

# CHAPTER NINE

## The Homestead Cave Ichthyofauna

by  
*Jack M. Broughton*

### INTRODUCTION

Biological evidence on the climatic and hydrographic history of the intermountain region would be much richer, if we had more than the present dribble of paleontological data on the fishes (Hubbs and Miller, 1948, p. 25).

In this passage from their landmark synthesis of historical fish biogeography in the Great Basin, Hubbs and Miller lament the dearth of available fish fossil evidence and suggest that a far more detailed picture of past climates and hydrography would emerge were this situation to change. To Hubbs and Miller, the geographic distributions of fishes, both past and present, held the "least assailable" evidence of past hydrographic connections and climatic history of the Great Basin since "...fishes appear to occur only in habitats which they have been able to reach through surface water connections, by means of either active or passive migration. The dispersal of fishes is therefore closely linked with the history of water courses." The key assumption of this approach followed the earlier pioneering work of Jordan (1905) and was succinctly paraphrased by Smith, G. R. (in press): "fish are where they can swim and stop there."

In this approach, climatic inferences are derived primarily by documenting previous hydrographic connections from the geographic distributions of fishes and deducing the levels of ancient lake systems that would have allowed for such connections. A richer fossil fish record would enhance our understanding of historical fish biogeography and ultimately lead to a greater understanding of regional paleohydrography and climate change.

Inferences on the nature of past climates can be derived from fossil (or subfossil) fish assemblages in ways other than those based strictly on biogeography. Fluctuations in the size and depth of a lake can, of course, have dramatic effects on water chemistry and temperature and, in turn, profoundly influence the nature of its fish populations. In addition to controlling whether a lake can support fish at all, water temperature and salinity, for example, play critical roles in determining the species composition, growth characteristics, and the age and size structure of fish populations. As a result, high-resolution fossil fish sequences from Lake Bonneville could provide fine-scale details on lake-level oscillations to test and refine hypotheses based on other sources. And since there is perhaps a no more sensitive measure of regional climate than the size of closed-basin lakes, paleofish faunas can potentially provide one of the more direct proxies of climate change.

Utilizing this ichthyological source of information on past climates in the Bonneville basin has not, however, been possible due to what has continued to be an extremely sparse late Quaternary paleontological fish record in the region.

While geological research of Lake Bonneville extends well back into the 19th century, knowledge of Lake Bonneville's fish fauna has been derived primarily from a single detailed analysis conducted by Smith and colleagues in the 1960s (Stokes and others, 1964; Smith and others, 1968). Smith's unique study of Quaternary fish biogeography in the Bonneville basin was based on the materials derived from two fossil fish localities in the northern Bonneville basin and provided our first glimpse of the fish fauna of Lake Bonneville. Smith identified eight species from these deposits and documented that the species composition of Lake Bonneville was very similar to that of the Recent fauna of Bear Lake, Utah-Idaho. This clearly confirmed the physiographic evidence that Bear Lake was tributary to Lake Bonneville during pluvial times. The analysis also revealed that the high degree of isolation and endemism among modern fishes of the Bonneville basin is recent in origin. The sites that produced the fish materials were, however, not well dated, nor were they internally stratified. Accordingly, no analysis of temporal variation in Lake Bonneville's fish fauna could be undertaken for any purpose.

The precisely dated ichthyofauna from Homestead Cave represents the largest, well-stratified, and richest Quaternary fish assemblage from the entire Bonneville basin and the only known terminal-Pleistocene fish fauna of the region. This fauna provides an unprecedented opportunity to examine the dynamics of Lake Bonneville's fish populations as it fluctuated toward the end of the Pleistocene and sheds light on both the nature and timing of fine-scale climatologically driven lake level oscillations and late Quaternary fish biogeography in the Bonneville basin. At last, we have far more than a dribble.

### DEPOSITIONAL ORIGIN OF THE HOMESTEAD CAVE FISHES

The analyses of the Homestead fishes that follow depend in many ways on an understanding of their depositional origin. As previously emphasized (Grayson, chapter seven; Livingston, chapter eight), the mammals and birds from Homestead Cave were apparently accumulated by raptorial birds, especially owls. Owl pellet cones were observed on the floor of the cave when the excavation began, the deposits contain numerous owl pellets, and many of the bones themselves still have owl pellet material adhering to them. Although it is possible that the fish materials may have washed into the cave as the lake descended past its mouth during the post-Provo recession, the available evidence does not support this scenario. Instead, like the other vertebrates, the fish remains from Homestead Cave appear to have resulted from the use of the cave by owls.

