106.85651	Eastern	Middle Rockies 3	orolestes11
ADH 37	38.65583	-106.85651	Eastern	Middle Rockies 3	orolestes11
ADH 38	38.65583	-106.85651	Eastern	Middle Rockies 3	orolestes11
ADH 39	38.65583	-106.85651	Eastern	Middle Rockies 3	orolestes12
ADH 4	46.57505	-114.15044	Western	Northern	cinerea5
ADH 40	38.65583	-106.85651	Eastern	Middle Rockies 3	orolestes12
ADH 42	40.63738	-108.63316	Eastern	Middle Rockies 1	cinn-oro1
ADH 43	41.43783	-109.3164	Eastern	Middle Rockies 2	cinnamomea1
ADH 44	41.43783	-109.3164	Eastern	Middle Rockies 2	cinnamomea1
ADH 45	41.43783	-109.3164	Eastern	Middle Rockies 2	cinnamomea1
ADH 46	41.43783	-109.3164	Eastern	Middle Rockies 2	cinnamomea2
ADH 47	41.43596	-109.31689	Eastern	Middle Rockies 1	cinnamomea3
ADH 48	41.45303	-109.30716	Eastern	Middle Rockies 1	ari-cinn1
ADH 49	41.45303	-109.30716	Eastern	Middle Rockies 1	ari-cinn1
ADH 5	46.57505	-114.15044	Western	Northern	cinerea5
ADH 50	41.45303	-109.30716	Eastern	Middle Rockies 2	cinnamomea4
ADH 51	41.45118	-109.30972	Eastern	Middle Rockies 2	cinnamomea1
ADH 52	42.51878	-108.79351	Eastern	Middle Rockies 2	cinnamomea9
ADH 53	42.51403	-108.79301	Eastern	Middle Rockies 2	cinnamomea5
ADH 54	42.51878	-108.79351	Eastern	Middle Rockies 1	cinnamomea6
ADH 55	42.5374	-108.79765	Eastern	Middle Rockies 2	cinn-oro2
ADH 56	42.5374	-108.79765	Eastern	Middle Rockies 2	cinn-oro2
ADH 57	42.53757	-108.79652	Eastern	Middle Rockies 2	cinn-oro2
ADH 58	42.53891	-108.79631	Eastern	Middle Rockies 2	cinn-oro2
ADH 59	42.53891	-108.79631	Eastern	Middle Rockies 2	cinn-oro2
ADH 6	48.24106	-113.49101	Western	Northern	cinerea8
ADH 60	44.18491	-111.31812	Western	Northern	cinerea6
ADH 61	44.1753	-111.31496	Western	Northern	cinerea7
ADH 62	39.22617	-117.14085	Western	Great Basin	acraea1

Specimen ID	Latitude	Longitude	Clade	Subclade	Haplotype
ADH 63	39.2191	-117.13041	Western	Great Basin	acraea2
ADH 64	41.61967	-117.54524	Western	Great Basin	alticola3
ADH 65	41.62096	-117.54611	Western	Great Basin	alticola4
ADH 66	41.62117	-117.54596	Western	Great Basin	alticola4
ADH 67	36.2538	-115.64824	Western	Great Basin	lucida1
ADH 7	48.24106	-113.49101	Western	Northern	cinerea8
ADH 8	48.24106	-113.49101	Western	Northern	cinerea8
ADH 9	48.24106	-113.49101	Western	Northern	cinerea8
BYU 13886	39.4394	-109.2741	Eastern	Middle Rockies 1	macrodon1
BYU 13887	39.4394	-109.2741	Eastern	Middle Rockies 1	macrodon2
BYU 13888	40.4595	-111.6678	Western	Great Basin	acraea3
BYU 14868	39.4394	-109.2741	Eastern	Middle Rockies 1	macrodon3
BYU 16617	39.66805556	-109.2333333	Eastern	Middle Rockies 1	macrodon4
BYU 16618	39.67083333	-109.2375	Eastern	Middle Rockies 1	macrodon5
BYU 17790	40.2558	-111.6586	Western	Great Basin	acraea4
BYU 18997	44.198	-121.2712	Western	Great Basin	alticola5
BYU 18998	44.198	-121.2712	Western	Great Basin	alticola6
CUMV 20269	45.1908989	-116.5725021	Western	Northern	alticola7
DMNS ZM.11178	38.8406	-105.0451	Eastern	Middle Rockies 3	orolestes13
DMNS ZM.11383	40.8295	-108.7349	Eastern	Middle Rockies 1	cinnamomea7
DMNS ZM.11517	39.0382	-107.9076	Eastern	Middle Rockies 3	orolestes14
DMNS ZM.11518	39.0382	-107.9076	Eastern	Middle Rockies 3	orolestes14
JHB 59	39.1174	-114.30383	Western	Great Basin	acraea5
JHB 60	39.1174	-114.30383	Western	Great Basin	acraea6
JHB 61	39.11444	-114.30054	Western	Great Basin	acraea5
JHB 62	39.1144	-114.29949	Western	Great Basin	acraea5
JHB 63	39.11702	-114.30418	Western	Great Basin	acraea6
LSUMZ M452	38.23234	-109.43364	Eastern	Middle Rockies 4	arizonae1
MDM 148	39.4468	-120.266	Western	Great Basin	alticola8
MSB 140843	35.274898	-106.387917	Eastern	Southern Rockies	orolestes15
MSB 141113	35.80743333	-106.5078667	Eastern	Southern Rockies	orolestes16
MSB 149469	60.72087	-135.053179	Western	Pacific Northwest	occidentalis1
MSB 152633	43.486	-116.229	Western	Great Basin	alticola9
MSB 152693	43.486	-116.229	Western	Great Basin	alticola9
MSB 152695	43.486	-116.229	Western	Great Basin	alticola9
MSB 70026	35.6741992	-105.6572036	Eastern	Southern Rockies	orolestes17
MSB 73684	35.5783334	-105.595	Eastern	Southern Rockies	orolestes18
MSB 74609	40.6333333	-108.3166667	Eastern	Middle Rockies 2	cinnamomea9
MSB 74610	40.6333333	-108.3166667	Eastern	Middle Rockies 2	cinnamomea8
MSB 74611	40.6333333	-108.3166667	Eastern	Middle Rockies 2	cinnamomea9
MSB 74612	40.6333333	-108.3166667	Eastern	Middle Rockies 1	cinnamomea10
MSB 74646	39	-104.8333333	Eastern	Middle Rockies 3	orolestes13

Specimen ID	Latitude	Longitude	Clade	Subclade	Haplotype
MSB 76526	39.597482	-108.8025017	Eastern	Middle Rockies 1	ari-cinn1
MSB 76527	39.597482	-108.8025017	Eastern	Middle Rockies 1	ari-cinn1
MSB 76967	37.2	-109.555	Eastern	Middle Rockies 4	arizonae2
MSB 76968	37.2	-109.555	Eastern	Middle Rockies 4	arizonae2
MSB 86004	35.81445	-106.5218667	Eastern	Southern Rockies	orolestes19
MSB 90783	38.25583	-119.23028	Western	Great Basin	acraea7
MSB 92136	35.807667	-106.507867	Eastern	Southern Rockies	orolestes20
MSB 92137	35.807667	-106.507867	Eastern	Southern Rockies	orolestes20
MSB 92140	35.807667	-106.507867	Eastern	Southern Rockies	orolestes21
MSB 92141	35.807667	-106.507867	Eastern	Southern Rockies	orolestes22
MSB 99135	35.80776667	-106.5078667	Eastern	Southern Rockies	orolestes23
MVZ 197092	41.76003	-114.7807	Western	Great Basin	alticola10
MVZ 199348	38.7113	-109.32825	Eastern	Middle Rockies 4	arizonae3
MVZ 201915	37.91355	-119.42225	Western	Great Basin	acraea8
MVZ 201916	37.91355	-119.42225	Western	Great Basin	acraea8
MVZ 206431	36.3869	-118.4107	Western	Northern	acraea9
MVZ 215473	40.7340055	-121.1357641	Western	Great Basin	alticola11
MVZ 216409	37.87078	-119.16125	Western	Great Basin	acraea10
MVZ 218378	40.888370	-120.181110	Western	Great Basin	alticola12
MVZ 218379	40.966360	-120.137450	Western	Great Basin	alticola15
MVZ 219950	37.531010	-118.165080	Western	Great Basin	acraea11
MVZ 219951	37.531010	-118.165080	Western	Great Basin	acraea12
MVZ 220134	37.841170	-119.412060	Western	Northern	acraea13
MVZ 220623	40.804340	-120.612350	Western	Great Basin	alticola13
MVZ 220746	40.446310	-121.409000	Western	Great Basin	alticola14
MVZ 220747	40.406370	-121.360860	Western	Great Basin	alticola15
MVZ 220748	40.406370	-121.360860	Western	Great Basin	alticola15
MVZ 222570	36.090649	-118.226099	Western	Great Basin	acraea14
MVZ 222572	35.946513	-118.324318	Western	Great Basin	acraea15
NMMNH 1006	56.851398	-131.655594	Western	Pacific Northwest	occidentalis2
NMMNH 614	47.019995	-113.132689	Western	Northern	cinerea9
OSU	43.879898	-122.36221	Western	Great Basin	occidentalis3
RAM 01.8.3	50.633333	-110.183333	Western	Northern	cinerea12
RAM 03.13.1	50.0772	-110.7781	Western	Northern	cinerea10
RAM 03.13.2	50.0405	-110.6735	Western	Northern	cinerea11
RAM 04.12.1	50.6438889	-110.1891667	Western	Northern	cinerea12
RAM 95.30.34	50.6	-110.3	Western	Northern	cinerea12
RBCM 20000	49.966667	-119.966667	Western	Northern	occidentalis4
RBCM R0207	49.045833	-123.790556	Western	Pacific Northwest	occidentalis5
UAM 24566	47.11388889	-120.9333333	Western	Northern	occidentalis11
UAM 24567	47.11388889	-120.9333333	Western	Northern	occidentalis11
UAM 35061	47.13333333	-120.9666667	Western	Pacific Northwest	occidentalis6

Specimen ID	Latitude	Longitude	Clade	Subclade	Haplotype
UAM 35063	47.11388889	-120.9333333	Western	Northern	occidentalis7
UAM 35116	47.15	-121.95	Western	Northern	occidentalis8
UAM 35117	47.15	-121.95	Western	Northern	occidentalis11
UAM 35118	47.15	-121.95	Western	Northern	occidentalis11
UAM 35134	58.18805556	-129.8880556	Western	Pacific Northwest	occidentalis9 / saxamans1
UAM 49980	47.11388889	-120.9333333	Western	Northern	occidentalis10
UAM 50132	47.11388889	-120.9333333	Western	Northern	occidentalis11
UAM 54423	47.11388889	-120.9333333	Western	Northern	occidentalis11
UAM 71646	60.71666667	-135.05	Western	Pacific Northwest	occidentalis12 / saxamans2
UCM 18902	40.0305	-105.276	Eastern	Middle Rockies 3	orolestes24
UMNH 29794	39.03200	-114.28970	Western	Great Basin	acraea16
UMNH 31172	38.43659	-111.46604	Western	Great Basin	acraea17
UMNH 31873	40.34539	-115.59535	Western	Great Basin	acraea18
UMNH 31874	40.34539	-115.59535	Western	Great Basin	acraea18
UMNH 31875	40.34539	-115.59535	Western	Great Basin	acraea18
UMNH 32187	40.68811	-115.47072	Western	Great Basin	acraea21
UMNH 32202	40.68811	-115.47072	Western	Great Basin	acraea19
UMNH 32468	40.51290	-115.43491	Western	Great Basin	acraea20
UMNH 32653	40.51290	-115.43491	Western	Great Basin	acraea21
UMNH 32654	40.51290	-115.43491	Western	Great Basin	acraea21
UMNH 32655	40.51290	-115.43491	Western	Great Basin	acraea21
UWBM 49066	48.6739498	-120.56647	Western	Pacific Northwest	occidentalis13
UWBM 72106	45.570195	-117.528619	Western	Great Basin	alticola9
UWBM 72108	45.570195	-117.528619	Western	Great Basin	alticola9
UWBM 72137	45.570195	-117.528619	Western	Great Basin	alticola9
UWBM 73810	47.1166667	-121.0666667	Western	Northern	occidentalis14
UWBM 75217	46.1325	-117.816	Western	Great Basin	alticola16
UWBM 76697	45.12816667	-117.6225	Western	Great Basin	alticola17
UWBM 76799	47.22916667	-120.0916667	Western	Pacific Northwest	occidentalis15
UWBM 76808	47.22916667	-120.0916667	Western	Northern	occidentalis16
UWBM 76811	47.22916667	-120.0916667	Western	Northern	occidentalis16
UWBM 76813	47.15416667	-119.9833333	Western	Northern	occidentalis17
UWBM 78001	44.65866667	-120.2571667	Western	Great Basin	alticola18
UWBM 78139	48.80966667	-117.129	Western	Northern	occidentalis18
UWBM 78604	47.95133333	-123.2556667	Western	Pacific Northwest	occidentalis19
UWBM 78606	47.94966667	-123.2645	Western	Pacific Northwest	occidentalis19
UWBM 78852	47.88216667	-123.1451667	Western	Pacific Northwest	occidentalis20
UWBM 79495	44.86016667	-123.8371667	Western	Northern	fusca1
UWBM 79658	42.08116667	-113.6816667	Western	Great Basin	acraea22

