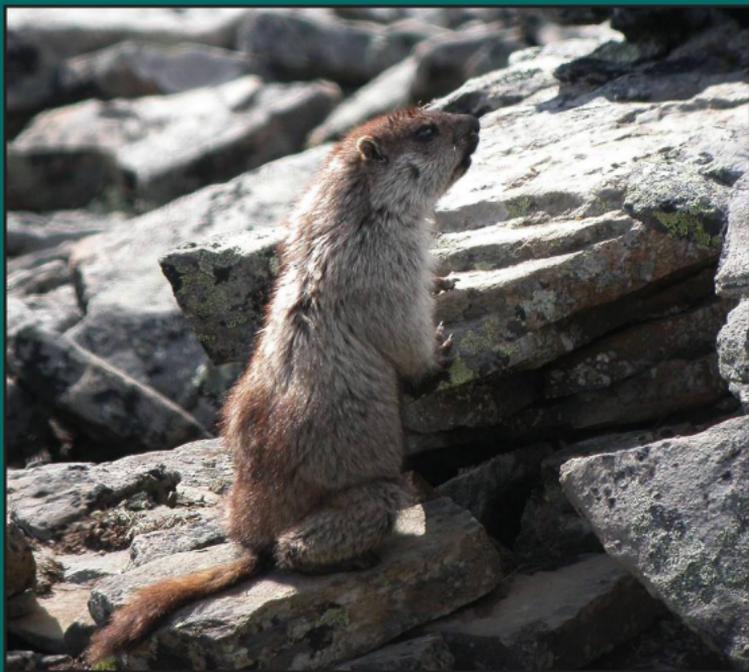


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REVISED DISTRIBUTION OF THE ALASKA MARMOT, *MARMOTA BROWERI*, AND CONFIRMATION OF PARAPATRY WITH HOARY MARMOTS

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The distribution and taxonomic status of the Alaska marmot (*Marmota broweri*) have been the subject of much debate and confusion since the taxon was 1st described as a subspecies of the hoary marmot (*M. caligata*). As a result of its early association with *M. caligata* and a lack of focused effort to determine its range, our current understanding of the distribution of *M. broweri* is vague at best and completely erroneous at worst. Through a review of all museum specimens and published accounts of this species, field surveys, and the identification of previously unidentified marmot specimens, we have determined that the current distribution of the Alaska marmot includes not only the Brooks Range, but also the Ray Mountains and Kokrines Hills of northern interior Alaska. We report the 1st confirmed records of this species outside of the Brooks Range and a commensurate range extension of 400 km southward. The Yukon River appears to form the current boundary between the parapatric distributions of *M. broweri* and *M. caligata* in Alaska, but additional fieldwork will be necessary to confirm that the 2 species are not allopatric.

Key words: Alaska marmot, climate change, hoary marmot, *Marmota broweri*, *Marmota caligata*

Alaska marmots (*Marmota broweri*) inhabit boulder fields, talus slopes, and rock outcrops in the alpine tundra of northern Alaska (Bee and Hall 1956). They are locally abundant and generally occur in loose communities (Bee and Hall 1956). *M. broweri* was 1st described by Hall and Gilmore (1934) based on 4 specimens collected by Charles D. Brower from Native residents of Point Lay and Cape Thompson on the northwestern coast of Alaska. Based on cranial morphology and pelage characters, Hall and Gilmore (1934) concluded that those 4 specimens constituted a new subspecies (*M. caligata broweri*) of the hoary marmot, previously known from southern Alaska, western Canada, and alpine areas of Washington, Idaho, and Montana. Since its description, the taxonomy and distribution of this marmot have been the subject of much debate and confusion. With relatively few voucher specimens available for morphological analyses, the taxonomic status of *M. broweri* was tentative for more than 30 years after its discovery. The distributions of *M. broweri* and *M. caligata* have been published erroneously due to this taxonomic

confusion and speculation surrounding *M. broweri*, and those errors have been perpetuated through the literature.

Montane and alpine-restricted small mammals, including marmots, were among the 1st taxa suggested as being particularly sensitive to climate change (McDonald and Brown 1992), and alpine marmots are increasingly recognized as potential harbingers thereof (e.g., Krajick 2004; Parmesan 2006). Although relatively few studies have addressed the effects of recent climate change on the distribution of any Alaskan mammal, the state includes the northernmost records of more than 40 species of terrestrial North American mammals (Patterson et al. 2007; Wilson and Ruff 1999), making it an ideal, albeit logistically challenging, venue for such studies. In contrast to the lack of knowledge surrounding their distributional stability, Alaskan mammals appear to be responding to climate change via changes in body size, as suggested by recent studies on Alaskan shrews (*Sorex cinereus*—Yom-Tov and Yom-Tov 2005), lynx (*Lynx canadensis*—Yom-Tov et al. 2007), and martens (*Martes americana*—Yom-Tov et al. 2008). As the only mammal species purportedly endemic to the Brooks Range (the northernmost mountain range in North America), and given its apparent reliance on rocky alpine tundra habitat, the Alaska marmot may be uniquely susceptible to the ongoing upslope and northward encroachment of the tree- and shrubline in Alaska

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(Sturm et al. 2001) and the pronounced effect recent climate change has had on Arctic ecosystems (reviewed by Parmesan 2006). However, the relative isolation and inaccessibility of the Alaska marmot's range has served to hinder research on its distribution and natural history, and it remains the most poorly studied marmot species in North America. In a 1st step toward ameliorating this, we have conducted extensive field surveys across much of northern and interior Alaska and have reviewed literature accounts, examined museum specimens, and conducted limited mitochondrial DNA (mtDNA) sequencing on putative extralimital specimens of *M. broweri* in order to obtain a more accurate estimate of its historic and current distribution.