A water-deposited origin for the Homestead fishes now

appears unlikely for three reasons. First, evidence from the sediments of Stratum I (chapter three), where the fish remains are concentrated (see below), show no evidence of water-laid deposits. In fact, the cave appears to have been completely scoured out as the lake regressed past its mouth. Second, a diversity of small mammal and bird species dominates the vertebrate faunal assemblage in Stratum I of Homestead Cave; these materials are unlikely to have been deposited by water. Finally, the high strontium ratios (0.7125-0.7129) of the Homestead fishes indicate they originated from a low-elevation lake, and postdate the late Pleistocene lake-splitting event (see Quade, chapters two and five). The water-deposited hypothesis, on the other hand, calls for a higher elevation lake - one of roughly the elevation of the mouth of the cave - and fish strontium ratios low enough to indicate they occupied Lake Bonneville before the time of the lake-splitting event.

The analysis of the Homestead avifauna has documented the presence of nine raptor taxa in the lower strata (I-III) of the deposit (chapter eight; table XXIV). Of these taxa, only two routinely roost and nest in open caves: *Bubo virginianus*, Great Horned Owl and *Tyto alba*, Barn Owl, (figures 77, 78). Although the diet of these owls is comprised predominantly of small mammals, both species have been reported to utilize fish.

Reports of barn owls taking fish are extremely rare. The only reference of which I am aware was provided by Gallup (1949, p. 150). In Escondido, California, Gallup (1949, p. 150) noted that: "Barn owls are common birds in the region. I have seen as many as 30 on the beach at night feeding on grunion when these were running."

Accounts of Great Horned Owls taking fish are far more common. Although fish remains have been reported in small quantities from the pellets of Great Horned Owls in a variety of settings in western North America (Marti, 1974; Knight and Jackman, 1984; Marti and Kochert, 1996; Bogiatto, in

prep.), the most detailed accounts come from eastern North America. For instance, in an analysis of 33 Great Horned Owl pellets collected in Wisconsin, Errington and others (1940, p. 806) indicate that fish were represented by at least 13 individuals comprising four different species. Similarly, a total of nine individual fish, also representing four species, were identified from a set of 21 Great Horned Owl pellets collected in Iowa (Errington and others, 1940, p. 850). Errington and others (1940, p. 806) indicate they "know little of the horned owl's technique in capturing fishes but have some reason to think that in winter it gets them mainly from concentrations about open springs or holes in the ice at the edge of lakes...It may be that the owls scavenge upon fishes stranded, washed ashore or left by other animals." Errington and others (1940) do not indicate what the reasons were for thinking this, but it is well known that Great Horned Owls are eager scavengers.

From an analysis of Great Horned Owl pellets from the Caney Creek roost in middle Tennessee, Klippel (personal communication 1998) indicates that fish remains comprise over 44% of the total vertebrate MNI (minimum number of individuals). The sample contains 33 individual fish, representing three families (Cyprinidae, Catostomidae and Centrarchidae) and 11 different species. Suckers, including *Hypentelium nigricans*, northern hog sucker, *Moxostoma duquesnei*, black redhorse, *Moxostoma* spp., redhorse, and unidentified catostomids, represent over 66% of the fish MNI. Klippel observed suckers spawning in the shallow water of Caney Creek near the roost that provided the pellets. While engaged in their spawning activities, adult fish became partially dewatered and would have made easy quarry for the owl (Klippel, personal communication 1998).



Figure 77. Great Horned Owl (*Bubo virginianus*).



Figure 78. Barn Owl (*Tyto alba*).

Figures 77 and 78 are from Udvardy, M.D.F. (1977). *Audubon Society Field Guide to North American Birds - Western region*. New York, Knopf distributed by Random House. All the fish figures are from Sigler and Sigler 1996, with one exception, figure 80, the picture of the bull trout. That figure is from Sternberg, D. (1987), *Freshwater Gamefish of North America*, Cy DeCosse, Incorporated, Minnetonka, Minnesota 553345. ISBN 0-86573-023-7. Distributed by Prentice Hall Press, a division of Simon and Schuster, Inc., NY, NY. ISBN 0-13-331125-2.

These limited data suggest that owls exploit fish resources only when the costs of taking them are substantially reduced, such as when fish are stranded (dead or alive) on shorelines or partially exposed in shallow streams (Gallup, 1949; Errington and others, 1940; Klippel, personal communication 1998). I am unaware of any accounts of these owls taking live fish from deep open water.