CHAPTER 3:
Morphological diversity of *Neotoma cinerea*

INTRODUCTION

Patterns of morphological variation can be key to understanding how organisms are related, how they react and evolve in accord with their environments, and whether the variation seen is caused by molecular factors, environment, or a complex interaction of both. The bushy-tailed woodrat, *Neotoma cinerea*, is a wide-ranging species which displays a variety of morphological and pelage differences among its 13 currently-recognized subspecies (Hall 1981). These differences have been cataloged through over 200 years of descriptive information, resulting in the formation of two primary consensus opinions: first, that there is a great deal of morphological variation in this species; and second, that this variation very rarely shows clear geographic breaks even at suggested subspecies boundaries, instead intergrading within and between subspecies throughout the range of *N. cinerea* (see Chapter 1).

Current intraspecific taxonomy of *N. cinerea* is based on phenotypic characteristics, including heavy reliance on extremely variable characteristics of the pelage. However, pelage is challenging to quantify and thus comparatively difficult to assess in a systematic way. Alternatively, craniodental characteristics also factor heavily into subspecies recognition but are easily measured and thus amenable to statistical analysis; yet, investigation of *N. cinerea* cranial morphology beyond simple descriptive statistics has been lacking. Powerful modern statistical techniques have been used to understand patterns of variation in other species or species groups of *Neotoma* (Hayes and Richmond 1993; Matocq 2002; Matocq and Murphy 2007; Patton *et al.* 2008) and may help provide ways to statistically explore and test patterns of variation within *N. cinerea*.

The purpose of this study is to determine whether there are consistent morphological differences between the members of the two major phylogenetic clades, the Eastern and Western clades (see Chapter 2), that would indicate whether morphological differentiation of these groups was concurrent with molecular differentiation. These clades show a level of genetic divergence and inferred independent population history that encourages further inquiry into whether they would best be described as separate species (see Chapter 2), a topic that can be further addressed with morphological analyses. I use qualitative, univariate (t-test, ANOVA), and multivariate (principal component analysis) approaches here to test for differences between the major groups and subspecies. Based on moderate genetic divergence, I expect to see the greatest morphological differences between the Eastern and Western groups, with the potential of discovering more subtle differences between the subspecies of each group.

METHODS

Sampling

Skulls for morphological analysis came from both museum and field collections. To begin choosing museum specimens, I first performed multi-institution searches for *Neotoma cinerea* through the Mammal Networked Information System (MaNIS) and Arctos databases (queried July-August 2007), supplemented by searches in the individual databases of several other museums not networked through MaNIS or Arctos. I plotted the trapping locations of these according to each specimen's geographic coordinates or locality, and performed field collections between July-November 2008 to fill in sampling from underrepresented areas of the distribution (see Chapter 2 for trapping procedures). I chose to revive the defunct subspecies *N. c. saxamans* for these analyses; synonymization of this taxon under *N. c. occidentalis* is the most recent change in *N. cinerea* taxonomy (Cowan and Guiguet 1960; see Chapter 1), although its incorporation was based on relatively ambiguous information and it is still recognized as a separate subspecies by some natural history museums.

I restricted measurements to animals of age classes 2-4 as determined by degree of wear on the upper molars (Matocq 2002). The youngest specimens representing age class 1 were excluded as they were most likely to display developmental allometry.

Categorical trait

I scored each skull according to one categorical trait, the sphenopalatine vacuity (SPV), as follows: closed = 0; narrow = 1; open = 2 (Figure 11). I mapped SPV scores of specimens age classes 2-4 onto a phylogenetic tree to investigate the degree of concordance between this trait and the major *N. cinerea* clades (see Chapter 2). The phylogeny was developed via maximum parsimony analysis on complete cytochrome *b* sequences (1143 bp) using MEGA v4.1 (Tamura *et al.* 2007) with 10 random-sequence addition preliminary trees, level 3 heuristic close neighbor interchange, and 1,000 bootstraps. Five outgroups included 4 previously-sequenced taxa (Matocq *et al.* 2007) and one taxon (*N. lepida*) for which SPV state was confirmed. I summarized equally-parsimonious outcomes in a single majority-rule consensus tree, and mapped SPV state onto this phylogeny manually.

Continuous traits: Principal component analysis

I took 10 continuous craniodental measurements from *N. cinerea* skulls using digital calipers with precision to 0.01 mm. Traits measured include: length of nasals; rostrum width; rostrum depth; interorbital breadth; length of palatal bridge; alveolar length of molar row; zygomatic breadth; occipital breath at mastoid processes; bullar length; and width of interpterygoid fossa (Matocq 2002). An eleventh measurement, basilar length, was also taken to represent overall body size and serve as a scaling factor for the remaining 10 traits (Matocq and Murphy 2007).

I performed all statistical analyses with SAS software v9.1.3 (SAS Institute Inc.). Unless otherwise noted, analyses on continuous traits were performed separately for males and females to avoid effects of sexual size dimorphism (Smith 1997). To confirm whether age classes within sexes could be reasonably grouped for analyses, I log-transformed all traits and compared age classes using CONTRAST statements in the generalized linear model PROC GLM. Within females, age class 2 differed significantly ($\alpha = 0.05$) from class 3 in 8 traits and class 4 in 9 traits; classes 3 and 4 differed in only one trait, and were therefore pooled for remaining analyses. Within males, age class 2 differed from classes 3 and 4 in 10 traits each; classes 3 and 4 differed in only 3 traits, and were therefore likewise pooled. Thus, specimens of age class 2 were omitted from all quantitative analyses. This pooling scheme was adopted for all continuous trait analyses, and has been supported for similar analyses of related species (Matocq 2002; Matocq and Murphy 2007).

I used principal component analysis (PCA) to simplify the continuous trait dataset by combining the several correlated variables into fewer principal components. To account for potential trait allometry based on the overall specimen size, I applied a regression-based adjustment developed by Thorpe (1975). Though more mathematically intensive than methods which account for body size by calculating trait proportions or allowing body size to dominate the first principal component, methods such as Thorpe's are preferred because they more effectively remove the effect of body size (Reist 1985).

To make these adjustments, I first regressed each log-transformed trait against log-transformed basilar length and noted the significance of the slope estimate; slopes with $P < 0.05$ indicated significant isometry which needed to be corrected for. Adjusted trait values were calculated by applying the slope estimate b in the following formula:

$$Y_{i,adj} = \log(Y_i) - b(\log(X_i) - \log(\overline{X}))$$

where $Y_{i,adj}$ is the adjusted trait value, Y_i is the original trait value, X_i is the basilar length, and $\overline{X}$ is the mean basilar length (Thorpe 1975). In cases where no significant isometric relationship was found ($P > 0.05$), the adjusted trait value was set equal to the original value. I then standardized values into Z scores with the following formula:

$$Z = (Y_{i,adj} - Y_{i,adj}\overline{X}) / s$$

where $Y_{i,adj}\overline{X}$ is the mean adjusted trait value and s is the standard deviation of the adjusted trait value. I conducted analyses on standardized values using PROC PRINCOMP.

Continuous traits: ANOVA and regression trait analyses

I used the original basilar length measurements in direct analyses of body size; all other continuous traits were transformed to proportional sizes (trait length divided by basilar length) prior to analysis. I used this comparatively simple method of correcting for body size to keep the univariate statistical analyses more directly aligned with the relative, qualitative descriptions given by previous authors. I used several different procedures to explore the dataset, including: PROC MEANS for basic statistics; PROC

T-TEST to compare trait means between the Eastern and Western subspecies groups; PROC GLM including Tukey-Kramer comparisons in ANOVA to test trait means between subspecies; and PROC GLM regressions to test the relationship between body size and latitude, to test the relationships between two traits (bullar length and occipital breadth), and to test the relationship between one trait (bullar length) and average annual precipitation. Precipitation data for the contiguous United States was determined for each specimen through the PRISM Climate Group data explorer, representing 30-year averages (1971-2000) modeled at 30-arcsecond (*ca*. 800 m) resolution (PRISM Climate Group, Oregon State University, http://www.prismclimate.org, queried July 2000). Precipitation data for Canada was estimated based on empirical data from the closest-available weather stations, also representing 30-year averages (1971-2000; National Climate Data and Information Archive, http://www.climate.weatheroffice.ec.gc.ca, queried July 2009). I excluded data from stations more than 400 m in elevation or 32 km in distance (*ca.* 10 miles) from the original collection point to avoid values that would poorly represent conditions at the specimen origins.

RESULTS

Of nearly 600 skulls examined, 385 skulls were of age classes 2-4 and sufficiently undamaged to include in analyses (Appendix VI). Cyt *b* sequences and SPV states were available from n = 97 specimens, which were used for phylogenetic mapping of the SPV trait, and additional specimens for a total n = 378 provided SPV information for geographic mapping. 235 specimens in age classes 3 and 4 were used for quantitative analyses, including 144 females and 91 males representing 14 subspecies.

Categorical trait

Within subspecies, SPV morphology is highly consistent with historical descriptions (Table 3). Additionally, this trait is quite consistent with the phylogeny and with the phylogenetic distribution of the major Eastern and Western clades (Figure 10; Figure 11; see Chapter 2). All Eastern clade members show open morphology, and most Western clade member show closed or narrow morphology. Exceptions of open SPV morphology in the Western clade include the following haplotypes: saxamans1 and saxamans2, which occur in northern British Columbia; cinerea12 which occurs in southern Alberta; and orolestes2, orolestes3, and rupicola1 which occur in southern Montana and western South Dakota (see Chapter 2). An additional specimen with open SPV morphology was collected from northwest Washington within the geographic Western group boundaries, although it is not represented in the phylogeny (Figure 11).

Continuous traits: Principal component analysis

PCA was restricted to specimens with a full complement of trait measurements, including n = 84 females and n = 66 males. In both sexes, only interorbital breadth showed no positive, significant relationship with body size; all other traits were size-corrected with the Thorpe method. The first 5 principle components in females and first 4 in males were presumably informative with eigenvalues greater than 1. Plots of principal component 2 against principal component 1 showed no separation of the major Eastern and Western clades (Figure 12). Plots of the remaining informative principal components showed a similar lack of separation between groups (not shown).

Continuous traits: ANOVA and regression trait analyses

Basilar length was explained fairly well by major group classification, with the

Eastern group overall smaller than the Western group (Table 4). Subspecies classification also showed a strong relationship with basilar length (Table 5). In ANOVA comparisons of subspecies, this outcome was echoed by trends of Eastern group *N. c. arizonae*, *N. c. cinnamomea*, and *N. c. orolestes* generally smaller than Western group *N. c. cinerea*, *N. c. drummondii*, and *N. c. occidentalis*. However, *N. c. acraea* within the Western group was also significantly smaller than some Western group subspecies, and all of these relationships were only noteworthy among females, not males (Table 6). Regression analyses of basilar length against latitude showed highly significant relationships (females: $F = 51.66$, $P < 0.0001$, $r^2 = 0.2806$; males: $F = 17.53$, $P < 0.0001$, $r^2 = 0.1645$).

