GEOGRAPHIC VARIATION AND EVOLUTION IN THE CALIFORNIA GULL (*LARUS CALIFORNICUS*)

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ABSTRACT.—The California Gull (*Larus californicus*), currently regarded as a monotypic species, is separable into a small, dark-mantled race (*L. c. californicus*) that breeds primarily in the Great Basin of the United States, and a larger, paler race (*L. c. albertaensis*) from the Great Plains of the north-central U.S. and south-central Canada. The breeding ranges of these two races, previously disjunct, have expanded recently, and a zone of secondary contact seems to be forming east of the Rocky Mountains in the northern United States. *Received 13 November 1986, accepted 23 January 1987.*

THE California Gull (*Larus californicus*) has a discontinuous breeding range in the western United States and Canada, extending from Great Slave Lake, N.W.T. (62°N) south to San Francisco Bay and Mono Lake, California (38°N) and east to the Dakotas (A.O.U. 1983, pers. obs.). Except for a brief study by Zink and Winkler (1983), who found only minor size and genetic differences between gulls from Mono Lake and Great Salt Lake, Utah, there has been no effort to investigate geographic variation in this species, which is pronounced.

METHODS

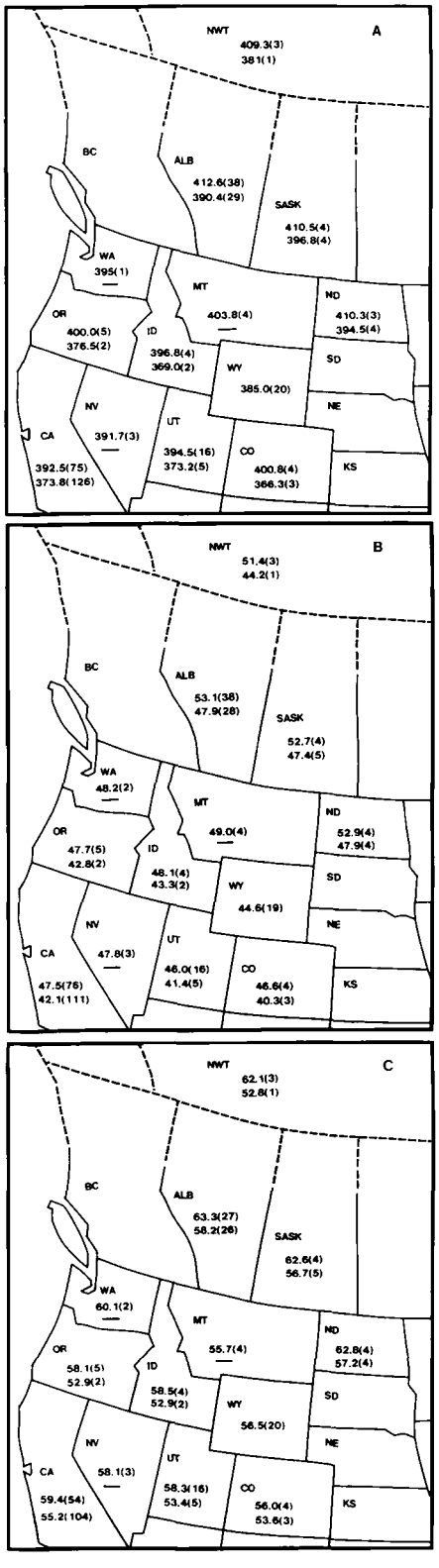
Museum specimens used in this analysis were taken in the breeding range between 1 April and 15 August. Because some gulls are still migrating to inland breeding stations in April, and because adults begin to move coastward by the last days of July, samples from western parts of the range may have included migrants. I took standard measurements on length of the exposed culmen, flattened wing and tarsus, depth of the bill at the gonys, and body mass. The large sample from Mono Lake is based mainly on birds found freshly dead on nesting islets; a representative series was preserved as museum specimens. Some California Gulls begin to show extensive wear of the primaries by March. Specimens whose wing length could not be determined accurately were excluded from the analysis. Additional size and mass data were extracted from the literature. I also noted the patterning of the primaries and the color of the mantle. Although variation in the latter was evident, I could not measure it consistently because of the generally soiled condition of most specimens.