In addition, many of the fish specimens recovered from Homestead Cave represent very large individuals (>2.6 kg estimated live weight), which suggests they could not have been taken and carried out of deep water by owls but instead reflect fish parts that were scavenged by these birds. For example, many of the salmonine vertebrae (most probably represent *Oncorhynchus clarki*) exceed 9.0 mm in maximum width, suggesting live weights over 2.6 kg; some exceed 11.0 mm, suggesting weights over 6.2 kg (see Follett, 1980: 115, 1982: figure 3). The large size also eliminates the possibility that these fish entered the cave in the stomachs of fish-eating birds (for example, *Phalacrocorax auritus*, *Aechmophorus occidentalis*) who had fallen prey to owls.

The maximum distance from roost to foraging areas reported for the Barn Owl is 5.6 km (Marti, 1992); that distance for the Great Horned Owl is 4.35 km (Smith, 1971). Thus, aquatic habitats that supported, but at least periodically lost, fish populations must have existed within a radius of ~6 km or less from Homestead Cave during the periods of their deposition.

In sum, the fishes from Homestead Cave appear to have been accumulated by scavenging owls. An owl-based origin of the Homestead fishes suggests that local fish populations

experienced substantial mortality (that is, die-offs) and/or were frequently exposed in very shallow water over the time the fauna accumulated. Strata in which the remains of Lake Bonneville fishes are abundant should thus signal recessionary periods of the lake's history. By dating those strata, inferences on the chronology of lake-level fluctuations and climate change can be derived.

## TAXONOMIC SUMMARY

The fish materials from Homestead Cave are heavily concentrated in the lowest stratum of the deposit, Stratum I. As I discuss in detail below, the extremely low representation of fish materials in the deposits above Stratum I appears to reflect the extinction of Lake Bonneville's fish fauna. All of the fish materials from the 6.3 mm and 3.1 mm sample fractions of Homestead Cave have been identified and are reported here.

Table XXVII provides a systematic list of the identified fish species in the Homestead Cave deposits; nomenclature follows Robins and others (1991). The total numbers of identified specimens per taxon by stratum are provided in table XXVIII. Table XXIX provides the numbers of identified specimens by provenience unit for Stratum I. The numbers of identified fish specimens by element and taxon for the Homestead Cave deposits are archived in electronic form at the Utah Geological Survey (see Broughton, 2000).

A total of 14,866 fish specimens have been identified from the Homestead Cave deposits (table XXVIII). The as-