Most other traits also showed strong relationships with subspecies classification (Table 5); however, fewer traits also displayed a significant difference between the major Eastern and Western groups (Table 4). Traits that showed the clearest relationships across sexes and in both subspecies and group analyses include length of palatal bridge, occipital breadth, and bullar length. Remaining traits showed less discernable patterns, and are summarized in Table 6.

Proportional palatal bridge length is greater in the Eastern clade in both males and females. (Table 4). Somewhat contrary to the overall pattern, the strongest trend at the subspecies level was of larger proportional measurements in Western group *N. c. fusca* than other Western group subspecies, although this is confined almost entirely to females (Table 6).

Proportional occipital breadth and bullar length are significantly larger across sexes in the Eastern group than the Western group (Table 4). The relationship between these variables is positive and highly significant (females: $F = 63.48$, $P < 0.0001$, $r^2 = 0.3315$; males: $F = 46.77$, $P < 0.0001$, $r^2 = 0.3779$), although of the two, bullar length shows more consistent trends in subspecies comparisons (Table 6). Bullar length comparisons illustrate the overall difference between Eastern and Western groups, with several Eastern subspecies showing larger proportional bullae than Western subspecies. However, there were no differences between Eastern subspecies and Western *N. c. acraea* and *N. c. lucida*, and *N. c. acraea* even showed significantly larger bullae than other Western subspecies (Table 6). Regression of proportional bullar size against average annual precipitation showed a highly significant negative relationship (females: $F = 34.98$, $P < 0.0001$, $r^2 = 0.2287$; males: $F = 23.17$, $P < 0.0001$, $r^2 = 0.2542$).

DISCUSSION

Categorical trait evolution

Overall, the single categorical trait differentiated the Eastern and Western groups better than any single continuous variable or combination thereof. The multivariate analyses failed to differentiate between the major groups, and the strongest patterns in univariate analyses can be explained by environmental variables; the SPV trait appears to offer the most evidence that the Eastern and Western clades differ morphologically in regard to phylogeny. Although the ancestral SPV morphology has been hypothesized as closed (Merriam 1894), it was likely open in the genus ancestor as this is the state seen in other *Neotoma* species (with some variation in size; True 1894). Generally speaking, the Eastern group and northernmost Western *N. cinerea* populations show the ancestral (open) SPV morphology, while the derived (narrow, closed) conditions are seen broadly across the remaining Western clade populations.

Several specimens that fall under the Western phylogenetic clade show open SPV morphology, thus appearing in a clade otherwise showing narrow or closed SPV's (Figure 10). I will consider these cases separately. Specimens with open SPV's from Alberta, South Dakota, and Montana were not surprising as *N. c. cinerea* in that region is said to show a range of SPV morphology intermediate between the Eastern and Western groups (Hooper 1940). Additionally, open SPV states of specimens from the Wyoming margins could be explained by interbreeding between the two major clades in this region of presumed contact (see Chapter 2).

Open SPV morphology in the far north of the *N. cinerea* range is also unsurprising, as it is consistent with the previous morphological description of the defunct subspecies *N. c. saxamans* in Yukon and northern British Columbia (Osgood 1900; Table 3). Several explanations for this finding are possible. First, there may have been back-mutation or character reversal to the ancestral state in these northern areas. Second, because *N. c. saxamans* appears derived from northward expansion of *N. c. occidentalis* (Figure 10), the open SPV may reflect a founder effect based on small initial population sizes and random genetic drift; the occurrence of one open-SPV specimen in the hypothesized Western clade point of origin around Washington (see Chapter 2) supports this possibility. Third, predominance of open SPV morphology in the far north could represent evidence of population persistence in a northern glacial refugium dating from around the time of Eastern and Western clade divergence; however, the phylogeny does not support this hypothesis (see Chapter 2).

Continuous trait patterns

The lack of differentiation between the Eastern and Western groups through PCA was unexpected given the presumed evolutionary independence of those clades. For the same reason, it was surprising that there was also a lack of unambiguous trends in most univariate trait analyses between the groups, although these tests in particular may have been severely hampered by small sample sizes (particularly *N. c. lucida* and *N. c. macrodon*). To illustrate the lack of differentiation, subspecies from the Eastern and Western groups and from the most disparate parts of the species range (*e.g*. *N. c. arizonae* in Arizona and *N. c. saxamans* in Yukon and northern British Columbia), presumably inhabiting markedly different environmental conditions, varied only sporadically in traits other than basilar length, occipital breadth, and bullar length.

Basilar length showed significant differences between the Eastern and Western groups, and between subspecies of those groups. However, the subspecies showing significant differences are arranged according to latitude, which was a very strong predictor of body size. Hence the differences between subspecies, and between the Eastern and Western groups generally, may just as easily be explained in the context of overall adherence to a well-known ecogeographic hypothesis, Bergmann's rule (1847). The most common interpretation of this rule is that of Mayr (1956), who suggested that intraspecific body size of homeotherms varies with environmental temperature: larger races inhabit cooler climates, and smaller races inhabit warmer climates. This has classically been considered a function of the surface area to mass ratio, and the need to retain heat in cooler climates (thus favoring low proportional surface area) and dissipate heat in warmer climates (thus favoring high proportional surface area; Mayr 1956). Sampled across portions of its range, *Neotoma cinerea* appears to adhere to Bergmann's rule based on such climate variables as mean annual temperature (Brown and Lee 1969) and average January and July temperatures (Smith *et al.* 1995; Smith and Betancourt 2006), for which latitude is a proxy. Thus, differences seen here between the groups and subspecies likely illustrate this trend, and in fact these data represent a more complete picture of Bergmann's rule across the entire species range than has been seen to date.

Occipital breadth and bullar length show a strong positive correlation, such that increased occipital breadth may simply reflect changes in bullar size. Bullar length was consistently larger in Eastern group taxa than Western, with the exception of Western group *N. c. acraea* which also had consistently larger bullae. There was a strong negative correlation of bullar size with average annual precipitation, which can be explained by the reported effect of inflated bullar size in response to auditory sensitivity needs and predation pressures in arid environments (see summary in Squarcia *et al.* 2007).

These data suggest that the most significant and consistent quantitative morphological differences in *N. cinerea* result from reaction to environmental variables, rather than resulting from strong patterns based on phylogenetic relationships. This is illustrated best by *N. c. acraea*, a Western group subspecies that showed morphological trends of the Eastern group, perhaps because its southern Great Basin habitat may more closely resemble habitats of the Eastern group than the remaining Western group. Although body size is believed to be highly canalized (Smith and Betancourt 2006), it is unknown whether the environmental correlations of any of these traits reflect evolutionary changes or plastic responses. Additionally, while we can hypothesize on the effects of variability and trends, very little can be concluded based on the likely complex functional significance of the continuous traits; for instance, while body size may be important for heat regulation in direct reaction to the environment, it can also affect or be affected by mating success, competition, digestive efficiency, and other factors (Matocq and Murphy 2007; Smith 1995). In contrast, SPV morphology may have maintained correspondence to the phylogeny because of its relative selective neutrality. Overall, the major clades found in phylogenetic analyses are not evidenced by morphological analyses, making it all the more likely that *Neotoma cinerea* represents a single, albeit highly variable, species, as hypothesized by Goldman (1910) almost a century ago.

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Table 3. Frequency and proportion of *N. cinerea* specimens displaying each state of sphenopalatine vacuity (SPV) morphology: 0 = closed; 1 = narrow; 2 = open. Fifteen taxa are represented, including *N. c. occidentalis* and *N. c. saxamans* (currently synonymized under *N. c. occidentalis*) both separately and pooled ("+ *saxamans*"). The major group designation of Eastern (E) or Western (W) is shown for each subspecies. Shaded cells indicate the expected SPV states per subspecies as suggested by historical literature.

Table 3.

Subspecies	Group	*n*	Frequency (*n*) SPV = 0	SPV = 1	SPV = 2	Proportion (%) SPV = 0	SPV = 1	SPV = 2
arizonae	E	10	0	0	10	0.0	0.0	100.0
cinnamomea	E	22	0	0	22	0.0	0.0	100.0
macrodon	E	4	0	0	4	0.0	0.0	100.0
orolestes	E	61	0	2	59	0.0	3.3	96.7
rupicola	E	5	0	1	4	0.0	20.0	80.0
acraea	W	87	84	3	0	96.6	3.4	0.0
alticola	W	79	70	9	0	88.6	11.4	0.0
cinerea	W	18	5	12	1	27.8	66.7	5.6
drummondii	W	15	6	9	0	40.0	60.0	0.0
fusca	W	9	8	1	0	88.9	11.1	0.0
lucida	W	2	2	0	0	100.0	0.0	0.0
occidentalis	W	36	24	11	1	66.7	30.6	2.8
+ *saxamans*	W	54	28	16	10	51.9	29.6	18.5
pulla	W	12	4	8	0	33.3	66.7	0.0
saxamans	W	18	4	5	9	22.2	27.8	50.0

Table 4. Outcomes of t-tests comparing trait means of the two major groups, Eastern and Western. Basilar length was analyzed alone, and used as a scaling factor to create proportional trait sizes for analyses. All *t*-tests were performed with pooled variances, except for italicized tests in which the Satterthwaite correction was applied to correct for significantly unequal variances. DF are degrees of freedom, and asterisks following *P*-values mark marginally significant (*α = 0.1), significant (**α = 0.05), and highly significant (***α = 0.01) results. The relative size relationship is included for all outcomes of at least marginal significance (P < 0.1), indicating whether the trait was larger in the Eastern (E) or Western (W) group based on proportional trait size.

Table 4.

	Females					Males				
Trait	DF	*t*	*P*		Size	DF	*t*	*P*		Size
Basilar length	142	-3.05	0.0027	***	E < W	89	-1.93	0.0564	*	E < W
Length of nasals	103	-0.68	0.5010			*27.5*	*0.91*	*0.3696*		
Rostrum width	*38.2*	*1.76*	*0.0871*	*	*E > W*	*65.9*	*2.21*	*0.0308*	**	*E > W*
Rostrum depth	*38.5*	*1.25*	*0.2181*			89	0.86	0.3943		
Interorbital breadth	141	2.55	0.0119	**	E > W	89	1.87	0.0647	*	E > W
Palatal bridge	138	2.43	0.0165	**	E > W	88	3.64	0.0005	***	E > W
Molar row	141	0.87	0.3870			89	0.42	0.6778		
Zygomatic breadth	135	0.60	0.5472			87	0.84	0.4014		
Occipital breadth	139	2.96	0.0036	***	E > W	85	2.54	0.0130	**	E > W
Bullar length	129	6.02	<0.0001	***	E > W	80	3.81	0.0003	***	E > W
Interpterygoid fossa	137	-0.59	0.5550			88	-2.02	0.0462	**	E < W

Table 5. Outcomes of ANOVA models with subspecies classification as the independent predictor of trait value. Taxa *N. c. occidentalis* and *N. c. saxamans* were analyzed as separate subspecies. Basilar length was analyzed alone, and used as a scaling factor to create proportional trait sizes for analyses. DF are degrees of freedom, and asterisks following *P*-values mark marginally significant (*α = 0.1), significant (**α = 0.05), and highly significant (***α = 0.01) results.

Table 5.