For analysis of size variation I separated mensural data by sex and used principal components analysis (BMDP4M; Dixon 1983) to test for patterns of variation. The analysis showed that the gulls fell into two distinct assemblages. I then used stepwise discriminant function analysis (BMDP7M; Dixon 1983) to determine which variables contributed to the separation of groups, using locality as the grouping variable.

RESULTS

Although California Gulls are well represented in museum collections, material from the breeding grounds is scanty. Even so, considerable geographic variation in size is obvious (Appendix). A preliminary comparison of the only two large samples, from Alberta and Mono Lake, showed that Alberta birds were significantly larger in culmen, wing, tarsus, and mass (t-test, $P < 0.05$); they also had a paler mantle.

Simple inspection of the data showed that the size differences did not conform to a simple latitudinal gradient, as might be expected from Bergmann's rule; some of the largest birds were from North Dakota (48°N) and some of the smallest from Utah (41°N) (Fig. 1). Principal components analysis showed that 58% of the variation in females and 61% in males was explained by a single factor and that within each sex two assemblages could be recognized (Fig. 2). These assemblages corresponded broadly to physiographic provinces in western North America. Gulls from the northern Great Plains of the north-central United States, the prairie provinces of Canada, and the Northwest Territories were large and clustered with the Alberta sample. Those from the Great Basin of the western United States (Washington, Oregon, Nevada, Utah, and California), as well as those from nearby regions in Colorado, Wyoming, and Idaho, were small like those from Mono



Lake. Although samples from many regions were very small, the available data did not reveal any indication of clinal variation.

External differences between the Great Basin and Great Plains forms are greater than those characterizing most currently recognized races of North American birds. I describe them as subspecies because morphological and historical (see below) data indicate they have had separate evolutionary histories. The type specimen of the species (Amer. Mus. Nat. Hist. No. 46070) was taken near Stockton, California, and is an adult (cf. Greenway 1978) female of the Great Basin population, which becomes *L. c. californicus*. Its measurements are: exposed culmen, 43.7 mm; depth of bill at gonys, 15.8 mm; tarsus, 55.4 mm; wing, 380 mm. For the larger form I propose the name:

Larus californicus albertaensis
ssp. nov.

Holotype.—University of Michigan Museum of Zoology No. 224,653, adult male, from Frog Lake, Alberta, 53°55'N, 110°15'W; collected by Philip H. R. Stepney, 9 July 1985.

Diagnosis.—Distinguished from *L. c. californicus* by greater size, particularly in bill dimensions and body mass (Table 1, Fig. 3). Mantle paler gray, less bluish than in *L. c. californicus*, approaching or matching the paleness of *L. argentatus* (Fig. 4). Measurements of holotype: exposed culmen, 52.5 mm; depth of bill at gonys, 18.7 mm; tarsus, 62.6 mm; wing, 424 mm; mass, 809 g. Using stepwise discriminant function analysis for the entire sample, I could determine the racial identification of a bird of known sex for 87.9% of the females of *L. c. albertaensis* and 95.3% of the females of *L. c. californicus*, and for 87.0% of the males of *L. c. albertaensis* and 92.4% of the males of *L. c. californicus* (Fig. 5) by the following formulas, where a score >0 is *albertaensis* and a score <0 is *californicus*: for females, 0.36 culmen (mm) + 0.31 bill depth (mm) + 0.06 wing (mm) − 45.60; for males, 0.25 culmen

←

Fig. 1. Mean dimensions of (A) wing length, (B) culmen length, and (C) tarsus length of California Gulls. For each state or province, data for males are listed above those for females. The sample for Wyoming was based on unsexed individuals. Sample sizes are in parentheses.