Table XXVII  
Systematic list of the fishes identified at Homestead Cave

### Osteichthyes

#### Salmoniformes

##### Salmonidae

##### Salmoninae

cf. *Salvelinus confluentus*

*Oncorhynchus clarki*

##### Coregoninae

*Prosopium spilonotus*

*Prosopium abyssicola*

*Prosopium spilonotus/abyssicola*

*Prosopium gemmifer*

Pikes, Smelts, Trouts and Allies

Trouts, Chars, Whitefishes and Allies

Trouts and Chars

Bull Trout

Cutthroat Trout

Whitefishes

Bonneville Whitefish

Bear Lake Whitefish

Bonneville or Bear Lake Whitefish

Bonneville Cisco

#### Cypriniformes

##### Cyprinidae

*Gila atraria*

*Richardsonius balteatus*

##### Catostomidae

*Catostomus ardens*

*Catostomus discobolus*

Minnows and Suckers

Minnows

Utah Chub

Redside Shiner

Suckers

Utah Sucker

Bluehead Sucker

#### Scorpaeniformes

##### Cottidae

*Cottus bairdi*

*Cottus extensus*

*Cottus extensus/echinatus*

Scorpionfishes, Sculpins and Allies

Sculpins

Mottled Sculpin

Bear Lake Sculpin

Bear Lake or Utah Lake Sculpin

Table XXVIII

Numbers of identified fish specimens per taxon by stratum at Homestead Cave

TAXON	STRATUM																				Total	
	I	Ia	Ib	I-II	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII		XVIII
Salmoninae	701	258	23	-	21	2	6	1	2	1	-	1	-	-	2	1	1	-	1	-	1	1022
<i>cf. Salvelinus confluentus</i>	1	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Oncorhynchus cf. clarki</i>	40	20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	60
<i>Oncorhynchus clarki</i>	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
<i>Prosopium</i> sp.	945	5944	449	-	111	19	32	-	10	6	3	5	2	2	-	1	4	-	-	2	1	7536
<i>Prosopium cf. spilonotus</i>	79	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	84
<i>Prosopium spilonotus</i>	27	10	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	41
<i>P. spilonotus/abyssicola</i>	93	87	2	-	14	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	198
<i>Prosopium abyssicola</i>	2	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
<i>Prosopium gemmifer</i>	225	499	37	-	15	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	778
Cypriniformes	1167	471	58	-	44	10	28	4	19	10	8	22	13	45	224	48	23	1	7	38	5	2245
Cyprinidae	34	35	3	-	3	3	5	-	1	1	-	1	-	2	14	4	2	-	-	12	-	120
<i>Gila atraria</i>	443	191	26	-	12	7	17	1	13	10	3	14	6	13	59	40	17	2	20	63	1	958
<i>Richardsonius balteatus</i>	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Catostomus</i> sp.	900	299	24	-	19	4	20	2	7	6	7	5	2	3	25	6	9	2	1	2	-	1343
<i>Catostomus ardens</i>	134	22	7	-	2	-	4	-	1	1	-	1	-	-	5	1	1	-	-	-	-	179
<i>Catostomus discobolus</i>	-	-	-	-	-	-	-	-	1	-	-	3	1	-	-	-	-	-	-	-	-	5
<i>Cottus</i> sp.	53	178	9	-	13	5	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	259
<i>Cottus cf. bairdi</i>	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Cottus bairdi</i>	2	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6
<i>Cottus extensus/echinatus</i>	3	9	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14
<i>Cottus extensus</i>	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5
Total	4850	8045	641	1	257	51	114	8	54	36	21	52	24	65	330	101	57	5	29	117	8	14,866

Table XXIX

Numbers of identified fish specimens per taxon by provenience unit for Stratum I at Homestead Cave

TAXON	PROVENIENCE UNIT										Total
	Stratum I		Stratum Ia						Stratum Ib		
	FS-47 (6.3 mm)	FS-63 (6.3 mm)	FS-63 (3.1 mm)	FS-64 (6.3 mm)	FS-93 (1.6 mm)	FS-94 (1.6 mm)	FS-75 (6.3 mm)	FS-75 (3.1mm)	FS-92 (1.6 mm)	FS-95 (1.6 mm)	
Salmoninae	210	203	276	12	207	25	13	13	1	22	982
cf. <i>Salvelinus confluentus</i>	-	1	-	-	-	-	-	-	-	-	1
<i>Oncorhynchus</i> cf. <i>clarki</i>	15	20	5	-	14	2	4	-	-	-	60
<i>Oncorhynchus clarki</i>	1	-	-	-	-	-	1	-	-	-	2
<i>Prosopium</i> sp.	103	72	768	2	4726	1008	6	204	48	401	7338
<i>Prosopium</i> cf. <i>sylonotus</i>	42	26	11	-	3	2	-	-	-	-	84
<i>Prosopium sylonotus</i>	3	9	14	1	5	1	-	4	-	3	40
<i>P. sylonotus/abyssicola</i>	8	6	79	-	59	14	3	11	-	2	182
<i>Prosopium abyssicola</i>	-	-	2	-	6	-	-	-	-	-	8
<i>Prosopium gemmifer</i>	1	4	220	-	349	100	-	50	3	34	761
Cypriniformes	229	161	772	5	317	50	16	88	9	49	1696
Cyprinidae	2	-	32	-	15	16	-	4	-	3	72
<i>Gila atraria</i>	150	68	221	4	140	29	5	17	3	23	660
<i>Catostomus</i> sp.	294	241	363	2	206	49	23	21	3	21	1223
<i>Catostomus ardens</i>	61	32	41	-	15	5	1	1	-	7	163
<i>Cottus</i> sp.	3	-	50	-	134	31	-	13	1	8	240
<i>Cottus</i> cf. <i>bairdi</i>	-	-	-	-	1	-	-	-	-	-	1
<i>Cottus bairdi</i>	-	-	2	-	2	2	-	-	-	-	6
<i>Cottus extensus/echinatus</i>	-	-	3	-	6	3	-	-	-	-	12
<i>Cottus extensus</i>	-	-	-	-	2	3	-	-	-	-	5
Total	1122	843	2859	26	6207	1340	72	426	68	573	13,536