	Females				Males			
Trait	DF	*F*	*P*		DF	*F*	*P*	
Basilar length	13	4.80	<0.0001	***	11	2.52	0.0090	***
Length of nasals	13	2.60	0.0041	***	11	1.27	0.2609	
Rostrum width	13	1.74	0.0598	*	11	3.06	0.0019	***
Rostrum depth	13	2.71	0.0020	***	11	2.03	0.0364	**
Interorbital breadth	13	2.40	0.0063	***	11	2.19	0.0229	**
Palatal bridge	13	3.75	<0.0001	***	11	4.06	0.0001	***
Molar row	13	1.88	0.0375	**	11	0.91	0.5342	
Zygomatic breadth	13	0.61	0.8392		11	1.46	0.1658	
Occipital breadth	13	4.46	<0.0001	***	11	3.17	0.0014	***
Bullar length	13	10.53	<0.0001	***	11	6.03	<0.0001	***
Interpterygoid fossa	13	1.38	0.1779		11	2.07	0.0321	**

Table 6. Outcomes of Tukey-Kramer multiple comparisons with subspecies classification as the independent predictor of trait value. Taxa *N. c. occidentalis* and *N. c. saxamans* were analyzed as separate subspecies. Basilar length was analyzed alone, and used as a scaling factor to create proportional trait sizes for analyses. Above the diagonal, asterisks marking marginally significant (*$\alpha = 0.1$), significant (**$\alpha = 0.05$), and highly significant (***$\alpha = 0.01$) differences. Below the diagonal, relative size relationships for comparisons of $P < 0.1$ indicate which subspecies showed the larger trait value in proportion to body size, coded as follows: AC = *acraea*; AL = *alticola*; AR = *arizonae*; CI = *cinerea*; CN = *cinnamomea*; DR = *drummondii*; FU = *fusca*; LU = *lucida*; MA = *macrodon*; OC = *occidentalis*; OR = *orolestes*; PU = *pulla*; RU = *rupicola*; and SA = *saxamans*. Shaded cells highlight comparisons between Eastern and Western group subspecies.

Table 6.

Females

Trait	Subspecies	Group	*n*	Mean	*arizonae*	*cinnamomea*	*macrodon*	*orolestes*	*rupicola*	*acraea*	*alticola*	*cinerea*	*drummondii*	*fusca*	*lucida*	*occidentalis*	*pulla*	*saxamans*
Basilar length	*arizonae*	E	3	38.14	-							***	***			**		*
	cinnamomea	E	9	40.01		-						**	**			*		
	macrodon	E	1	40.00			-											
	orolestes	E	14	40.41				-				**	*					
	rupicola	E	3	40.02					-									
	acraea	W	46	40.40						-		***	**			**		
	alticola	W	26	41.33							-							
	cinerea	W	8	43.22	CI	CI		CI		CI		-					**	
	drummondii	W	7	43.22	DR	DR		DR		DR			-				*	
	fusca	W	6	41.69										-				
	lucida	W	1	37.34											-			
	occidentalis	W	11	42.73	OC	OC				OC						-	*	
	pulla	W	5	39.59								CI	DR			OC	-	
	saxamans	W	4	42.87	SA													-
Length of nasals (proportional)	*arizonae*	E	3	0.470	-													
	cinnamomea	E	9	0.477		-												
	macrodon	E	1	0.445			-											
	orolestes	E	13	0.473				-										
	rupicola	E	2	0.468					-									
	acraea	W	29	0.464						-	**		*			*		
	alticola	W	19	0.480						AL	-							
	cinerea	W	6	0.474								-						
	drummondii	W	3	0.495						DR			-					
	fusca	W	3	0.491										-				
	lucida	W	1	0.482											-			
	occidentalis	W	8	0.484						OC						-		
	pulla	W	4	0.480													-	
	saxamans	W	4	0.484														-

Males

Trait	Subspecies	Group	*n*	Mean	*arizonae*	*cinnamomea*	*macrodon*	*orolestes*	*rupicola*	*acraea*	*alticola*	*cinerea*	*drummondii*	*fusca*	*lucida*	*occidentalis*	*pulla*	*saxamans*
Basilar length	*arizonae*	E	2	39.47	-													
	cinnamomea	E	6	41.03		-												*
	macrodon	E	0	-			-											
	orolestes	E	15	42.50				-										
	rupicola	E	1	45.50					-									
	acraea	W	25	42.32						-								
	alticola	W	15	43.51							-							
	cinerea	W	2	47.27								-						
	drummondii	W	6	44.81									-					
	fusca	W	2	44.40										-				
	lucida	W	0	-											-			
	occidentalis	W	4	43.54												-		
	pulla	W	7	41.59													-	
	saxamans	W	6	46.08		SA												-
Length of nasals (proportional)	*arizonae*	E	1	0.458	-													
	cinnamomea	E	6	0.473		-												
	macrodon	E	0	-			-											
	orolestes	E	13	0.476				-										
	rupicola	E	1	0.449					-									
	acraea	W	24	0.467						-								
	alticola	W	13	0.467							-							
	cinerea	W	1	0.457								-						
	drummondii	W	3	0.457									-					
	fusca	W	2	0.475										-				
	lucida	W	0	-											-			
	occidentalis	W	2	0.478												-		
	pulla	W	5	0.487													-	
	saxamans	W	6	0.464														-

Table 6. Continued.

Females

Trait	Subspecies	Group	*n*	Mean	*arizonae*	*cinnamomea*	*macrodon*	*orolestes*	*rupicola*	*acraea*	*alticola*	*cinerea*	*drummondii*	*fusca*	*lucida*	*occidentalis*	*pulla*	*saxamans*
Rostrum width (proportional)	*arizonae*	E	3	0.122	-													
	cinnamomea	E	9	0.116		-												
	macrodon	E	1	0.129			-											
	orolestes	E	14	0.117				-										
	rupicola	E	3	0.117					-									
	acraea	W	45	0.116						-								
	alticola	W	25	0.115							-							
	cinerea	W	8	0.112								-						
	drummondii	W	7	0.109									-					
	fusca	W	6	0.112										-				
	lucida	W	1	0.111											-			
	occidentalis	W	11	0.115												-		
	pulla	W	5	0.116													-	
	saxamans	W	4	0.111														-
Rostrum depth (proportional)	*arizonae*	E	3	0.203	-													
	cinnamomea	E	9	0.199		-												
	macrodon	E	1	0.192			-											
	orolestes	E	14	0.201				-										
	rupicola	E	3	0.203					-									
	acraea	W	45	0.197						-	**							
	alticola	W	25	0.202						AL	-	*	**					
	cinerea	W	8	0.194							AL	-						
	drummondii	W	7	0.192							AL		-	*				
	fusca	W	6	0.203									FU	-				
	lucida	W	1	0.205											-			
	occidentalis	W	11	0.198												-		
	pulla	W	5	0.202													-	
	saxamans	W	4	0.199														-

Males

Trait	Subspecies	*n*	Mean	*arizonae*	*cinnamomea*	*macrodon*	*orolestes*	*rupicola*	*acraea*	*alticola*	*cinerea*	*drummondii*	*fusca*	*lucida*	*occidentalis*	*pulla*	*saxamans*
Rostrum width (proportional)	*arizonae*	2	0.118	-													
	cinnamomea	6	0.120		-												
	macrodon	0	-			-											
	orolestes	15	0.116				-										
	rupicola	1	0.118					-									
	acraea	25	0.117						-								*
	alticola	15	0.111							-							
	cinerea	2	0.114								-						
	drummondii	5	0.107									-					
	fusca	2	0.117										-				
	lucida	0	-											-			
	occidentalis	4	0.106												-	*	
	pulla	7	0.120												PU	-	*
	saxamans	6	0.107						AC							PU	-
Rostrum depth (proportional)	*arizonae*	2	0.204	-													
	cinnamomea	6	0.203		-												
	macrodon	0	-			-											
	orolestes	15	0.200				-										
	rupicola	1	0.188					-									
	acraea	25	0.200						-								
	alticola	15	0.202							-							
	cinerea	2	0.194								-						
	drummondii	6	0.193									-					
	fusca	2	0.203										-				
	lucida	0	-											-			
	occidentalis	4	0.198												-		
	pulla	7	0.203													-	
	saxamans	6	0.195														-

Table 6. Continued.

			Females																Males															
	Subspecies	Group	*n*	Mean	*arizonae*	*cinnamomea*	*macrodon*	*orolestes*	*rupicola*	*acraea*	*alticola*	*cinerea*	*drummondii*	*fusca*	*lucida*	*occidentalis*	*pulla*	*saxamans*	*n*	Mean	*arizonae*	*cinnamomea*	*macrodon*	*orolestes*	*rupicola*	*acraea*	*alticola*	*cinerea*	*drummondii*	*fusca*	*lucida*	*occidentalis*	*pulla*	*saxamans*
Interorbital breadth (proportional)	*arizonae*	E	3	0.153	-													**	2	0.144	-													
	cinnamomea	E	9	0.139		-													6	0.140		-												*
	macrodon	E	1	0.144			-												0	-			-											
	orolestes	E	14	0.145				-											15	0.138				-										**
	rupicola	E	3	0.145					-										1	0.118					-									
	acraea	W	45	0.141						-								*	25	0.136						-								*
	alticola	W	26	0.141							-							*	15	0.133							-							
	cinerea	W	8	0.135								-							2	0.120								-						
	drummondii	W	7	0.135									-						6	0.131									-					
	fusca	W	6	0.141										-					2	0.127										-				
	lucida	W	1	0.147											-				0	-											-			
	occidentalis	W	11	0.137												-			4	0.138												-		
	pulla	W	5	0.140													-		7	0.138													-	
	saxamans	W	4	0.126	AR					AC	AL							-	6	0.119		CN		OR		AC								-
Length of palatal bridge (proportional)	*arizonae*	E	3	0.218	-														2	0.230	-													
	cinnamomea	E	9	0.222		-													6	0.226		-					**							
	macrodon	E	1	0.227			-												0	-			-											
	orolestes	E	13	0.220				-						*					14	0.226				-			***							**
	rupicola	E	3	0.236					-		**		**					**	1	0.236					-									
	acraea	W	45	0.217						-				***					25	0.221						-	***							
	alticola	W	25	0.213					RU		-			***					15	0.205		CN		OR		AC	-			**				
	cinerea	W	8	0.218								-		*					2	0.214								-						
	drummondii	W	7	0.211					RU				-	***					6	0.212									-					
	fusca	W	6	0.238				FU		FU	FU	FU	FU	-	*	**		***	2	0.238							FU			-				*
	lucida	W	1	0.199										FU	-				0	-											-			
	occidentalis	W	10	0.217										FU		-			4	0.222												-		
	pulla	W	5	0.221													-		7	0.217													-	
	saxamans	W	4	0.207					RU					FU				-	6	0.206				OR						FU				-

Table 6. Continued.

Females

Character	Subspecies	Group	*n*	Mean	*arizonae*	*cinnamomea*	*macrodon*	*orolestes*	*rupicola*	*acraea*	*alticola*	*cinerea*	*drummondii*	*fusca*	*lucida*	*occidentalis*	*pulla*	*saxamans*
Length of molar row (proportional)	*arizonae*	E	3	0.236	-													
	cinnamomea	E	9	0.238		-												
	macrodon	E	1	0.240			-											
	orolestes	E	13	0.236				-										
	rupicola	E	3	0.242					-									
	acraea	W	46	0.237						-		*						
	alticola	W	26	0.240							-	**						
	cinerea	W	8	0.222						AC	AL	-						
	drummondii	W	7	0.231									-					
	fusca	W	6	0.240										-				
	lucida	W	1	0.236											-			
	occidentalis	W	11	0.228												-		
	pulla	W	5	0.234													-	
	saxamans	W	4	0.225														-
Zygomatic breadth (proportional)	*arizonae*	E	3	0.622	-													
	cinnamomea	E	7	0.618		-												
	macrodon	E	1	0.614			-											
	orolestes	E	14	0.621				-										
	rupicola	E	3	0.633					-									
	acraea	W	43	0.621						-								
	alticola	W	26	0.621							-							
	cinerea	W	8	0.612								-						
	drummondii	W	6	0.617									-					
	fusca	W	6	0.622										-				
	lucida	W	1	0.636											-			
	occidentalis	W	10	0.612												-		
	pulla	W	5	0.623													-	
	saxamans	W	4	0.620														-

Males

Character	Subspecies	Group	*n*	Mean	*arizonae*	*cinnamomea*	*macrodon*	*orolestes*	*rupicola*	*acraea*	*alticola*	*cinerea*	*drummondii*	*fusca*	*lucida*	*occidentalis*	*pulla*	*saxamans*
Length of molar row (proportional)	*arizonae*	E	2	0.227	-													
	cinnamomea	E	6	0.241		-												
	macrodon	E	0	-			-											
	orolestes	E	15	0.228				-										
	rupicola	E	1	0.224					-									
	acraea	W	25	0.231						-								
	alticola	W	15	0.233							-							
	cinerea	W	2	0.209								-						
	drummondii	W	6	0.224									-					
	fusca	W	2	0.243										-				
	lucida	W	0	-											-			
	occidentalis	W	4	0.227												-		
	pulla	W	7	0.229													-	
	saxamans	W	6	0.223														-
Zygomatic breadth (proportional)	*arizonae*	E	2	0.622	-													
	cinnamomea	E	6	0.619		-												
	macrodon	E	0	-			-											
	orolestes	E	15	0.614				-										
	rupicola	E	1	0.596					-									
	acraea	W	24	0.619						-								
	alticola	W	15	0.605							-							
	cinerea	W	2	0.599								-						
	drummondii	W	5	0.608									-					
	fusca	W	2	0.600										-				
	lucida	W	0	-											-			
	occidentalis	W	4	0.606												-		
	pulla	W	7	0.621													-	
	saxamans	W	6	0.596														-

Table 6. Continued.