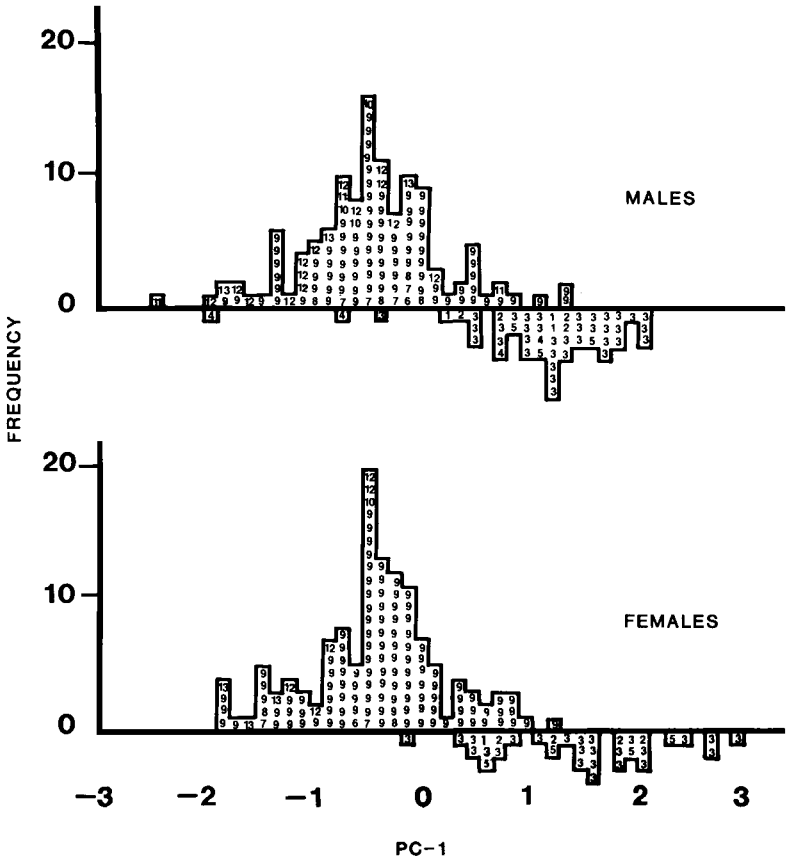


Fig. 2. Plot of first principal component of male and female California Gulls. Numbers refer to localities: 1 = Northwest Territories, 2 = Saskatchewan, 3 = Alberta, 4 = Montana, 5 = North Dakota, 6 = Washington, 7 = Oregon, 8 = Idaho, 9 = Mono Lake, California, 10 = other California, 11 = Nevada, 12 = Utah, and 13 = Colorado.

(mm) + 0.15 tarsus (mm) + 0.05 wing (mm) − 40.21.

Range.—Nests on lakes, often of slight to moderate alkalinity or salinity, in North (and South?) Dakota, Manitoba, Saskatchewan, Alberta, and the Northwest Territories (Fig. 6). Southern and western limits unknown, as the range of the species is changing rapidly. Presumably winters through the range of the species, mainly along the Pacific coast from British Columbia to Baja California.

Variation.—*Larus c. albertaensis* averages 5–12% larger than *L. c. californicus* in linear dimensions and 27% greater in body mass. All of these differences are highly significant (t-test, $P < 0.0001$). Indeed, females of *albertaensis* exceed male *californicus* in mean culmen length and mass. In addition, *albertaensis* has a paler mantle, and the gray areas on the inner vane of the primaries average larger and paler, although the latter differences are minor. The pattern of white markings ("mirrors") on the primaries of adults is variable (see Dwight 1925: figs. 115, 117, 119, 120), though not geographically. I found no differences in color or pattern in the downy and juvenile plumages of 10 gulls from Mono Lake and 10 from Beaverhill Lake that were hatched and reared in captivity. Among wild-taken birds, juvenile and subadult plumages were too variable for analysis. Juveniles from Mono Lake, for example, range from pale tan to dark brown in their general coloration, which may be modified dramatically by exposure to alkaline water and intense sunlight.

Studies of allozyme variability revealed no diagnostic genetic differences between the two populations (Karl et al. 1987).