Taxonomic history.—As part of their original description, Hall and Gilmore (1934:58) stated, "... it might be maintained with some justice that *broweri* should be accorded full specific rank. However, the differences distinguishing the 2 forms [*M. caligata caligata* and *M. broweri*] are of much the same nature as those which distinguish other subspecies of the *caligata* group." Therefore, the new marmot was described as a subspecies of the hoary marmot, *M. c. broweri*. No new specimens were collected until 1950 when Robert Rausch made an effort to collect marmots from the central Brooks Range. Based on the morphology of a series of Eurasian and North American marmot skulls and the conclusions of Ognev (1947) and Ellerman and Morrison-Scott (1951) that *M. caligata*, *M. camtschatica*, and *M. marmota* constituted a single species, Rausch (1953) concluded that all named subspecies of *M. caligata*, including *broweri*, the Olympic marmot (*M. olympus*), and the Vancouver Island marmot (*M. vancouverensis*), were subspecies of a single marmot species, *M. marmota*, that also included 3 forms from Europe and Asia. *Marmota marmota broweri* was the new name given to the marmots found in northern Alaska. Bee and Hall (1956) were reluctant to adopt this new name, citing a lack of sufficient evidence that the purported subspecies intergraded geographically or could interbreed if in contact. They maintained the name *M. caligata broweri* for marmots found in the Brooks Range. The application of karyology settled the taxonomic issues surrounding *M. broweri*. Rausch and Rausch (1965) found *M. broweri* to have $2n = 36$ chromosomes, whereas *M. caligata* had $2n = 42$. They therefore recognized *M. broweri* as a distinct species. This specific distinction has since been confirmed through molecular phylogenetic analyses (see below).

Two competing hypotheses have been suggested for the origin of *M. broweri*. Rausch and Rausch (1971:96) considered *M. broweri* "to be probably a relict North American species which became established in the Brooks Range during pre-Würm time, rather than a late Pleistocene invader of middle Asian derivation ..." based on the fact that *M. broweri* shared 2 species of cestodes with the North American species *M. caligata*, *M. flaviventris*, *M. olympus*, and *M. vancouverensis*. They (Rausch and Rausch 1971:96) claimed that the diverse and distinct cestode faunas of the North American and Eurasian marmots were "indicative of a long period of

separation of the two groups." Hoffmann and Nadler (1968) and Hoffmann et al. (1979) proposed an alternative origin for *M. broweri*—namely, that it dispersed into North America from Asia during the Pleistocene and is most closely related to the Russian species *M. camtschatica*.

The 1st molecular study to investigate the relationships among all 14 currently recognized marmot species, conducted by Steppan et al. (1999), supported the full species status of *M. broweri* and determined that Alaska marmots are more closely related to all Asian marmots and the woodchuck (*M. monax*; subgenus *Marmota*) than to other North American species (subgenus *Petromarmota*). However, the position of *M. broweri* within the subgenus *Marmota* remained unresolved and the question of its origin remains unanswered.

Distributional history.—Three species of marmots are known to occur in Alaska. These include *M. broweri* and *M. caligata*, both largely restricted to alpine areas (Hoffmann 1999; Svendsen 1999a), and the woodchuck, which occupies edge habitats at lower elevations and has not been recorded from alpine areas in Alaska (Svendsen 1999b). Prior to the research presented here, the distribution of the Alaska marmot had been described as restricted to the Brooks Range (e.g., Anderson 1934; Barash 1989; Rausch 1953). Earlier reports of marmots occurring north of the known range of *M. caligata* claimed that *M. caligata* was the species observed (Bailey and Hendee 1926; Hall 1929; Howell 1915), and Hall and Gilmore (1934:58) thought "it probable that [geographic] intergradation will be found to exist between *M. c. broweri* and *M. c. caligata*." Consequently, Anderson (1934) expanded the distribution of hoary marmots to include the Alaska Range, the Brooks Range and much of the area in between (Fig. 1). In 1951, after having collected and observed marmots from the central and eastern Brooks Range, Rausch (1951:178) concluded, "it is clear that *M. caligata broweri* is the form found throughout the Brooks Range, probably as far as the Alaska-Canada boundary." Rausch (1953) later published a map of this distribution that more accurately portrayed the geographic separation between *M. c. broweri* and *M. c. caligata* (Fig. 1). Unfortunately, the map published by Rausch (1953) and the specific distinction of *M. broweri* from Rausch and Rausch (1965) were not reflected in the species account of *M. caligata* in *The Mammals of North America* (Hall 1981), which instead relied on outdated information on the distribution of *M. caligata* (Fig. 1) and failed to recognize *M. broweri* as a distinct species. This has been perpetuated such that the respective distributions of *M. broweri* and *M. caligata* have continued to be confused in modern scientific publications and field guides (e.g., Fisher et al. 2000; Foresman 2001; Hoffmann 1999; Smith 2008; Fig. 1).

In their original description of *M. c. broweri*, Hall and Gilmore (1934) cite Point Lay as the type locality. Point Lay is a coastal community, far from suitable marmot habitat. Based on his personal communications with "old Utukamiut, or Kukmiut, Eskimo," Rausch (1953:117) assumed the likely origin of these specimens, and type locality, to be near the head of the Kukpowruk River, an area frequently traveled by