			Females																Males															
	Subspecies	Group	*n*	Mean	*arizonae*	*cinnamomea*	*macrodon*	*orolestes*	*rupicola*	*acraea*	*alticola*	*cinerea*	*drummondii*	*fusca*	*lucida*	*occidentalis*	*pulla*	*saxamans*	*n*	Mean	*arizonae*	*cinnamomea*	*macrodon*	*orolestes*	*rupicola*	*acraea*	*alticola*	*cinerea*	*drummondii*	*fusca*	*lucida*	*occidentalis*	*pulla*	*saxamans*
Occipital breadth (proportional)	*arizonae*	E	3	0.491	-													**	2	0.496	-							*						*
	cinnamomea	E	9	0.486		-						***				*		**	6	0.484		-												*
	macrodon	E	1	0.467			-												0	-			-											
	orolestes	E	14	0.482				-				***						**	14	0.483				-										**
	rupicola	E	3	0.488					-			**							1	0.461					-									
	acraea	W	43	0.481						-		***				*		**	24	0.480						-								**
	alticola	W	26	0.480							-	***						*	15	0.475							-							
	cinerea	W	8	0.456		CN		OR	RU	AC	AL	-							2	0.446	AR							-						
	drummondii	W	7	0.471									-						4	0.468									-					
	fusca	W	6	0.475										-					2	0.486										-				
	lucida	W	1	0.466											-				0	-											-			
	occidentalis	W	11	0.467		CN				AC						-			4	0.458												-		
	pulla	W	5	0.474													-		7	0.475													-	
	saxamans	W	4	0.457	AR	CN		OR		AC	AL							-	6	0.454	AR	CN		OR		AC								-
Bullar length (proportional)	*arizonae*	E	3	0.205	-						**	***	***	***		***	***	**	2	0.203	-								**			**	**	*
	cinnamomea	E	9	0.201		-					***	***	***	***		***	***	**	6	0.199		-					**	*	***			***	***	***
	macrodon	E	1	0.201			-												0	-			-											
	orolestes	E	14	0.192				-				***	***	***		**			12	0.190				-					**			*		
	rupicola	E	3	0.203					-		**	***	***	***		***	**	*	1	0.169					-									
	acraea	W	36	0.192						-		***	***	***		***			20	0.190						-			***			**	*	*
	alticola	W	23	0.186	AR	CN			RU		-	*		*					15	0.183		CN					-							
	cinerea	W	8	0.175	AR	CN		OR	RU	AC	AL	-							2	0.173		CN						-						
	drummondii	W	7	0.176	AR	CN		OR	RU	AC			-						6	0.172	AR	CN		OR		AC			-					
	fusca	W	6	0.174	AR	CN		OR	RU	AC	AL			-					2	0.178										-				
	lucida	W	1	0.195											-				0	-											-			
	occidentalis	W	11	0.180	AR	CN		OR	RU	AC						-			3	0.169	AR	CN		OR		AC						-		
	pulla	W	5	0.182	AR	CN			RU								-		7	0.176	AR	CN				AC							-	
	saxamans	W	4	0.183	AR	CN			RU									-	6	0.176	AR	CN				AC								-

Table 6. Continued.

Females

	Subspecies	Group	*n*	Mean	*arizonae*	*cinnamomea*	*macrodon*	*orolestes*	*rupicola*	*acraea*	*alticola*	*cinerea*	*drummondii*	*fusca*	*lucida*	*occidentalis*	*pulla*	*saxamans*
Interpterygoid fossa (proportional)	*arizonae*	E	3	0.076	-													
	cinnamomea	E	9	0.071		-												
	macrodon	E	1	0.078			-											
	orolestes	E	13	0.073				-										
	rupicola	E	3	0.070					-									
	acraea	W	44	0.072						-								
	alticola	W	24	0.077							-							
	cinerea	W	8	0.073								-						
	drummondii	W	7	0.071									-					
	fusca	W	6	0.072										-				
	lucida	W	1	0.067											-			
	occidentalis	W	11	0.073												-		
	pulla	W	5	0.076													-	
	saxamans	W	4	0.072														-

Males

Subspecies	*n*	Mean	*arizonae*	*cinnamomea*	*macrodon*	*orolestes*	*rupicola*	*acraea*	*alticola*	*cinerea*	*drummondii*	*fusca*	*lucida*	*occidentalis*	*pulla*	*saxamans*
arizonae	2	0.075	-													
cinnamomea	6	0.069		-												
macrodon	0	-			-											
orolestes	14	0.067				-										
rupicola	1	0.061					-									
acraea	25	0.070						-								
alticola	15	0.076							-							
cinerea	2	0.064								-						
drummondii	6	0.072									-					
fusca	2	0.076										-				
lucida	0	-											-			
occidentalis	4	0.076												-		
pulla	7	0.073													-	
saxamans	6	0.066														-

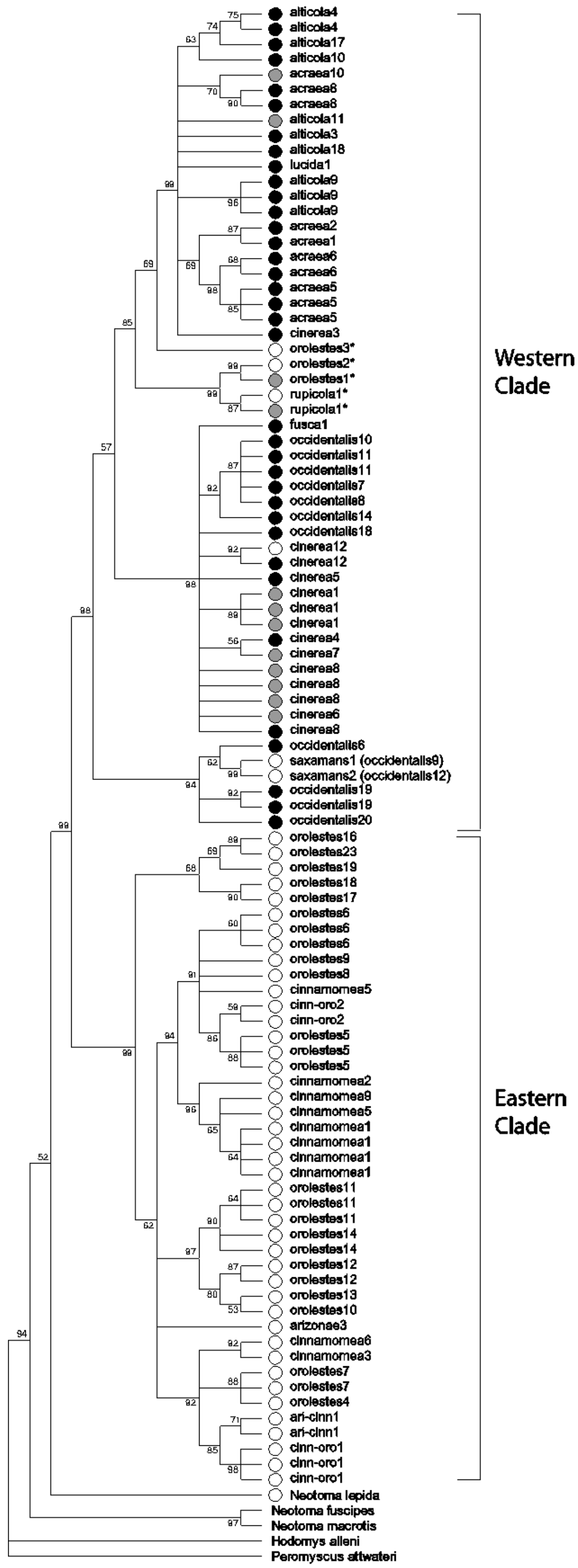

alticola4
alticola4
alticola17
alticola10
acraea10
acraea8
acraea8
alticola11
alticola3
alticola18
lucida1
alticola9
alticola9
alticola9
acraea2
acraea1
acraea6
acraea6
acraea5
acraea5
acraea5
cinerea3
orolestes3*
orolestes2*
orolestes1*
rupicola1*
rupicola1*
fusca1
occidentalis10
occidentalis11
occidentalis11
occidentalis7
occidentalis8
occidentalis14
occidentalis18
cinerea12
cinerea12
cinerea5
cinerea1
cinerea1
cinerea1
cinerea4
cinerea7
cinerea8
cinerea8
cinerea8
cinerea6
cinerea8
occidentalis6
saxamans1 (occidentalis9)
saxamans2 (occidentalis12)
occidentalis19
occidentalis19
occidentalis20
orolestes16
orolestes23
orolestes19
orolestes18
orolestes17
orolestes6
orolestes6
orolestes6
orolestes9
orolestes8
cinnamomea5
cinn-oro2
cinn-oro2
orolestes5
orolestes5
orolestes5
cinnamomea2
cinnamomea9
cinnamomea5
cinnamomea1
cinnamomea1
cinnamomea1
cinnamomea1
orolestes11
orolestes11
orolestes11
orolestes14
orolestes14
orolestes12
orolestes12
orolestes13
orolestes10
arizonae3
cinnamomea6
cinnamomea3
orolestes7
orolestes7
orolestes4
ari-cinn1
ari-cinn1
cinn-oro1
cinn-oro1
cinn-oro1
Neotoma lepida
Neotoma fuscipes
Neotoma macrotis
Hodomys alleni
Peromyscus attwateri
Western Clade
Eastern Clade

Figure 10.

Figure 10. Maximum parsimony consensus tree of *N. cinerea*, with tip symbols coding each sphenopalatine vacuity (SPV) morphology: black = closed; gray = narrow; white = open. Haplotypes are labeled by the subspecies from which they were collected. Asterisks mark samples that grouped within the Western phylogenetic clade but were collected within Eastern group subspecies boundaries (see Chapter 2). Nodes are labeled with bootstrap support; those with < 50% support are collapsed.