Specimens examined.—The type series of 9 males

TABLE 1. Size differences between races of California Gulls (*Larus californicus*).[a]

Race	Sex	Wing (mm)				Culmen (mm)			
		No.	Mean	Range	SD	No.	Mean	Range	SD
albertaensis[b]	M	48	412.2	385–431	9.6	49	53.0	47.3–57.4	2.1
	F	38	391.3	369–408	9.7	38	47.8	41.2–52.0	2.4
californicus[c]	M	146	393.7	365–415	9.6	145	47.3	40.5–59.2	2.5
	F	202	372.3	341–390	8.2	165	42.6	38.0–48.4	1.8

[a] Pooled data from Appendix.
[b] Northwest Territories, Saskatchewan, Alberta, and North Dakota.
[c] Washington, Oregon, Idaho, California, Utah, Nevada, and Colorado.

and 3 females from Frog Lake and Beaverhill Lake, Alberta, is housed in the University of Michigan Museum of Zoology (2 skins), the Provincial Museum of Alberta (2 skins), and the San Diego Museum of Natural History (4 skins, 4 skeletons). Other specimens examined are in the museums acknowledged below. Tissue samples of both forms, including the type of *L. c. albertaensis*, have been deposited in the Museum of Zoology, Louisiana State University.

Etymology.—Named for Alberta, Canada, province of the type locality.

DISCUSSION

Evolution and subspeciation in the California Gull: a hypothesis.—Rapid speciation among large gulls in the Northern Hemisphere is presumed to have resulted from the splitting of ancestral populations by events in the Pleistocene (Mayr 1963, Smith 1964). I postulate that when the California Gull stock was divided, one population (*albertaensis*) became isolated in the northern lakes on outwash plains near the margins of the glaciers. Until recently *albertaensis* bred mainly at lakes near the edge of the boreal forest (see Fig. 6). The other population (*californicus*) became isolated around lakes in the steppe-desert of the western United States, where the species is currently most abundant (Conover 1983).

In the pleniglacial period (ca. 12,500–15,000 yr B.P.) the refugium for the cold-desert flora characteristic of the modern Great Basin, and presumably for *L. c. californicus*, was in a small area of the present Mohave Desert (Wells 1983). As the climate ameliorated in the Holocene, steppe-desert conditions shifted north into the Great Basin, where extensive lakes of varied hydrology provided breeding habitat for gulls (Hubbs and Miller 1948, Hubbs et al. 1974). I infer that the absence of suitable nesting habitat in the High Plains helped isolate the Great Plains and Great Basin gulls, which as recently as 1915 were 700 km apart (Cooke 1915; Fig. 6). Shortly thereafter a major range expansion began, abet-

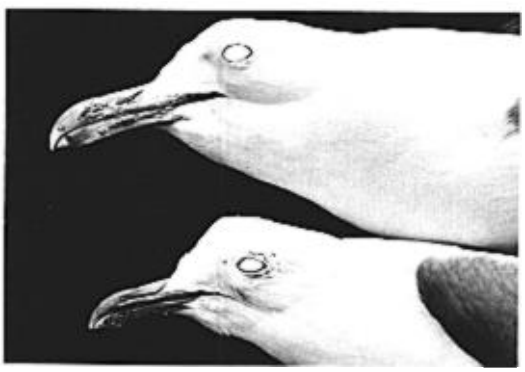


Fig. 3. Extremes of geographic and sexual variation in bill dimensions in California Gulls. Top: *L. c. albertaensis*, male, Frog Lake, Alberta (UMMZ No. 226,654). Bottom: *L. c. californicus*, female, Mono Lake, California (SDNHM No. 44123).

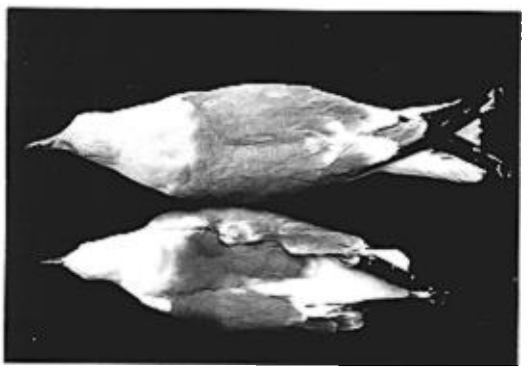


Fig. 4. Variation in body size and mantle color in California Gulls. Top: *L. c. albertaensis*. Bottom: *L. c. californicus*. Specimens as in Fig. 3.