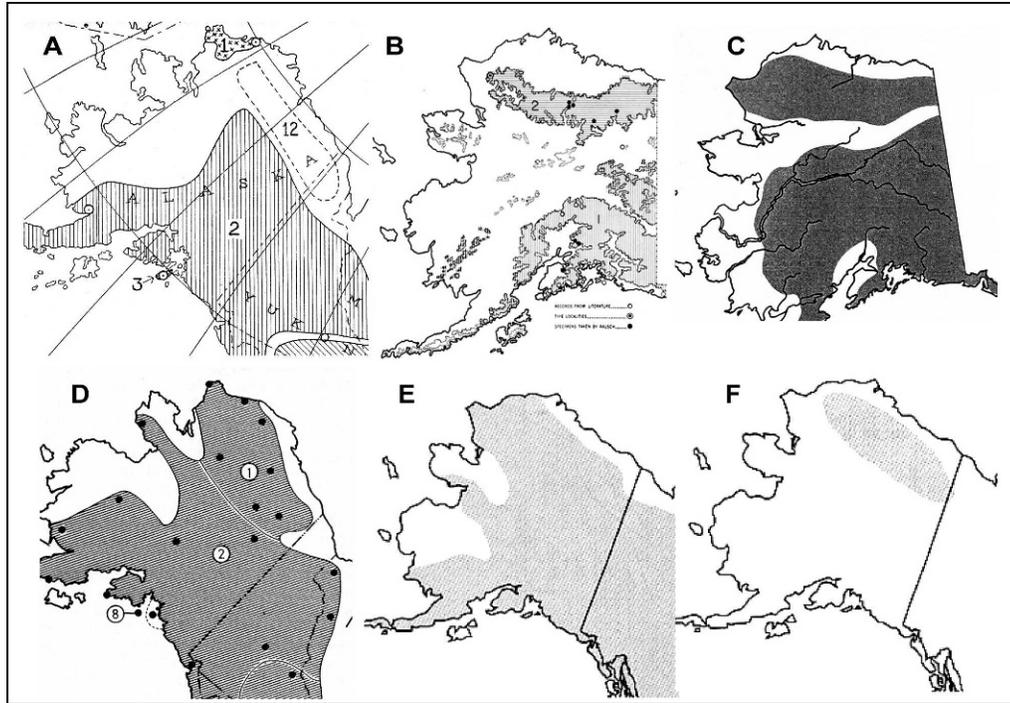


FIG. 1.—Published distribution maps for *Marmota broweri* and *M. caligata*. A) Distribution of *M. caligata* (taken directly from Howell 1915), including *M. c. broweri* from northwestern Alaska (Anderson 1934). B) Distribution of *M. marmota caligata* (south) and *M. m. broweri* (north—Rausch 1953). C) Distribution of *M. caligata* (ADFG 1978). D) Distribution of *M. caligata* (Hall 1981). E) Distribution of *M. caligata* (Svendsen 1999a). F) Distribution of *M. broweri* (Hoffmann 1999).

Native people. Prior to our study, 86 voucher specimens had been collected to verify the occurrence of Alaska marmots at 15 locations in the Brooks Range (see Appendix I for a list of all known specimens). Many of those specimens ($n = 34$) came from the central Brooks Range at Anaktuvuk Pass, 520 km east of the putative type locality (Rausch 1951, 1953), or were captive animals from Anaktuvuk Pass stock maintained by Rausch at Barrow, Alaska. The northern- and easternmost specimens were collected at Lake Peters, 160 km west of the Alaska–Yukon border (Bee and Hall 1956; this study). The westernmost specimens came from the Lisburne Peninsula at the edge of the Brooks Range bordering the Chukchi Sea (Childs 1969; Hall and Gilmore 1934; Pruitt 1966). Prior to the research presented here, the only locality on the south side of the Brooks Range from which a specimen had been collected is Arctic Village (Rausch 1951). It has often been speculated that *M. broweri* occurs in the British and Richardson Mountains of northern Yukon Territory (Anderson 1946; Rausch 1951; Rausch and Rausch 1971; Youngman 1975) and perhaps as far east as the Northwest Territories (Hoffmann et al. 1979). Many observational records can be found in the literature citing *M. broweri* in areas outside their known distribution or from new localities in the Brooks Range (Bailey and Hendee 1926; Bee and Hall 1956; Howell 1915; Juday 1984), but none has been revisited to verify the presence of marmots. Since the work of Robert Rausch, James W. Bee, and E. Raymond Hall in the 1950s and 1960s, there has been no focused effort to collect new specimens or to determine the distributional limits of this

species. The geographic distribution of Alaska marmots therefore remains poorly understood.

As a consequence of the original description of *M. broweri* as a subspecies of *M. caligata*, the respective distributions of hoary marmots (*M. caligata*) and Alaska marmots (*M. broweri*) are often confused in both the popular and scientific literature (Fig. 1). The distribution of *M. caligata* has frequently been portrayed as including all of the Brooks Range in northern Alaska, although it is not known from north of the Yukon River (see below). In addition, it was previously assumed that marmots of some subspecies of *M. caligata* would be found between the Alaska Range and the Brooks Range (Anderson 1934, 1946; Hall and Gilmore 1934), and thus the distribution of *M. caligata* was displayed as including that area (e.g., Alaska Department of Fish and Game 1978; Anderson 1934; Hoffmann 1999). The distribution of the hoary marmot is much broader than that of the Alaska marmot. Hoary marmots are found from their southern extent in Washington, northern Idaho, and Montana, northward through the White Mountains of interior Alaska. *M. broweri* and *M. caligata* are not known to occur in sympatry. Currently, hoary marmots in Alaska are known only from areas south of the Yukon River, whereas Alaska marmots occur north of the Yukon River. Hoary marmots can be found north of the Yukon River in the Oglvie Mountains in Yukon Territory.

In their original description of *M. c. broweri*, Hall and Gilmore (1934) listed several qualitative cranial and pelage characters that putatively distinguish it from other (sub)species

of *M. caligata*, including lighter coloration on the feet, lack of a white patch on the forehead, and the shape of the ventral margin of the mandible. We found these to be inconsistent and often unreliable given the variation in pelage characters we have observed in *M. caligata*, and particularly with incomplete specimens (e.g., crania without associated mandibles). Hoffmann et al. (1979) cite the shape of the labial margin of the nasal bones (concave in *M. broweri* and convex in *M. caligata*) as a reliable diagnostic character. Although we found this to be consistent in adult specimens, its utility in subadults has yet to be fully examined. Because of this lack of diagnostic characters distinguishing *M. broweri* from *M. caligata*, many published keys have relied heavily on locality (e.g., Frase and Hoffmann 1980).

Two specimens in the University of Alaska Museum confirm the presence of alpine marmots in the Kokrines Hills and Ray Mountains of central Alaska, discontinuous from and far to the south of the Brooks Range. These 2 alpine areas lie directly north of and adjacent to the Yukon River, between the Alaska Range and the Brooks Range. A skin and skull were collected from the Kokrines Hills (UAM 15044), which had tentatively been identified as *M. broweri* based on pelage characters and locality. A marmot cranium (with no associated mandible) was collected as part of a broad environmental survey of the Ray Mountains conducted in 1979 (Farquhar and Schubert 1980). These authors reported that marmots were common in alpine areas of the Ray Mountains and assumed them to be *M. broweri* because of their occurrence north of the Yukon River, but could not reliably identify which species they were observing. The identity of this specimen has heretofore remained unconfirmed due to the lack of reliable cranial features from which *M. caligata* and *M. broweri* can be distinguished (but see above). In the only published morphometric analysis of marmots to include representatives of both *M. broweri* and *M. caligata*, Cardini and O'Higgins (2004) found the 2 species to be distinctive and nonoverlapping in geometric morphospace, but their sample size of the former was small ($n = 2$) and the species was consequently excluded from several analyses. Those that did readily differentiate the 2 relied heavily, if not exclusively, on mandibular measurements, and the authors suggested that future studies would be necessary to confirm cranial distinction. Thus, crania lacking associated mandibles remain difficult to identify using qualitative or quantitative characters. If either of these specimens were confirmed to be *M. broweri*, they would represent the only records of this species outside the Brooks Range and a range extension of 400 km southward. Conversely, if either were determined to be *M. caligata*, it would represent the 1st documented occurrence of hoary marmots north of the Yukon River (in Alaska), a heretofore-unrecognized biogeographic barrier.