semblage is represented by three orders (Salmoniformes, Cypriniformes and Scorpaeniformes), four families (Salmonidae, Cyprinidae, Catostomidae and Cottidae) and eleven species. The species represented include cf. *Salvelinus confluentus*, bull trout, *Oncorhynchus clarki*, cutthroat trout, *Prosopium sylonotus*, Bonneville whitefish, *Prosopium abyssicola*, Bear Lake whitefish, *Prosopium gemmifer*, Bonneville cisco, *Gila atraria*, Utah chub, *Richardsonius balteatus*, redbside shiner, *Catostomus ardens*, Utah sucker, *Catostomus discobolus*, bluehead sucker, *Cottus bairdi*, mottled sculpin, and *Cottus extensus*, Bear Lake sculpin. As a group, the whitefish dominate the assemblage comprising 58.2% of the identified specimens. The percentage composition of the other major taxonomic groups are as follows: minnows and suckers, 32.6%, trout 7.4%, and sculpin, 1.9%.

In this section, I discuss the osteological criteria I used to identify the Homestead Cave fishes<sup>1</sup> and provide information on the modern and fossil geographic distributions, habitat requirements, and other data on the life histories of the represented species.

### Salmoninae - Chars and Trouts

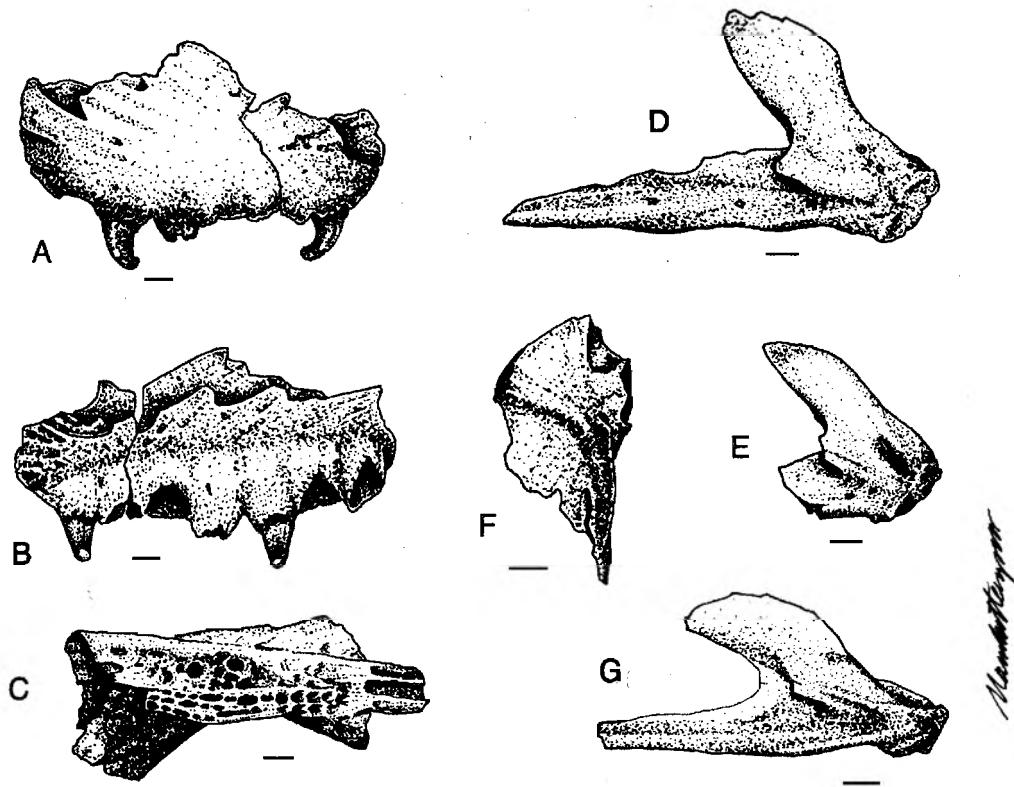
*Salvelinus confluentus* - Bull Trout, and *Oncorhynchus clarki* - Cutthroat Trout

**Osteological notes:** The single premaxilla fragment (figure 79, A, B) identified as cf. *Salvelinus confluentus* is similar to Recent material of this species and differs from that of *Oncorhynchus clarki*, the abundant and widely distributed

salmonine of the Great Basin. The teeth of the premaxilla specimen project mesially, as in *S. confluentus*, rather than more directly ventral (that is, in the same plane as the main body of the bone) as in *O. clarki*. Also similar to *S. confluentus*, the mesial surface of the premaxilla exhibits a well-developed shelf or spine that extends from the anterior margin of the bone, just dorsal to the tooth row, to the posterior base of the ascending process (Norden, 1961, p. 753); *O. clarki* lacks this feature. Unfortunately, the dorsal margin of this specimen has been fragmented so that it cannot be determined whether or not it possessed the most diagnostic feature of *S. confluentus*, the well-developed ascending process (Norden, 1961, p. 753). Gerald R. Smith (1998, personnel communication) has examined this specimen and concurs with the identification as *S. confluentus*. However, because of the fragmentary condition of the single specimen I have included the prefixal cf.