TABLE 1. Extended.

Depth (mm)				Tarsus (mm)				Mass (g)			
No.	Mean	Range	SD	No.	Mean	Range	SD	No.	Mean	Range	SD
48	17.7	15.6–19.2	0.7	48	63.1	56.8–72.0	3.3	32	841	653–1,045	103.3
36	15.8	14.8–17.0	0.6	36	57.7	52.8–65.1	2.4	19	710	568–903	91.2
142	16.6	13.7–18.8	0.9	132	59.0	47.7–65.0	2.3	64	657	490–885	85.3
157	14.9	13.1–16.3	0.6	153	54.8	43.8–60.5	2.6	84	556	432–695	53.4

ted by the creation of nesting habitat. By 1932 the Great Basin birds had bred in Washington (Decker and Bowles 1932), and some had spread across the Rockies, forming colonies in Wyoming and Colorado (Bailey and Niedrach 1965), a process that continues today (Findholt 1986, C. Chase pers. comm.). The regularity of nonbreeders summering in New Mexico suggests that colonization may be imminent (J. P. Hubbard pers. comm.); at least 5 of 6 specimens taken there in the summer of 1981 represent *L. c. californicus*. Data for the Great Plains birds are scanty, but the recent establishment of a colony in South Dakota (Harris 1982) suggests that their range, too, is expanding.

Between 1930 and 1980 the U.S. population increased from 101,000 gulls in 15 colonies to 276,000 in 80 colonies, and the hiatus that existed in the High Plains began to fill (Conover 1983). The increased abundance and range expansion apparently resulted in a zone of secondary contact east of the Continental Divide, with birds in that region being derived from breeding areas to the northeast and from the southwest. The small sample from Montana (4 males only), for example, includes two birds that clump with the Great Basin birds, one with the Great Plains birds, and one that is intermediate (Fig. 2).

The ancestry of the California Gull is uncertain. Most authors have considered it a member of the Herring Gull complex (Stegmann 1934,

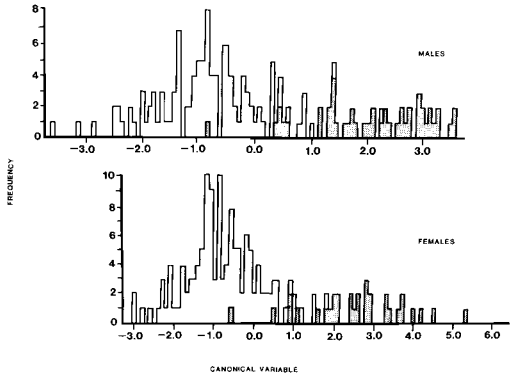


Fig. 5. Results of discriminant function analysis. Stippled areas refer to samples from the range ascribed to *L. c. albertaensis*, open areas to range of *L. c. californicus*.