The objectives of this study are to clarify the taxonomy and distribution of the Alaska marmot, *M. broweri*, with a review of all literature and museum records and to establish the current distributional limits of the Alaska marmot through field surveys and the identification of previously unidentified

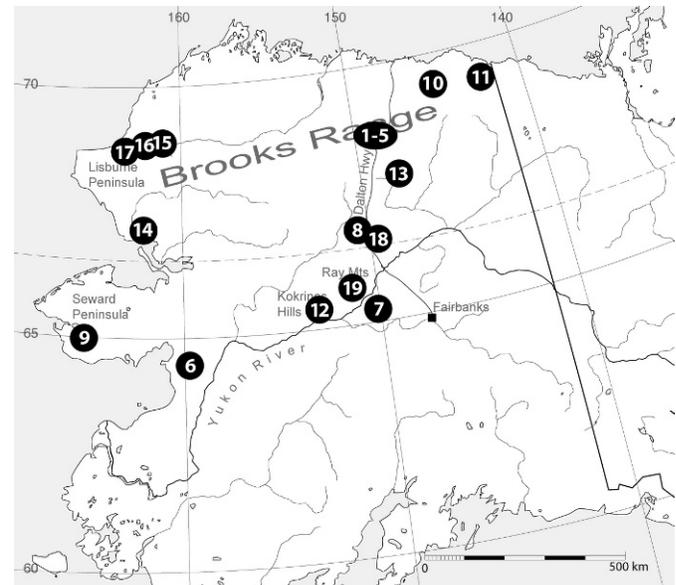


FIG. 2.—Areas where field surveys were conducted. The numbers correspond to survey sites in Table 1.

museum specimens via DNA sequencing. The distribution of hoary marmots is discussed in relation to that of the Alaska marmot, and a new extralimital record of *M. caligata* that renders the 2 species essentially parapatric also is reported.

MATERIALS AND METHODS

Field surveys.—Field surveys were conducted during the summer months of 2005–2007 (Fig. 2). Survey areas were chosen based on their proximity to known Alaska marmot populations or reported observations of marmots outside the established range of this species. Where marmots were observed, a limited number of specimens was collected using firearms. All fieldwork was carried out in accordance with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007) and with the approval of the Institutional Animal Care and Use Committee of the University of Alaska Fairbanks. Table 1 contains information regarding specific survey efforts. All voucher specimens were deposited at the University of Alaska Museum (see Table 2 for a list of specimens cited herein).

Molecular methods.—To verify the identity of the marmot specimen collected from the Kokrines Hills and the cranium collected from the Ray Mountains, DNA was extracted and sequenced from each. Extractions were performed in the Ancient DNA Laboratory at the University of Alaska Museum (UAM; a polymerase chain reaction-free building). A small subsample (approximately 25 mm²) was removed with flame-sterilized forceps and scissors from the ventral incision of the study skin (UAM 15044). The skin subsample was digested in a 1.6-ml tube with 600 μ l of Cell Lysis Solution (PureGene Genomic DNA Purification Kit; Gentra Systems, Minneapolis, Minnesota), 10 μ l of proteinase-K (20 mg/ml), and 30 μ l of dithiothreitol (100 mM) for 24 h with shaking at 55°C. Approximately 20 mg of maxilloturbinal bone was removed from the nasal cavity of the cranium specimen (UAM 15043)

TABLE 1.—Summary of field survey effort. Numbers at left correspond to Fig. 2. Additional details are available in field notes archived at the University of Alaska Museum (UAM). Most, but not all, surveys were conducted by UAM researchers, who kept detailed field notes about observations.

	Survey area	Dates surveyed	Latitude	Longitude	Results
1	Dalton Highway, Slope Mountain	18 June 2005	68°43'46"N	149°1'57"W	3 <i>Marmota broweri</i> collected, others observed
1	Dalton Highway, Slope Mountain	27 June 2006	68°44'13"N	149°1'38"W	1 <i>M. broweri</i> collected, others observed
2	Dalton Highway, Jade Mountain	28 June 2006	68°37'4"N	149°40'33"W	No marmots observed
3	Dalton Highway, Galbraith Lake	24 August 2006	68°31'4"N	149°27'9"W	3 <i>M. broweri</i> collected, others observed
4	Dalton Highway, Imnavait Mountain	25 August 2006	68°44'40"N	149°24'55"W	No marmots observed
5	Dalton Highway, Toolik Field Station	6 August 2007	68°36'51"N	149°29'53"W	1 <i>M. broweri</i> captured and released
6	Nulato Hills	5–12 July 2005	64°22'22"N	159°32'43"W	No marmots observed
7	Elephant Mountain	16–19 June 2006	65°15'30"N	150°3'28"W	2 <i>M. caligata</i> collected, others observed
8	Dalton Highway, Beaver Slide	29 June 2006	66°28'45"N	150°43'34"W	No marmots observed
9	Kigluaik Mountains	21–24 July 2006	65°2'27"N	165°25'58"W	No marmots observed
10	Lake Peters	21 July–1 August 2006	69°17'31"N	145°0'38"W	2 <i>M. broweri</i> collected, others observed
11	Kongukut River	31 July–10 August 2006	69°14'54"N	141°44'24"W	No marmots observed
12	Kokrines Hills	10–14 June 2007	64°57'0"N	154°51'0"W	No marmots observed
13	Little Squaw Lake	7 June, 31 July 2007	67°33'57"N	148°11'0"W	2 <i>M. broweri</i> collected
14	Mulik Hills	1 July 2007	67°9'53"N	162°19'13"W	No marmots observed
15	Utukok River	3 July 2007	68°57'38"N	161°19'18"W	4 <i>M. broweri</i> observed, none collected
16	Tupikchak Mountain	3–4 July 2007	68°51'42"N	161°49'22"W	6 <i>M. broweri</i> collected, others observed
17	Kukpowruk River	4 July 2007	68°56'55"N	162°53'27"W	2 <i>M. broweri</i> collected, others observed
18	Dalton Highway, Finger Mountain	4 August 2007	66°21'27"N	150°27'38"W	No marmots observed
19	Ray Mountains	7–12 September 2007	65°42'41"N	151°7'14"W	6 <i>M. broweri</i> collected, others observed

TABLE 2.—Summary of specimen data (newly reported in this study). Measurements (in mm) are from skin tags, database, or collectors notes (F = female, M = male, TL = total length, tail = length of tail, HF = hind foot length, EFN = length of ear from notch, and X = not recorded).