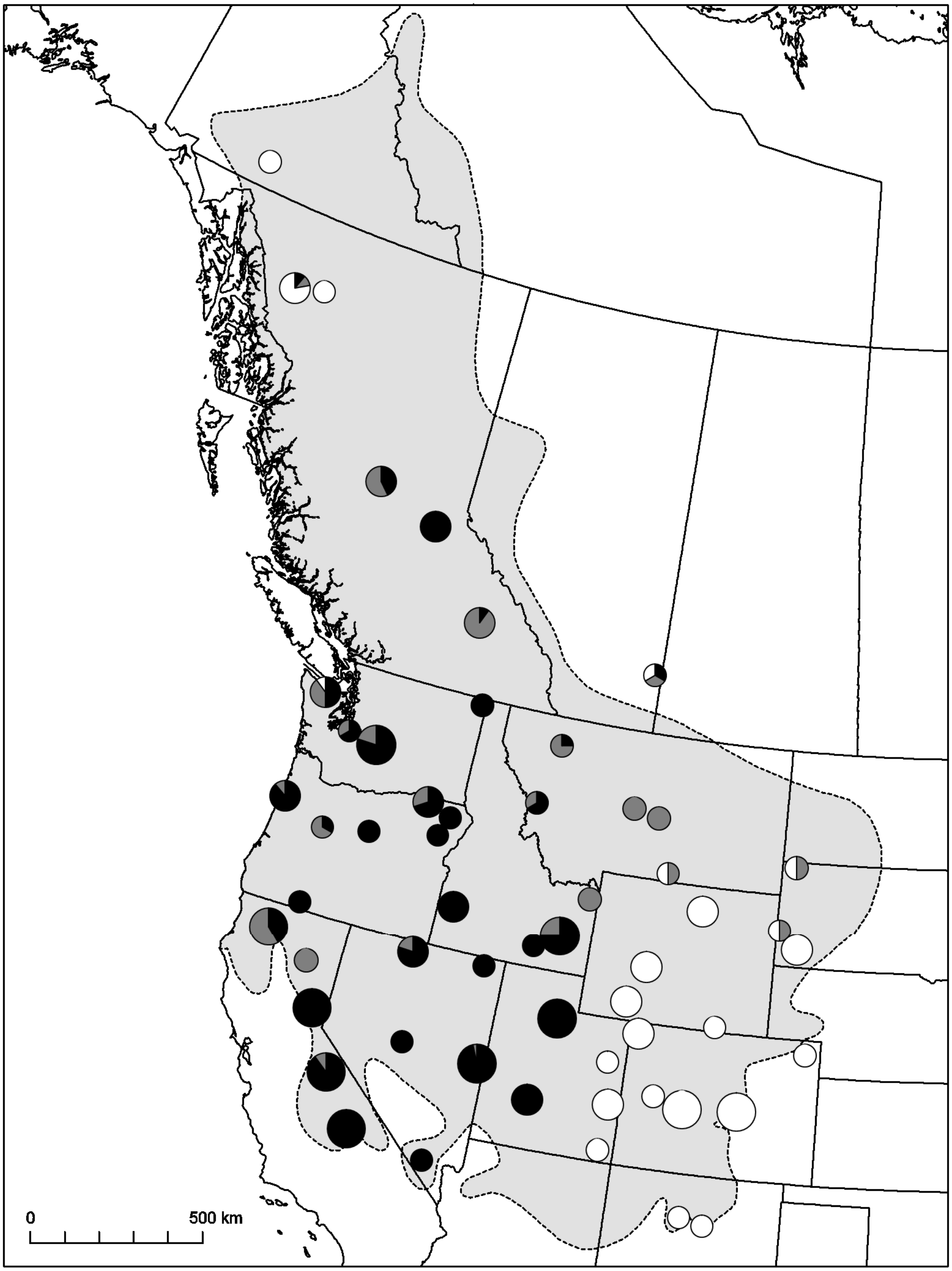
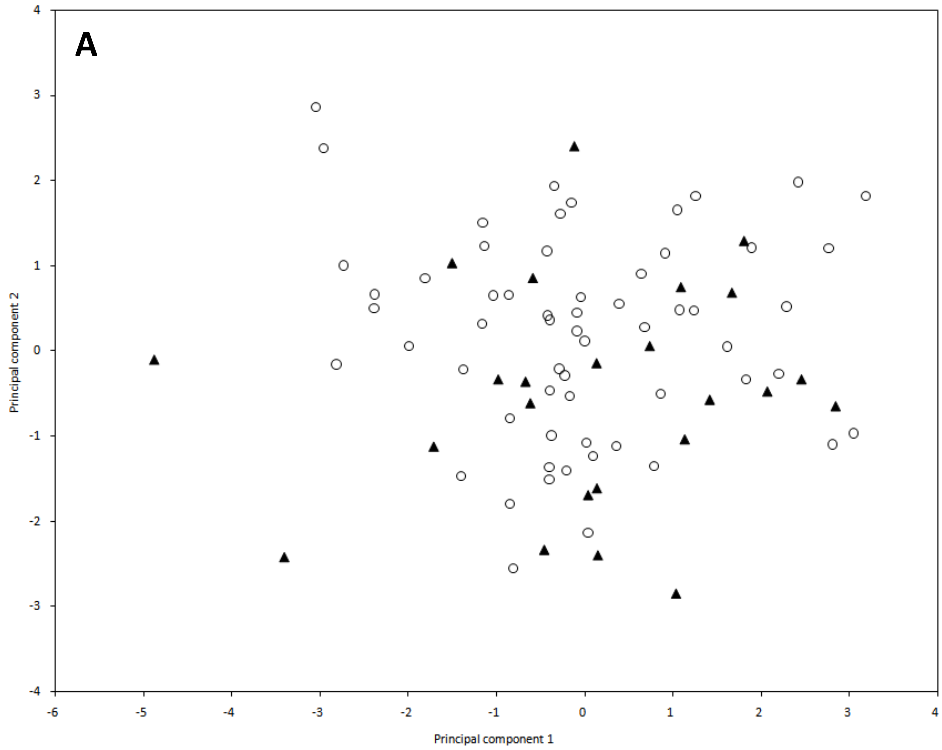


Figure 11.

Figure 11. Geographic distribution of sphenopalatine vacuity (SPV) morphology in *N. cinerea*. Pie charts show the proportion of skulls exhibiting each SPV morphology: white, open; gray, narrow; black, closed. Pie chart size corresponds to sample size: $n < 5$, small; $n = 5\text{-}10$, medium; $n > 10$, large. The shaded light gray area depicts the range of *N. cinerea* (redrawn from Hall 1981).


A
Principal component 2
Principal component 1
4
3
2
1
0
-1
-2
-3
-4
-6
-5
-4
-3
-2
-1
0
1
2
3
4

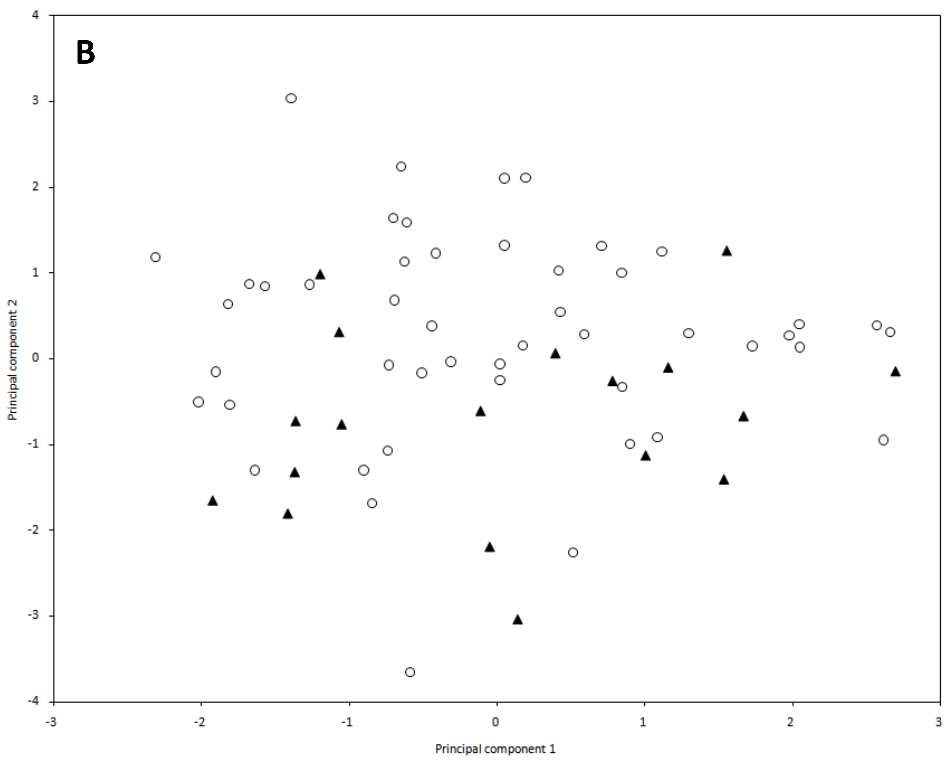

B
Principal component 2
Principal component 1
4
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3

Figure 12.

Figure 12. PCA plots of the first two principal component scores based on female (A) and male (B) *N. cinerea* skull measurements, including 10 traits adjusted for size by the Thorpe (1975) method. Specimens from the Eastern group are represented by black triangles, which specimens from the Western group are represented by open circles. Membership in each group was determined by taxonomic classification or geographic location in reference to subspecies boundaries from Hall (1981).

APPENDIX VI: *Neotoma cinerea* skulls used in analyses

See Appendix V for specimen ID codes.

Specimen ID	Latitude	Longitude	Age class	Sex	Subspecies
ADH 10	46.83469	-110.2774	4	F	*cinerea*
ADH 11	46.83244	-110.2806	2	M	*cinerea*
ADH 12	46.83244	-110.2806	4	F	*cinerea*
ADH 13	45.21292	-108.51588	4	F	*orolestes*
ADH 14	45.21292	-108.51588	3	M	*orolestes*
ADH 16	45.87466	-103.48643	4	M	*rupicola*
ADH 17	45.87466	-103.48643	4	F	*rupicola*
ADH 19	44.04304	-103.88467	3	M	*orolestes*
ADH 2	42.68404	-112.97845	2	F	*cinerea*
ADH 20	44.3018	-106.94785	2	M	*orolestes*
ADH 21	44.3018	-106.94785	2	M	*orolestes*
ADH 22	44.3238	-106.91302	4	M	*orolestes*
ADH 23	44.28702	-106.9648	2	M	*orolestes*
ADH 24	44.28463	-106.94404	2	F	*orolestes*
ADH 25	44.30178	-106.95128	2	M	*orolestes*
ADH 26	44.30178	-106.95128	2	F	*orolestes*
ADH 27	44.16916	-106.89883	2	M	*orolestes*
ADH 28	44.27757	-106.94853	2	F	*orolestes*
ADH 29	44.27757	-106.94853	4	F	*orolestes*
ADH 3	46.59677	-114.16418	2	F	*cinerea*
ADH 32	41.14354	-106.05341	3	F	*orolestes*
ADH 33	41.14354	-106.05341	3	M	*orolestes*
ADH 34	41.14354	-106.05341	4	M	*orolestes*
ADH 35	41.14354	-106.05341	2	F	*orolestes*
ADH 36	38.65583	-106.85651	4	M	*orolestes*
ADH 37	38.65583	-106.85651	2	F	*orolestes*
ADH 38	38.65583	-106.85651	4	F	*orolestes*
ADH 39	38.65583	-106.85651	4	M	*orolestes*
ADH 4	46.57505	-114.15044	2	F	*cinerea*
ADH 40	38.65583	-106.85651	2	F	*orolestes*
ADH 42	40.63738	-108.63316	2	F	*cinnamomea*
ADH 43	41.43783	-109.3164	2	F	*cinnamomea*
ADH 44	41.43783	-109.3164	3	F	*cinnamomea*
ADH 45	41.43783	-109.3164	4	F	*cinnamomea*
ADH 46	41.43783	-109.3164	2	M	*cinnamomea*
ADH 47	41.43596	-109.31689	2	M	*cinnamomea*
ADH 48	41.45303	-109.30716	3	F	*cinnamomea*
ADH 49	41.45303	-109.30716	4	F	*cinnamomea*

Specimen ID	Latitude	Longitude	Age class	Sex	Subspecies
ADH 50	41.45303	-109.30716	3	M	*cinnamomea*
ADH 51	41.45118	-109.30972	4	F	*cinnamomea*
ADH 52	42.51878	-108.79351	4	M	*cinnamomea*
ADH 53	42.51403	-108.79301	2	M	*cinnamomea*
ADH 54	42.51878	-108.79351	2	M	*cinnamomea*
ADH 56	42.5374	-108.79765	2	M	*cinnamomea*
ADH 59	42.53891	-108.79631	3	F	*orolestes*
ADH 6	48.24106	-113.49101	4	M	*cinerea*
ADH 60	44.18491	-111.31812	2	F	*cinerea*
ADH 61	44.1753	-111.31496	2	M	*cinerea*
ADH 62	39.22617	-117.14085	2	M	*acraea*
ADH 63	39.2191	-117.13041	3	F	*acraea*
ADH 64	41.61967	-117.54524	2	F	*alticola*
ADH 65	41.62096	-117.54611	2	F	*alticola*
ADH 66	41.62117	-117.54596	3	F	*alticola*
ADH 67	36.2538	-115.64824	2	M	*lucida*
ADH 7	48.24106	-113.49101	3	F	*cinerea*
ADH 8	48.24106	-113.49101	4	F	*cinerea*
ADH 9	48.24106	-113.49101	4	F	*cinerea*
DMNS ZM.11178	38.8406	-105.0451	3	F	*orolestes*
DMNS ZM.11383	40.8295	-108.7349	2	M	*cinnamomea*
DMNS ZM.11517	39.0382	-107.9076	3	F	*orolestes*
DMNS ZM.11518	39.0382	-107.9076	3	M	*orolestes*
FMNH 20120	57.9	-131.1667	2	M	*saxamans*
FMNH 6294	48.0089	-123.685	4	M	*occidentalis*
FMNH 6295	48.0089	-123.685	2	M	*occidentalis*
FMNH 6296	48.0089	-123.685	3	M	*occidentalis*
FMNH 6297	48.0089	-123.685	4	F	*occidentalis*
FMNH 6303	48.0089	-123.685	3	F	*occidentalis*
FMNH 6304	48.0089	-123.685	3	M	*occidentalis*
JHB 59	39.1174	-114.30383	4	F	*acraea*
JHB 60	39.1174	-114.30383	3	F	*acraea*
JHB 61	39.11444	-114.30054	4	M	*acraea*
JHB 62	39.1144	-114.29949	2	F	*acraea*
JHB 63	39.11702	-114.30418	2	F	*acraea*
MSB 107867	40.72056	-108.74972	3	M	*cinnamomea*
MSB 108275	40.72056	-108.74972	3	F	*arizonae*
MSB 108276	40.72056	-108.74972	3	F	*cinnamomea*
MSB 108277	40.72056	-108.74972	4	M	*cinnamomea*
MSB 108278	40.72056	-108.74972	3	F	*cinnamomea*
MSB 108279	40.72056	-108.74972	3	M	*cinnamomea*
MSB 108280	40.72056	-108.74972	3	M	*cinnamomea*