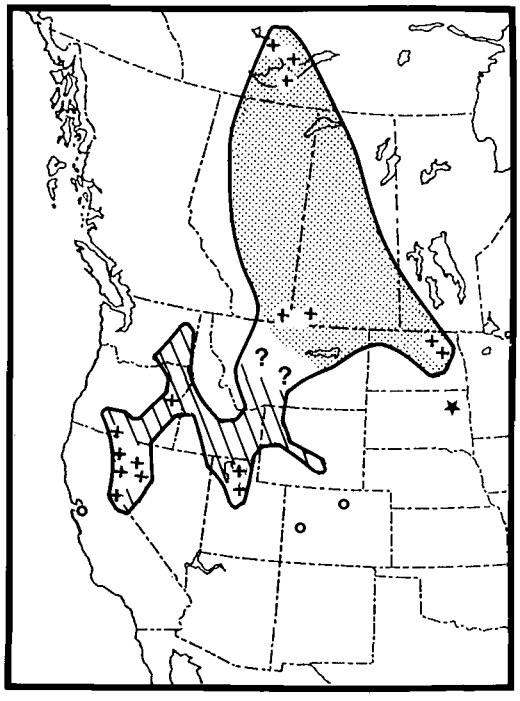


Fig. 6. Breeding range of California Gull, based on Conover (1983), Findholt (1986), Godfrey (1966), Harris (1982), C. Chase, III (pers. comm.), and original observations. The main range of *L. c. californicus* is hatched; outlying colonies are indicated by open circles. The range of *L. c. albertaensis* is stippled; a colony in South Dakota (★) is presumed of be of this race. For precise location of U.S. colonies see Conover (1983). Colonies known to Cooke (1915) are indicated by crosses.

Fisher and Lockley 1954, A.O.U. 1983), and among extant forms it is reminiscent of Thayer's Gull (*L. thayeri*) in its small size, dark iris, relatively dark mantle, juvenile and subadult plumages, east-west migration route, and west coast wintering range. Schnell (1970, pers. comm.), on the other hand, using only specimens that I would classify as *L. c. californicus*, found that the species clustered more closely with the smaller Ring-billed (*L. delawarensis*) and Mew (*L. canus*) gulls than with the Herring Gull. While I suspect a reanalysis that included large specimens from the Great Plains might lead to a different result, I doubt any conclusions will be fully satisfactory until the possible relationship of *L. californicus* to two small Pleistocene species, *L. oregonus* and *L. robustus*, is considered. Those species are known only from inland localities in the Great Basin (Howard 1946, Jefferson 1985), the area now inhabited by *L. c. californicus*.

Sampling procedures.—The paucity of preserved material from many parts of the gulls' range is deplorable but easily remedied. Collecting east of the Continental Divide, especially, is needed to document current morphological variation more precisely and to determine whether the differences described above will be swamped or reinforced as the species continues its increase and range expansion.

Considerable sampling bias in currently available material is manifested by the sex ratios of specimens used in this study, which vary among localities (see Appendix); indeed, females were unrepresented in some samples. The high incidence of males (109 males vs. 69 females) from localities other than Mono Lake probably stems from their greater aggressiveness and likelihood to approach within shotgun range (Butler and Janes-Butler 1982, Burger 1983). By contrast, the high incidence of females in the Mono Lake (72 males vs. 124 females) sample, derived largely from birds dying of trauma or predation in the colony, reflects the females' greater risk of mortality early in the nesting season (Jehl and Chase 1987, Jehl MS). These contradictory ratios illustrate further the inherent risks in drawing inferences about social structure from the sex ratios of preserved specimens, when bias in collection or preservation is not, or cannot be, known (Burger 1983; cf. Conover and Hunt 1984).

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APPENDIX. Measurements of California Gulls (*Larus californicus*).