UAM catalog no.	Species	Locality	Sex	TL-tail-HF-EFN = weight (kg)
85514	<i>Marmota broweri</i>	Dalton Highway, Galbraith Lake	F	404-95-67-23 = X
86397	<i>M. broweri</i>	Dalton Highway, Galbraith Lake	F	628-130-83-28 = 3.30
86399	<i>M. broweri</i>	Dalton Highway, Galbraith Lake	F	615-136-88-28 = 4.25
85224	<i>M. broweri</i>	Dalton Highway, Slope Mountain	F	635-145-88-35 = 3.85
85225	<i>M. broweri</i>	Dalton Highway, Slope Mountain	F	640-160-87-22 = 3.75
85226	<i>M. broweri</i>	Dalton Highway, Slope Mountain	M	640-166-90-33 = 3.70
85760	<i>M. broweri</i>	Dalton Highway, Slope Mountain	M	517-140-74-27 = 1.60
87946	<i>M. broweri</i>	Dalton Highway, Toolik Field Station	F	X-X-X-X = 3.09
85858	<i>M. caligata</i>	Elephant Mountain	M	715-190-96-34 = 4.50
85859	<i>M. caligata</i>	Elephant Mountain	M	527-50-85-27 = X
15044	<i>M. broweri</i>	Kokrines Hills	M	591-152-83-35 = 2.83
87313	<i>M. broweri</i>	Kukpowruk River	F	640-160-80-25 = 4.6
100922	<i>M. broweri</i>	Kukpowruk River	?	X
85847	<i>M. broweri</i>	Lake Peters	F	552-147-80-18 = 2.12
85848	<i>M. broweri</i>	Lake Peters	F	X-121-71-26 = X
87311	<i>M. broweri</i>	Little Squaw Lake	M	488-129-76-15 = X
87314	<i>M. broweri</i>	Little Squaw Lake	M	625-160-85-27 = X
15043	<i>M. broweri</i>	Ray Mountains	?	X
100000	<i>M. broweri</i>	Ray Mountains	F	567-120-78-27 = 3.15
87303	<i>M. broweri</i>	Ray Mountains	M	519-123-82-24 = 2.6
87305	<i>M. broweri</i>	Ray Mountains	F	504-127-77-23 = 2.0
87307	<i>M. broweri</i>	Ray Mountains	F	526-129-76-23 = 2.2
87308	<i>M. broweri</i>	Ray Mountains	M	537-125-78-26 = 2.4
87309	<i>M. broweri</i>	Ray Mountains	M	635-148-83-28 = 3.65
87300	<i>M. broweri</i>	Tupikchak Mountain	F	607-143-83-27 = 4.8
87301	<i>M. broweri</i>	Tupikchak Mountain	M	654-158-87-28 = 4.7
87304	<i>M. broweri</i>	Tupikchak Mountain	M	700-172-90-32 = 5.9
87306	<i>M. broweri</i>	Tupikchak Mountain	F	658-184-87-27 = 5.1
87310	<i>M. broweri</i>	Tupikchak Mountain	M	622-193-93-32 = 3.4
87312	<i>M. broweri</i>	Tupikchak Mountain	F	583-155-87-30 = 3.1

as described in Wisely et al. (2004). The bone sample was digested in 600 μ l of Cell Lysis Solution, 20 μ l of proteinase-K, and 30 μ l of dithiothreitol for 72 h with shaking at 55°C, with the addition of 20 μ l of proteinase-K every 24 h (60 μ l total). After digestion, both extractions proceeded according to the PureGene Genomic DNA Purification Kit protocol for DNA purification from 5–10 mg of fresh or frozen solid tissue with the following modifications: RNase treatment was omitted and all reagent and solution volumes were doubled (protein precipitation solution, isopropanol, ethanol, and DNA hydration solution). Each extraction included a negative control to test for contamination that might result from the extraction procedure. For comparative purposes, DNA was extracted from frozen tissue of 4 specimens of *M. broweri* (UAM 35015, 78513, 85226, and 85848) and 5 specimens of *M. caligata* (UAM 35130, 38304, 49848, 57693, and 78240) in a separate facility using the PureGene Genomic DNA Purification Kit protocol for DNA purification from 5–10 mg of fresh or frozen solid tissue. A 5th sequence from *M. broweri* was obtained from GenBank (accession number AF143918).

Because of the degraded nature of the DNA extracted from the skin and bone specimens, we amplified and sequenced the first 556 base pairs (bp) of the mitochondrial cytochrome-*b* gene in 3 overlapping sections (39 bp and 61 bp of overlap between adjacent fragments) using the following primer pairs: CB-F1 (5' CTCACCGTTGTTATTCAACTA 3') and CB-R4AG (5' TGTGGGCAACTGATGAGAAA 3'), CB-F4AG (5' ATCCAAATCTTTACCGGACT 3') and CB-R5AG (5' TGACCTCAGGGGAGGACATA 3'), and CB-F5AG (5' CTACGGCTCATATACTACTC 3') and CB-R6AG (5' TAGGGCTGCGATGATAAAGG 3'). We amplified and sequenced the entire length of cytochrome-*b* (1,140 bp) for the 4 specimens of *M. broweri* and 5 specimens of *M. caligata* used for comparison in 2 overlapping segments (104 bp of overlap) using the primer pairs CB-F1 and CB-AGR1 (5' GGGATTTTGTCTGAGTCAGA 3'), and CB-AGF1 (5' CAAAGCCACTCTAACACGAT 3') and CB-R3AG (5' GGTTTACAAGGCCAGGGTAATG 3'). Volumes and concentrations of reagents used in the amplifications were as follows: 1 μ l of DNA template, 1 μ l of each of primers (10 μ M), 2.5 μ l of 10 \times Promega reaction buffer (Promega, Madison, Wisconsin), 1 μ l of MgCl₂ (25 mM), 0.5 μ l of deoxynucleoside triphosphates (10 mM), 0.25 μ l Promega GoTaq polymerase (5 U/ μ l), and 17.75 μ l of H₂O for a total reaction volume of 25 μ l. The reactions were run on an MJ Research PTC-200 Peltier thermal cycler (Bio-Rad Laboratories, Inc., Hercules, California) with the following cycling parameters: 94°C for 3 min, then 40 cycles of 94°C for 1 min, 55°C for 1 min, and 72°C for 1 min. The extraction negatives were run along with DNA extracts, and each polymerase chain reaction also included a negative control to determine if any contaminating DNA was introduced from the polymerase chain reaction reagents.