Specimen ID	Latitude	Longitude	Age class	Sex	Subspecies
MSB 108282	40.72056	-108.74972	3	F	*cinnamomea*
MSB 108430	43.18456944	-116.3783306	4	F	*alticola*
MSB 108432	43.18456944	-116.3783306	2	M	*alticola*
MSB 108435	43.18456944	-116.3783306	2	M	*alticola*
MSB 108436	43.18456944	-116.3783306	4	M	*alticola*
MSB 108437	43.18456944	-116.3783306	4	F	*alticola*
MSB 141113	35.80743333	-106.5078667	4	M	*orolestes*
MSB 70026	35.6741992	-105.6572036	2	M	*orolestes*
MSB 73684	35.5783334	-105.595	2	M	*orolestes*
MSB 86004	35.81445	-106.5218667	2	M	*orolestes*
MSB 99135	35.80776667	-106.5078667	2	F	*orolestes*
MVZ 109054	36.45162	-118.40694	4	F	*acraea*
MVZ 118889	39.438	-120.2111667	2	M	*alticola*
MVZ 118986	39.438	-120.2111667	2	M	*alticola*
MVZ 125882	38.6898058	-106.8789134	2	F	*orolestes*
MVZ 126809	39.43877	-120.23311	4	M	*alticola*
MVZ 126810	39.43877	-120.23311	2	F	*alticola*
MVZ 126811	39.43877	-120.23311	2	F	*alticola*
MVZ 128766	39.4319423	-120.2418191	2	F	*alticola*
MVZ 128769	39.438	-120.2111667	2	M	*alticola*
MVZ 128770	39.438	-120.2111667	4	F	*alticola*
MVZ 128771	39.438	-120.2111667	2	F	*alticola*
MVZ 128772	39.438	-120.2111667	3	M	*alticola*
MVZ 128773	39.438	-120.2111667	2	F	*alticola*
MVZ 128774	39.438	-120.2111667	3	F	*alticola*
MVZ 128775	39.438	-120.2111667	2	F	*alticola*
MVZ 128776	39.43159	-120.22386	2	F	*alticola*
MVZ 128777	39.45158	-120.18423	2	M	*alticola*
MVZ 13363	41.2609747	-122.9413938	4	F	*pulla*
MVZ 13364	41.2609747	-122.9413938	4	M	*pulla*
MVZ 13365	41.2609747	-122.9413938	3	M	*pulla*
MVZ 13366	41.2609747	-122.9413938	4	M	*pulla*
MVZ 13367	41.2609747	-122.9413938	3	M	*pulla*
MVZ 13368	41.2609747	-122.9413938	3	F	*pulla*
MVZ 13370	41.1675636	-122.8607265	3	F	*pulla*
MVZ 13371	41.1675636	-122.8607265	4	M	*pulla*
MVZ 13372	41.1675636	-122.8607265	4	F	*pulla*
MVZ 13374	41.1675636	-122.8607265	3	F	*pulla*
MVZ 13376	41.1675636	-122.8607265	3	M	*pulla*
MVZ 13377	41.1675636	-122.8607265	4	M	*pulla*
MVZ 134170	39.4319423	-120.2418191	2	M	*alticola*
MVZ 134171	39.4319423	-120.2418191	4	F	*alticola*

Specimen ID	Latitude	Longitude	Age class	Sex	Subspecies
MVZ 134172	39.4319423	-120.2418191	3	F	*alticola*
MVZ 134173	39.4319423	-120.2418191	2	F	*alticola*
MVZ 134174	39.4319423	-120.2418191	3	M	*alticola*
MVZ 134175	39.4319423	-120.2418191	3	M	*alticola*
MVZ 134176	39.4319423	-120.2418191	3	F	*alticola*
MVZ 134177	42.2089	-122.0921	3	F	*alticola*
MVZ 134180	42.2089	-122.0921	2	M	*alticola*
MVZ 134634	39.438	-120.2111667	2	F	*alticola*
MVZ 138894	39.44433	-120.22159	4	M	*alticola*
MVZ 138895	39.44433	-120.22159	2	M	*alticola*
MVZ 138896	39.44433	-120.22159	2	F	*alticola*
MVZ 138897	39.44433	-120.22159	2	F	*alticola*
MVZ 140101	39.43708	-120.22907	3	M	*alticola*
MVZ 149746	39.42763	-120.19853	2	F	*alticola*
MVZ 15546	36.498353	-118.219906	4	M	*acraea*
MVZ 15547	36.498353	-118.219906	2	M	*acraea*
MVZ 15549	36.498353	-118.219906	4	M	*acraea*
MVZ 15550	36.498353	-118.219906	4	F	*acraea*
MVZ 15551	36.498353	-118.219906	4	M	*acraea*
MVZ 15552	36.498353	-118.219906	3	F	*acraea*
MVZ 15554	36.498353	-118.219906	3	F	*acraea*
MVZ 15555	36.498353	-118.219906	4	M	*acraea*
MVZ 15556	36.498353	-118.219906	4	F	*acraea*
MVZ 15559	36.498353	-118.219906	2	M	*acraea*
MVZ 15562	36.473421	-118.119206	2	M	*acraea*
MVZ 15563	36.473421	-118.119206	4	F	*acraea*
MVZ 15565	36.473421	-118.119206	2	M	*acraea*
MVZ 165897	39.438	-120.2111667	3	F	*alticola*
MVZ 181489	39.4319691	-120.2399175	2	F	*alticola*
MVZ 181490	39.4319691	-120.2399175	4	F	*alticola*
MVZ 181491	39.4319691	-120.2399175	3	F	*alticola*
MVZ 181492	39.4328608	-120.2162179	2	F	*alticola*
MVZ 197092	41.76003	-114.7807	2	M	*alticola*
MVZ 199348	38.7113	-109.32825	2	M	*arizonae*
MVZ 201915	37.91355	-119.42225	4	F	*acraea*
MVZ 201916	37.91355	-119.42225	2	F	*acraea*
MVZ 201918	37.9007	-119.43205	2	F	*acraea*
MVZ 215473	40.7340055	-121.1357641	2	F	*alticola*
MVZ 216409	37.87078	-119.16125	2	M	*acraea*
MVZ 22326	37.7769743	-119.2608776	4	F	*acraea*
MVZ 22327	37.7769743	-119.2608776	3	F	*acraea*
MVZ 22328	37.7649446	-119.2506065	3	F	*acraea*

Specimen ID	Latitude	Longitude	Age class	Sex	Subspecies
MVZ 22329	37.7769743	-119.2608776	3	M	*acraea*
MVZ 22330	37.7741135	-119.2597501	4	F	*acraea*
MVZ 22332	37.875501	-119.354783	3	F	*acraea*
MVZ 22333	37.875501	-119.354783	3	F	*acraea*
MVZ 23097	37.739477	-119.397231	2	M	*acraea*
MVZ 23101	37.788547	-119.3445	3	M	*acraea*
MVZ 23104	37.788547	-119.3445	2	F	*acraea*
MVZ 23108	37.903599	-119.51566	2	M	*acraea*
MVZ 23109	37.788547	-119.3445	4	F	*acraea*
MVZ 23110	37.87115	-119.17166	3	F	*acraea*
MVZ 23112	37.87115	-119.17166	3	F	*acraea*
MVZ 23114	37.90417	-119.12495	3	F	*acraea*
MVZ 23116	37.916703	-119.440162	2	M	*acraea*
MVZ 30706	57.9167	-131.1833	3	M	*saxamans*
MVZ 30708	57.9167	-131.1833	3	F	*saxamans*
MVZ 30709	57.9167	-131.1833	3	M	*saxamans*
MVZ 30710	57.9167	-131.1833	3	F	*saxamans*
MVZ 30711	57.9167	-131.1833	3	F	*saxamans*
MVZ 30713	57.9167	-131.1833	3	M	*saxamans*
MVZ 30715	57.8333	-131.3833	2	F	*saxamans*
MVZ 30716	57.8333	-131.3833	2	M	*saxamans*
MVZ 40241	53.2667	-121.2667	4	M	*drummondii*
MVZ 40242	53.2667	-121.2667	2	M	*drummondii*
MVZ 41084	53.2333	-121.3833	2	M	*drummondii*
MVZ 41401	38.29444	-112.40139	4	M	*acraea*
MVZ 41402	38.29444	-112.40139	4	F	*acraea*
MVZ 41983	38.9889	-114.215	3	M	*acraea*
MVZ 41987	38.9889	-114.215	4	M	*acraea*
MVZ 41988	38.9889	-114.215	3	F	*acraea*
MVZ 41989	38.9889	-114.215	4	M	*acraea*
MVZ 41990	38.9889	-114.215	3	F	*acraea*
MVZ 41991	38.9889	-114.215	3	F	*acraea*
MVZ 41993	38.96917	-114.28	4	M	*acraea*
MVZ 41994	38.96917	-114.28	3	F	*acraea*
MVZ 41995	38.96917	-114.28	4	F	*acraea*
MVZ 41996	38.96917	-114.28	4	M	*acraea*
MVZ 41997	38.96917	-114.28	4	M	*acraea*
MVZ 41998	38.96917	-114.28	4	F	*acraea*
MVZ 41999	38.96917	-114.28	4	M	*acraea*
MVZ 42000	38.96917	-114.28	4	F	*acraea*
MVZ 42001	38.96917	-114.28	4	F	*acraea*
MVZ 42002	38.96917	-114.28	3	F	*acraea*