Locality	Sex	Wing (mm)				Culmen (mm)				Depth (mm)				Tarsus (mm)				Mass (g)[a]			
		No.	Mean	Range	SD	No.	Mean	Range	SD	No.	Mean	Range	SD	No.	Mean	Range	SD	No.	Mean	Range	SD
Northwest Territories	M	3	409.3	408–410		3	51.4	50.5–52.7		3	17.6	17.0–18.4		3	62.1	57.3–66.1					
	F	1		381		1		44.2		1		16.9		1		52.8					
Saskatchewan	M	4	410.5	400–417		4	52.7	49.3–55.1		4	17.1	16.7–17.6		4	62.6	60.4–64.2		1		790	
	F	4	396.8	385–404		5	47.4	45.2–48.9		5	15.6	14.8–16.6		5	56.7	55.3–57.7					
Alberta	M	28	410.3	385–425	10.6	28	52.6	47.3–55.6	2.1	27	17.7	15.6–19.2	0.8	27	64.0	56.8–72.0	3.7	23	818	653–1,045	125
	F	26	390.2	369–408	9.8	25	47.9	41.2–52.0	2.7	23	15.9	15.0–16.9	0.5	23	58.6	54.7–65.0	2.5	17	716	568–914	108
Frog Lake[b]	M	10	419.5	412–431	6.6	10	54.7	52.4–57.4	1.6	10	17.9	17.2–18.5	0.5	10	61.4	58.3–65.0	2.2	9	880	809–965	52.6
	F	3	392.0	380–399		3	48.3	47.1–49.2		3	15.2	15.0–15.4		3	55.2	54.7–55.5		3	743	728–754	
Miquelon Lake[c]	M					15	54.6											23	826		
	F					10	48.8											16	688		
Montana	M	4	403.8	390–415		4	49.0	45.0–53.0		4	17.7	16.2–18.2		4	55.7	48.1–61.6		2	758	648–864	
North Dakota	M	3	410.3	408–415		4	52.9	50.8–54.7		4	17.8	16.8–18.7		4	62.8	59.4–65.3					
	F	4	394.5	380–405		4	47.9	45.6–48.7		4	15.8	15.0–17.0		4	57.2	56.4–57.5					
Washington	M	1		395		2	48.9	48.5–49.3		2	16.5	15.8–17.2		2	60.1	59.1–61.0					
Oregon	M	5	400.0	388–409		5	47.7	46.0–48.8		5	16.3	16.0–16.8		5	58.1	55.0–59.7					
	F	2	376.5	372–381		2	42.8	42.6–42.9		2	13.6	13.1–14.2		2	52.9	51.5–54.2					
California	M	3	396.7	388–405		3	47.4	46.5–48.7		3	16.4	15.5–17.4		3	57.2	54.7–58.7					
	F	2	375.0	372–378		2	44.0	44.3–43.5		2	14.7	14.2–15.2		2	52.4	51.0–53.7					
Mono Lake[d]	M	72	392.3	370–415	9.6	73	47.4	43.2–59.5	2.5	71	16.6	14.6–18.0	0.7	56	59.5	49.8–65.0	2.2	31	696	500–885	81
	F	124	373.8	350–390	7.2	109	42.7	38.0–47.1	1.7	102	14.9	13.4–16.3	0.6	102	55.2	44.8–60.0	2.3	45	575	477–695	47
Nevada	M	3	391.7	365–415		3	47.8	44.3–50.6		3	15.8	14.5–17.1		3	58.1	55.5–61.5		1		641	
Utah	M	16	394.5	382–408	7.4	16	46.0	40.5–49.1	2.5	14	15.7	13.7–17.0	1.1	16	58.3	55.3–62.0	1.9				
	F	5	373.2	370–379		5	41.4	40.0–42.3		5	14.6	13.5–15.6		5	53.4	52.5–55.3					
Great Salt Lake[e]	M	15	398.1	375–420[f]		15	48.6	45–54						15	59.0	55–67		15	653	556–748	
	F	17	383.3	359–400		17	44.2	40–48						16	54.3	49–62		17	526	425–625	
Idaho	M	4	396.8	385–405		4	48.1	45.6–50.8		4	16.6	15.7–17.7		4	58.5	56.8–59.4					
	F	2	369.0	358–380		2	43.3	43.3		2	14.3	13.8–14.8		2	52.9	52.2–53.6					
Wyoming	M																	13[g]	671	574–719	
	F																	14[g]	551	462–551	
	Unsexed[d]	20	385.1	370–424	14.2	19	44.6	41.4–47.8	1.9	19	15.1	14.5–17.1	22.5	20	56.5	52.0–60.8	2.3				
														101[g]	55.7			101	609	486–775	
Colorado	M	4	400.8	378–414		4	46.6	42.4–49.1		4	15.5	14.4–17.0		4	56.0	55.5–56.5					
	F	3	366.3	356–380		3	40.3	39.0–41.3		3	13.6	13.4–14.0		3	53.6	51.6–56.0					

[a] Based on museum specimens, except as indicated.
[b] Type series; Frog Lake, Alberta.
[c] Vermeer 1970.
[d] Jehl unpubl. data.
[e] Behle 1958.
[f] Measured as flattened.
[g] Smith and Diem 1972.