Before cycle sequencing, polymerase chain reaction products were purified with Exo-SAP-IT (USB, Cleveland, Ohio)

according to the manufacturer's protocol. Purified polymerase chain reaction products (1–2 μ l) were cycle sequenced in both directions (forward and reverse) using BigDye Terminator (2 μ l; Perkin-Elmer, Boston, Massachusetts), 5 \times reaction buffer (1 μ l), water (6 μ l), and the same polymerase chain reaction primers used in amplifications (1 μ l of each). Sequencing reactions were purified using ethanol–sodium acetate precipitation and electrophoresed on an ABI 3100 sequencer (Applied Biosystems, Foster City, California). DNA sequences generated in this study have been deposited in GenBank (accession numbers FJ438931–438941).

Data analysis.—The DNA sequences were aligned with reference to the sequence from *M. broweri* obtained from GenBank and checked by eye using Sequencher (version 4.7; Gene Codes, Ann Arbor, Michigan). Maximum-likelihood and maximum-parsimony trees were produced, and average pairwise differences were calculated using PAUP* (version 4.0—Swofford 2003). A sequence from *Spermophilus parryii* obtained from GenBank (AY427977) was used as an outgroup for rooting trees. Heuristic maximum-parsimony and maximum-likelihood tree searches were conducted using stepwise addition of 100 random addition sequences with the tree bisection-reconnection branch-swapping algorithm. For the maximum-likelihood analysis a model of nucleotide substitution (GTR+I) and associated parameters were estimated using Modeltest 3.7 (Posada and Buckley 2004; Posada and Crandall 1998) under the Akaike information criterion.

RESULTS

Field surveys.—Six previously unknown marmot populations were documented as a result of field surveys (see Fig. 2 for a map of localities surveyed; Table 1). The northernmost Alaska marmots along the Dalton Highway were found at Slope Mountain. We collected 3 voucher specimens on 18 June 2005 at 990 m in elevation and 1 specimen on 27 June 2006 at 1,080 m. Another colony of Alaska marmots was found 40 km south (by road), near Galbraith Lake airstrip, on 24 August 2006, from which 3 specimens were collected at 1,020 m elevation. A single marmot was livetrapped from the east side of the Dalton Highway, across from Toolik Field Station (administered by the University of Alaska Fairbanks), on 6 August 2007. We obtained a tissue (skin) voucher from that individual. Other areas surveyed along the Dalton Highway were the mountains directly west of Galbraith Lake airstrip, Jade Mountain west of Toolik Field Station, Innvait Mountain, Finger Mountain, and the alpine areas north and west of the Kanuti River bridge near Beaver Slide. No marmots were observed in these areas.

The Kigluai Mountains north of Nome, Alaska, on the Seward Peninsula, were surveyed on foot from the road system and by helicopter from 21 to 24 July 2006. We searched the area where Juday (1984) claimed to have observed marmots. The habitat in that area, on the north side of the mountains and southeast of Windy Cove, seemed suitable for marmots, although we did not find any marmots or signs of marmot activity.

We surveyed approximately 58 km of the Kongakut River drainage from Drain Creek to Caribou Pass between 31 July and 10 August 2006. The habitat in this area appeared marginal for supporting marmots (boulder fields and talus slopes generally did not feature friable soils suitable for burrows). Although some areas appeared suitable, no marmots were found.

The mountainous areas surrounding Lake Peters were surveyed from 21 July to 1 August 2006. Two marmots were observed in the Chamberlin Creek drainage at the south end of Lake Peters at 1,035 m elevation. Two marmots were observed in the Kelly Creek drainage at 1,190 m elevation. One voucher specimen was collected from each drainage. No other marmots, or marmot signs, were found, although we surveyed the area from the Whistler Creek drainage to the peak of Mount Chamberlin. The habitat in many areas without marmots appeared identical to that in areas supporting marmots.

The Kokrines Hills were surveyed from 10 to 14 June 2007 at the same locality from where the marmot skin (UAM 15044) tentatively identified as *M. broweri* was collected in 1983. We found the habitat to be well suited for marmots with rock outcrops and large boulder fields, but no marmots or evidence of recent marmot activity were found. The habitat we surveyed was fairly small and relatively isolated from other, more expansive alpine areas to the northeast. Marmots may still be present in the Kokrines Hills although farther north and east of where UAM 15044 was collected.

On 3–4 July 2007, we surveyed 3 localities in the northwestern Brooks Range, including the type locality, “near the head of the Kukpowruk River” (Rausch 1953:117). No other specimens have been collected from this area since the type specimen was delivered to Charles D. Brower by a Native hunter in Point Lay, Alaska, in 1931 (Hall and Gilmore 1934). We collected 1 specimen from the bluffs above the Kukpowruk River north of Tupikchak Creek. A 2nd specimen consisting of a single dentary was found near the entrance of a presumptive arctic ground squirrel (*S. parryii*) burrow at the same locality. Six specimens were collected 44 km to the east, at Tupikchak Mountain. A single specimen of *M. broweri* (UAM 13425) was collected in June 1981 from south of Archimedes Ridge near the Utukok River. We surveyed the same area, although not the exact locality, and observed 4 marmots (but did not collect any) at 2 locations near the Utukok River.

Gardner (1974) reported marmots from the Mulik Hills, north of Kotzebue near the Noatak River. We surveyed that area on 2 July 2007 but found no evidence of marmot activity. It is possible marmots will be found in the Igichuk Hills, a larger alpine range just north of the Mulik Hills. In 1963, Dean and Chesemore (1974) stated that an active marmot den was present in the highlands south of the Noatak River near Nakolik Mountain, northeast of the Igichuk Hills. Farther to the west and south, pilot Eric D. Sieh of Kotzebue claimed to have seen marmots at the headwaters of the Eli River.