Specimen ID	Latitude	Longitude	Age class	Sex	Subspecies
MVZ 42003	38.96917	-114.28	3	F	*acraea*
MVZ 42005	38.99731	-114.30682	4	M	*acraea*
MVZ 42006	38.96917	-114.28	4	M	*acraea*
MVZ 42007	38.96917	-114.28	3	M	*acraea*
MVZ 42008	38.96917	-114.28	4	F	*acraea*
MVZ 42010	38.96917	-114.28	3	F	*acraea*
MVZ 42011	38.96917	-114.28	4	F	*acraea*
MVZ 42013	38.96917	-114.28	4	F	*acraea*
MVZ 42014	38.96917	-114.28	4	M	*acraea*
MVZ 42612	53.2667	-121.2667	3	M	*drummondii*
MVZ 44080	37.28441	-109.55312	4	F	*arizonae*
MVZ 44081	37.28441	-109.55312	4	M	*arizonae*
MVZ 45799	39.23861	-116.98667	4	F	*acraea*
MVZ 45800	39.23861	-116.98667	3	F	*acraea*
MVZ 46510	42.8714	-112.3856	2	F	*alticola*
MVZ 46511	42.8714	-112.3856	3	F	*alticola*
MVZ 46513	42.8714	-112.3856	2	F	*alticola*
MVZ 46514	42.795	-112.3333	3	F	*alticola*
MVZ 46515	42.9016	-112.2723	3	F	*alticola*
MVZ 46516	42.9016	-112.2723	4	M	*alticola*
MVZ 46517	42.795	-112.3333	3	M	*alticola*
MVZ 46583	42.8714	-112.3856	3	F	*alticola*
MVZ 46584	42.795	-112.3333	3	M	*alticola*
MVZ 46585	42.8714	-112.3462	4	M	*alticola*
MVZ 47060	42.8714	-112.3462	2	F	*alticola*
MVZ 47061	42.795	-112.3333	3	F	*alticola*
MVZ 47063	42.8714	-112.3856	3	F	*alticola*
MVZ 51944	42.7805	-112.3628	3	M	*alticola*
MVZ 51945	42.7805	-112.3628	3	F	*alticola*
MVZ 51946	42.7805	-112.3628	3	F	*alticola*
MVZ 68516	41.69648	-117.53361	4	F	*alticola*
MVZ 68518	41.68199	-117.53361	2	F	*alticola*
MVZ 7064	38.81554248	-104.9922254	4	F	*orolestes*
MVZ 72094	53.0667	-121.5167	3	F	*drummondii*
MVZ 78198	46.5101	-114.0922	3	F	*cinerea*
MVZ 93085	35.96583	-115.50028	4	F	*lucida*
MVZ 95145	37.36698	-109.4512	2	M	*arizonae*
PSM 13513	45.03337972	-123.922106	3	F	*fusca*
PSM 13805	45.037	-123.917	3	F	*fusca*
PSM 13903	45.03337972	-123.922106	3	M	*fusca*
PSM 13904	45.037	-123.917	4	M	*fusca*
PSM 13905	45.037	-123.917	3	F	*fusca*

Specimen ID	Latitude	Longitude	Age class	Sex	Subspecies
PSM 13906	45.037	-123.917	3	F	*fusca*
PSM 13907	45.0334	-123.9323	2	F	*fusca*
PSM 13908	45.0334	-123.9323	4	F	*fusca*
PSM 3039	53.9167	-124.15	2	M	*saxamans*
PSM 3697	53.9167	-124.15	3	M	*saxamans*
PSM 3698	53.9167	-124.15	2	M	*saxamans*
PSM 4611	53.9167	-124.15	2	M	*saxamans*
PSM 5751	44.4017	-122.0067	2	F	*occidentalis*
PSM 5765	47.94889	-123.25806	2	M	*occidentalis*
PSM 8646	44.4017	-122.0067	4	F	*occidentalis*
PSM 8647	44.4017	-122.0067	2	F	*occidentalis*
RAM 01.8.3	50.63	-110.18	4	F	*cinerea*
RAM 04.12.1	50.6438889	-110.1891667	4	M	*cinerea*
RAM 95.30.34	50.6	-110.3	2	M	*cinerea*
RBCM 2178	50.997	-118.1978	3	F	*drummondii*
RBCM 2179	50.997	-118.1978	3	M	*drummondii*
RBCM 2180	50.997	-118.1978	3	M	*drummondii*
RBCM 2181	50.997	-118.1978	4	M	*drummondii*
RBCM 2182	50.997	-118.1978	3	F	*drummondii*
RBCM 2183	50.997	-118.1978	3	F	*drummondii*
RBCM 2184	50.997	-118.1978	4	F	*drummondii*
RBCM 2185	50.997	-118.1978	3	F	*drummondii*
RBCM 2487	50.997	-118.1978	4	M	*drummondii*
RBCM 2488	50.997	-118.1978	3	F	*drummondii*
ROM 21361	53.9166667	-124.15	3	F	*saxamans*
ROM 30229	53.9166667	-124.15	2	F	*saxamans*
ROM 30231	53.9166667	-124.15	3	M	*saxamans*
UAM 24566	47.11388889	-120.9333333	2	F	*occidentalis*
UAM 35061	47.13333333	-120.9666667	2	F	*occidentalis*
UAM 35063	47.11388889	-120.9333333	2	F	*occidentalis*
UAM 35116	47.15	-121.95	4	F	*occidentalis*
UAM 35117	47.15	-121.95	4	F	*occidentalis*
UAM 35118	47.15	-121.95	2	F	*occidentalis*
UAM 35134	58.18805556	-129.8880556	2	F	*saxamans*
UAM 49980	47.11388889	-120.9333333	4	M	*occidentalis*
UAM 71646	60.71666667	-135.05	3	M	*saxamans*
UCM 10000	40.5721229	-102.6445196	2	M	*rupicola*
UCM 10003	38.86970858	-106.9878231	3	F	*orolestes*
UCM 10004	38.86970858	-106.9878231	2	M	*orolestes*
UCM 10006	38.86970858	-106.9878231	2	M	*orolestes*
UCM 10008	38.80980684	-104.9035309	3	M	*orolestes*
UCM 10009	38.81804511	-104.8944317	3	F	*orolestes*

Specimen ID	Latitude	Longitude	Age class	Sex	Subspecies
UCM 10011	38.8155397	-104.9927565	3	M	*orolestes*
UCM 10013	38.8543388	-104.7516569	2	F	*orolestes*
UCM 10014	38.8155397	-104.9927565	2	F	*orolestes*
UCM 10028	38.8155397	-104.9927565	3	M	*orolestes*
UCM 10029	38.8155397	-104.9927565	3	M	*orolestes*
UCM 10030	38.8155397	-104.9927565	2	M	*orolestes*
UCM 10046	38.86962698	-106.9488282	3	M	*orolestes*
UCM 10055	38.86962698	-106.9488282	2	M	*orolestes*
UCM 9996	40.5721229	-102.6445196	4	F	*rupicola*
UCM 9997	40.5721229	-102.6445196	3	F	*rupicola*
UMMZ 104407	43.8039	-103.7838	3	M	*orolestes*
UMMZ 104408	43.8039	-103.7838	3	F	*orolestes*
UMMZ 115640	38.63944	-109.40833	2	F	*arizonae*
UMMZ 115641	38.63944	-109.40833	2	M	*arizonae*
UMMZ 115642	38.63944	-109.40833	3	F	*arizonae*
UMMZ 115643	38.63944	-109.40833	2	M	*arizonae*
UMMZ 56190	38.8494289	-104.9588949	2	F	*orolestes*
UMMZ 56191	38.8494289	-104.9588949	2	M	*orolestes*
UMMZ 56192	38.8494289	-104.9588949	2	M	*orolestes*
UMMZ 56193	38.8494289	-104.9588949	2	M	*orolestes*
UMMZ 56194	38.8494289	-104.9588949	2	M	*orolestes*
UMMZ 87619	46.7403	-109.3459	2	M	*cinerea*
UMMZ 87620	46.7139	-109.3451	4	F	*cinerea*
UMMZ 93224	43.5811	-103.4144	4	F	*orolestes*
UMMZ 93225	43.5811	-103.4144	2	F	*orolestes*
UMMZ 93226	43.5811	-103.4144	2	F	*orolestes*
UMMZ 96084	43.5811	-103.4144	2	F	*orolestes*
UMMZ 97140	43.5811	-103.4144	4	F	*orolestes*
UMMZ 97141	43.5811	-103.4144	3	F	*orolestes*
UMMZ 97142	43.5811	-103.4144	2	F	*orolestes*
UMMZ 97143	43.5811	-103.4144	2	M	*orolestes*
UMMZ 99519	38.7369603	-106.8878335	2	M	*orolestes*
UMMZ 99520	38.7369603	-106.8878335	4	M	*orolestes*
UMMZ 99815	46.9464	-121.1100771	3	F	*occidentalis*
UMNH 1128	40.80525	-111.86195	3	F	*acraea*
UMNH 11781	38.63944	-109.40833	4	F	*arizonae*
UMNH 1275	40.71194	-111.79722	4	F	*acraea*
UMNH 15022	41.46668	-109.38349	2	M	*cinnamomea*
UMNH 15456	39.72605	-109.5609	4	F	*macrodon*
UMNH 16677	40.77615	-111.8382	3	M	*acraea*
UMNH 16678	40.77615	-111.8382	4	F	*acraea*
UMNH 17078	38.55754	-112.43592	2	M	*acraea*

Specimen ID	Latitude	Longitude	Age class	Sex	Subspecies
UMNH 17080	38.3167	-112.36116	3	F	*acraea*
UMNH 17081	38.3167	-112.36116	3	F	*acraea*
UMNH 17082	38.5625	-112.35694	4	F	*acraea*
UMNH 17083	38.5625	-112.35694	2	F	*acraea*
UMNH 17084	38.5625	-112.35694	4	M	*acraea*
UMNH 17085	38.42417	-112.51722	3	M	*acraea*
UMNH 2299	40.68895	-111.78595	4	M	*acraea*
UMNH 2300	40.68895	-111.78595	3	M	*acraea*
UMNH 2322	40.69556	-111.67222	2	M	*acraea*
UMNH 2403	40.70685	-111.68975	3	F	*acraea*
UMNH 2405	40.70685	-111.68975	4	F	*acraea*
UMNH 24281	40.79025	-111.56302	2	F	*acraea*
UMNH 24283	40.88944	-111.84181	3	F	*acraea*
UMNH 2962	40.88944	-111.84181	3	M	*acraea*
UMNH 5852	40.69205	-111.7538	2	M	*acraea*
UMNH 6658	39.79155	-109.62275	2	M	*macrodon*
UMNH 6659	39.79155	-109.62275	2	F	*macrodon*
UMNH 6660	39.74945	-109.60625	2	F	*macrodon*
UMNH 967	38.63944	-109.40833	4	M	*arizonae*
UWBM 12789	45.7806	-118.1744	4	F	*alticola*
UWBM 12790	45.7806	-118.1744	4	M	*alticola*
UWBM 51172	46.905123	-120.9513899	2	F	*occidentalis*
UWBM 52120	46.8797	-120.9056	2	F	*occidentalis*
UWBM 61438	45.7806	-118.1744	4	M	*alticola*
UWBM 61469	46.9619	-121.0828	2	M	*occidentalis*
UWBM 61470	46.9619	-121.0828	2	F	*occidentalis*
UWBM 61471	46.9619	-121.0828	3	F	*occidentalis*
UWBM 61472	46.9619	-121.0828	4	F	*occidentalis*
UWBM 61473	46.9619	-121.0828	2	F	*occidentalis*
UWBM 61474	46.9619	-121.0828	2	M	*occidentalis*
UWBM 61475	46.9619	-121.0828	2	F	*occidentalis*
UWBM 61476	46.9619	-121.0828	3	F	*occidentalis*
UWBM 61480	46.9619	-121.0828	2	F	*occidentalis*
UWBM 61615	45.7878	-118.1331	3	M	*alticola*
UWBM 61616	45.7806	-118.1744	3	F	*alticola*
UWBM 61619	45.7806	-118.0917	4	M	*alticola*
UWBM 61623	45.7806	-118.1744	3	F	*alticola*
UWBM 61624	45.8113	-118.1356	2	F	*alticola*
UWBM 61625	45.8215	-118.1502	2	F	*alticola*
UWBM 61628	45.8139	-118.0923	4	F	*alticola*
UWBM 61638	46.9619	-121.0828	2	F	*occidentalis*
UWBM 72106	45.570195	-117.528619	2	F	*alticola*

Specimen ID	Latitude	Longitude	Age class	Sex	Subspecies
UWBM 72108	45.570195	-117.528619	2	F	*alticola*
UWBM 72137	45.570195	-117.528619	3	F	*alticola*
UWBM 73257	46.9619	-121.0828	3	F	*occidentalis*
UWBM 73810	47.1166667	-121.0666667	4	F	*occidentalis*
UWBM 76697	45.12816667	-117.6225	4	F	*alticola*
UWBM 78001	44.65866667	-120.2571667	2	M	*alticola*
UWBM 78139	48.80966667	-117.129	2	F	*occidentalis*
UWBM 78604	47.95133333	-123.2556667	2	F	*occidentalis*
UWBM 78606	47.94966667	-123.2645	2	F	*occidentalis*
UWBM 78852	47.88216667	-123.1451667	2	F	*occidentalis*
UWBM 79495	44.86016667	-123.8371667	3	F	*fusca*