In 1979, Farquhar and Schubert (1980) conducted a biological survey of the Ray Mountains. They collected a single, unidentifiable marmot cranium from Spooky Valley (UAM 15043). We revisited the Ray Mountains from 7 to 11

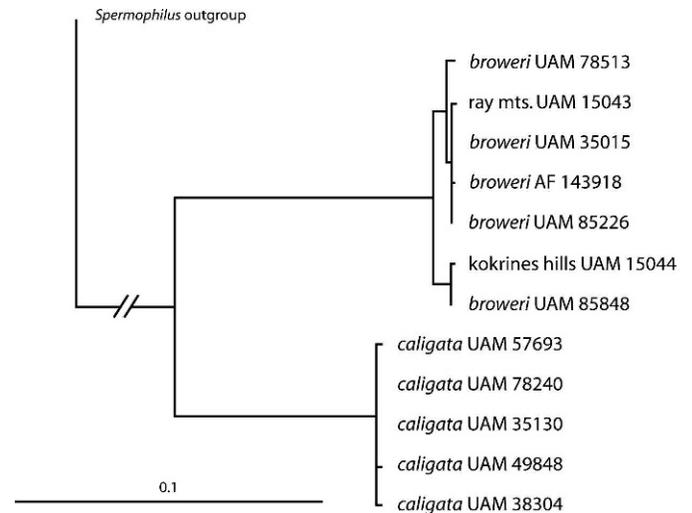


FIG. 3.—The maximum-likelihood tree for 5 *Marmota broweri*, 5 *M. caligata*, and the museum specimens from central Alaska. Both specimens (Ray Mountains and Kokrines Hills) are confirmed to be *M. broweri*.

September 2007. A population of *M. broweri* was found on the south-facing slope of the ridge south of the source of Gishna Creek. We observed 10 individuals, including adults, yearlings, and juveniles, documented 12 separate burrows, and collected 6 specimens. All the marmots were observed between 975 m and 1,340 m in elevation.

A previously unknown population of hoary marmots (*M. caligata*) was discovered at Elephant Mountain, just south of the Yukon River. We surveyed this area from 16 to 19 June 2006. We observed 8 individual hoary marmots during a 12-mile transect of the mountain's ridge at elevations between 915 m and 1,130 m and collected 2 voucher specimens. This extends the known range of *M. caligata* 240 km west of the nearest known hoary marmot population in the White Mountains, north of Fairbanks, Alaska.

We surveyed the Nulato Hills from 5 to 12 July 2005. Habitat in this area appeared to be unsuitable for marmots, and none was found.

Specimen identification.—Maximum-parsimony and maximum-likelihood analyses produced the same tree topology, grouping both the Ray Mountains and Kokrines Hills museum specimens with *M. broweri* and not *M. caligata* (Fig. 3). The average pairwise distances of the mtDNA sequences from the Ray Mountains and Kokrines Hills specimens to the *M. broweri* sequences were 0.4% and 1.1%, respectively, whereas the average distances from the *M. caligata* sequences were 10.1% and 11.3%, respectively. These results indicate that both museum specimens are *M. broweri*, not *M. caligata*.

DISCUSSION

A revised distribution of the Alaska marmot based on the new records and museum specimen identifications is reported (Fig. 4). Based on museum specimens and all published observations of *M. broweri*, Alaska marmots are patchily

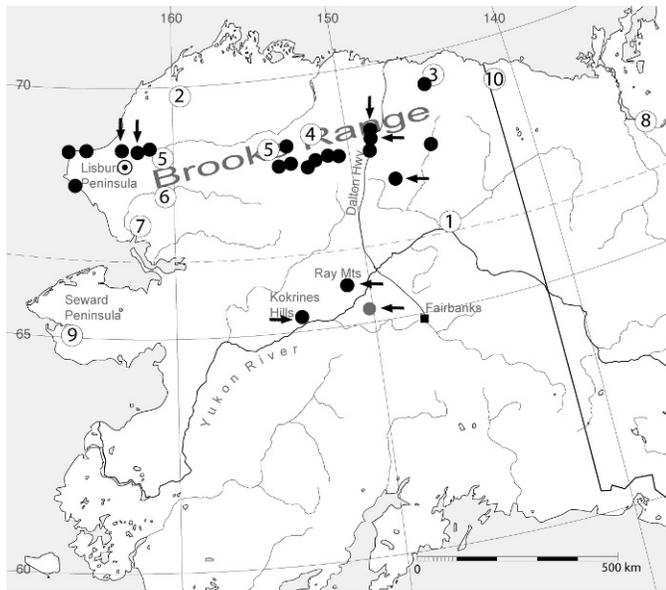


FIG. 4.—The current distribution of *Marmota broweri*. The black circles represent localities with museum voucher specimens (see Appendix I). The double black circle is the type locality as determined by Rausch (1953). The numbered circles represent authoritative but unconfirmed observations of *M. broweri* and the numbers correspond to the following references: 1, Howell (1915); 2, Bailey and Hendee (1926); 3, Anderson (1934); 4, Rausch (1951); 5, Bee and Hall (1956); 6, Dean and Chesemore (1974); 7, Gardner (1974); 8, Hoffmann et al. (1979; see text); 9, Juday (1984); 10, B. Smith, Fish and Wildlife Branch, Yukon Environment (pers. comm.). Arrows indicate previously undocumented localities. The gray circle represents a newly documented population of *M. caligata*.

distributed across the Brooks Range, from Cape Lisburne in the west to Lake Peters in the east, and in the Ray Mountains and Kokrines Hills of interior Alaska. This species likely occurs east of Lake Peters, perhaps into Yukon Territory (see below), but we were unable to find them within the Kongakut River drainage in northeastern Alaska near the United States–Canada border. Further field surveys are necessary to establish the eastern distributional limits of *M. broweri*.

Alaska marmots were previously assumed to be restricted to the Brooks Range (Anderson 1934; Barash 1989; Rausch 1953). The positive identification of the museum specimens from the Kokrines Hills and the Ray Mountains as *M. broweri*, and the discovery of a population of Alaska marmots currently inhabiting the Ray Mountains, extends the documented range of this species 400 km to the south. These are the 1st specimens of this species to be collected outside the Brooks Range. Additionally, with the discovery of hoary marmots (*M. caligata*) inhabiting Elephant Mountain, directly south of the Ray Mountains across the Yukon River (see Fig. 4), the Kokrines Hills and Ray Mountains apparently represent the southern limit of the Alaska marmot's current distribution. The ecological similarity of the 2 species makes it unlikely that they will be found in sympatry. It appears that the Yukon River forms the boundary between the parapatric distributions of *M. broweri* and *M. caligata* in Alaska, although its present and historical influence on their distributions is unknown. The

swimming abilities of *M. caligata* and *M. broweri* are unknown, but woodchucks (*M. monax*) are capable swimmers (Kwiecinski 1998) and hoary marmots have been observed swimming in alpine lakes in Lake Clark National Park in southcentral Alaska (M. Robinson, National Park Service, pers. comm.). It therefore seems unlikely that the Yukon River forms a significant barrier to dispersal for either species.

From 29 July through 15 August 1952, Bee and Hall (1956) surveyed the Lake Peters area for marmots. They reported observing marmots in 11 locations surrounding the lake and that “the marmot was common and lived in loose communities” (Bee and Hall 1956:37). Lake Peters lies at an elevation of 885 m with the peak of Mount Chamberlin to the southeast at 2,745 m. Despite this elevation range, Bee and Hall found marmots only inhabiting the mountainsides between 990 m and 1,220 m with an average elevation of 1,130 m. During a 10-day survey effort in July 2006, we searched the area from Whistler Creek to the peak of Mount Chamberlin and observed 4 marmots at just 2 locations. These marmots occurred within the elevation range reported by Bee and Hall, although they were not common and no community structure was apparent at either of the 2 locations. Fifty-four years after Bee and Hall's original survey, Alaska marmots appear to have declined in both distribution and abundance in the Lake Peters area.

Observations and reports of marmots east of Lake Peters and in northwestern Canada (Anderson 1934; Hoffmann et al. 1979; B. Smith, Fish and Wildlife Branch, Yukon Environment, pers. comm.) as well as the presence of seemingly suitable habitat suggests that marmots occur farther east of the Kongakut River drainage, where we did not find marmots. Hoffmann et al. (1979) claimed to have examined a specimen of *M. broweri* from the Northwest Territories, Canada, archived at The Natural History Museum, London (BMNH). If that specimen's locality and species identity were verified, it would represent the easternmost and only occurrence of *M. broweri* outside Alaska. However, Hoffmann et al. (1979) did not publish the catalog number of that, or any, specimen they examined and there are currently no records of specimens of *M. broweri* from Canada at BMNH (P. Jenkins, The Natural History Museum, London, pers. comm.). An effort by the Yukon Fish and Wildlife Branch to find marmots in the Firth River region of northern Yukon Territory has yielded no evidence of marmot activity (B. Smith, Fish and Wildlife Branch, Yukon Environment, pers. comm.). Further field surveys are needed to establish the eastern boundary of the Alaska marmot's distribution. Although we failed to find marmots in the area cited by Juday (1984), we did not have sufficient time to exhaustively search the Kigluaiik Mountains or other alpine areas of the Seward Peninsula. Marmot incisors or molars or both have been found in cave deposits at Cape Deceit (Guthrie and Matthews 1971) and in Trail Creek Caves, on the Seward Peninsula, dating to 13,000 years ago (Vinson 1993). This fossil evidence and the presence of suitable habitat and reliable observations leave us unconvinced that marmots are completely absent from that area.

Knowledge of where a species naturally occurs is essential to understanding that species' ecology, evolution, and

historical biogeography. Museum voucher specimens establish species' distributions and provide a historical baseline for evaluating changes in geographic distributions and organismal attributes over time. Because specimens represent populations, the value of large series of specimens increases through time, particularly as the habitat quality of many localities is degraded. Not surprisingly, data derived from museum specimens are proving to be increasingly valuable to studies of organismal responses to climate change, even over recent decadal time scales (e.g., Millien et al. 2006; Parra and Monahan 2008). Without the historic collection and preservation of specimens, field surveys such as this would have extremely limited value; without continued field- and specimen-based studies, monitoring ongoing and future responses to environmental change will be all but impossible. Funding used for biodiversity assessments is therefore most efficiently spent if funding agencies recognize the continued critical need for vouchers and provide support in both field and museum budgets for their preservation and maintenance.

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APPENDIX I

A list of all known museum specimens of *Marmota broweri* and their collecting localities. BMNH = The Natural History Museum; KU = University of Kansas Natural History Museum; MCZ = Museum of Comparative Zoology, Harvard; MSB = Museum of the Southwestern Biology, University of New Mexico; MVZ = Museum of Vertebrate Zoology, University of California Berkeley; PSM = Slater Museum of Natural History, University of Puget Sound; UAM = University of Alaska Museum, University of Alaska Fairbanks; USNM = National Museum of Natural History, Smithsonian Institution; UWBM = University of Washington Burke Museum, YPM = Yale Peabody Museum.

Specific locality, catalog numbers.—Alaska, USNM 290273, 290274; Anaktuvuk Pass, BMNH 1953.585, MCZ 47133, PSM 3201, 4161, 4162, 4163, UWBM 39676, MSB 136435, 25899, USNM 583154, 583155; Arctic Village, PSM 27500, MSB 136465; Brooks Range, UWBM 39793, YPM 523, 524; Cape Lisburne, UAM 12612, 12613, 12614, 12615; Cape Sabine, MVZ 123895; Cape Thompson, MVZ 39719, UAM 7014; Captive from Anaktuvuk Pass stock, MSB 137443, 137455, 137456, 137457, 137460, 137461, 137463, 137464, 137470, 137472, 137473, 141142, 141144, 141145, 141146, 141147, 141148, 141150, 141151, 141152, 141155, 141156, 141160; Chandler Lake, KU 43227, MSB 85689, 137454, 137645, 137646, 137647, 137649, 137651, 141158, USNM 305036; Fortress Mountain, UAM 78513, 79182; Galbraith, UAM 35015, 85514, 86397, 86399; Kokrines Hills, UAM 15044; Kukpowruk River, UAM 100922, 87313; Lake Peters, KU 50417, 50418, 50419, 50420, 50421, UWBM 32251, MSB 85688,

85707, 141153, UAM 85847, 85848; Little Squaw Lake, UAM 87311, 87314; Mount Wachsmuth, UWBM 39810; Nanushuk River, UAM 79245; Point Lay, MVZ 51654, 51655, 51675 (type specimen); Ray Mountains, UAM 15043, 87303, 87305, 87307, 87308, 87309, 100000; Slope Mountain, UAM 85224, 85225,

85226, 85227, 85760; Tolugak Lake, USNM 290275, 290276; Toolik Field Station, UAM 87946; Tupikchak Mountain, UAM 87300, 87301, 87304, 87306, 87310, 87312; Ukuminilagat Creek, MSB 141159; Utukok River, UAM 13425; no specific locality recorded, MSB 137385, 137732, UAM 13725.