The cranial elements of trout at Homestead Cave are heavily abraded and fragmentary, owing perhaps to the low mineral densities of the salmonine crania (Butler and Chatters, 1994). Accordingly, species-level identifications were not possible for many elements that are diagnostic when they are intact. The elements I identified as *O. cf. clarki* exhibited features that are similar to both *O. clarki* and *O. mykiss*, rainbow trout, but unlike those of *S. confluentus*. The designation as *O. cf. clarki* for these specimens is based on the known Quaternary distribution of these trout species in the Great Basin (see below).

I assigned the lingual plate specimens to *Oncorhynchus* on the basis of the pronounced medial-lateral ridge on the



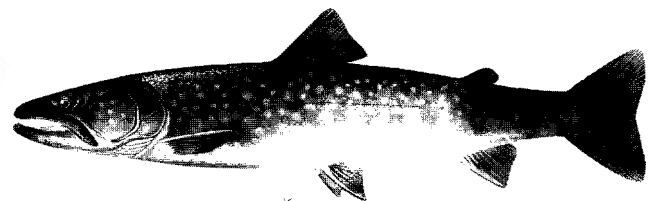
**Figure 79.** Selected diagnostic salmonid fish elements from Homestead Cave: (A) lateral view of right premaxilla of cf. *Salvelinus confluentus*, (B) mesial view of right premaxilla of cf. *Salvelinus confluentus* (same specimen as A), (C) basibranchial of *Oncorhynchus clarki*, (D) left dentary of *Prosopium spilonotus*, (E) left dentary of *Prosopium abyssicola*, (F) left hyomandibular of *Prosopium gemmifer*, (G) left dentary of *Prosopium gemmifer*, Scale: bar length = 1 mm.

ventral-anterior surface of these elements; the corresponding surface in *S. confluentus* is smooth. The salmonine vomers were identified as *Oncorhynchus* since the specimens exhibited a long, zigzag row of substantial teeth on an elongated vomeral shaft (Stearley and Smith, 1993, p. 17). In *Salvelinus*, teeth occur in a patch on the head of the vomer and the posterior extension of teeth is not supported by the vomeral shaft but, instead, by a crest ventral to the shaft that is attached to the head of the vomer (Stearley and Smith, 1993, p. 17). The ceratohyal specimens are relatively deep for their length, as in *Oncorhynchus*; these elements are more slender (dorsal-ventrally compressed) in *S. confluentus* (Stearley and Smith, 1993, figure 17). The maxillae are referable to *Oncorhynchus* on the basis of the orientation of the premaxillary process. In *Oncorhynchus*, this feature is oriented dorsally less than  $10^\circ$  from the main axis of the maxilla. In *Salvelinus*, the premaxillary process is oriented greater than  $10^\circ$  from the main axis of the maxilla (Stearley and Smith, 1993). As in *Oncorhynchus*, the Homestead salmonine basioccipitals exhibit paired ventrolateral walls that form a deep V-shaped furrow along the ventral portion of the element. In *Salvelinus*, the ventrolateral walls are less elevated and are flattened ventrally to form a shelf for articulation with the posterior parasphenoid.

I used only a single diagnostic element, the basibranchial, to provide species level identifications of the Homestead trout. The two basibranchial specimens (figure 79C) were identified as *O. clarki* since they were toothed; the basibranchials are untoothed in *O. mykiss* (Norden, 1961; Stearley and Smith, 1993). The basibranchials lack a sharp-edged

ventral keel as in *S. confluentus*.

**Distribution and habitat:** *Salvelinus confluentus* (figure 80) is a large piscivorous char that can attain lengths of over 1 m and weights of up to 18.3 kg (Cavender, 1978). Historically, *Salvelinus confluentus* was widely distributed in western North America from northern California to the south, north to Alaska, and east to Alberta (Cavender, 1978; Hass and McPhail, 1991). They have affinities for cold, clear lakes and streams that are fed by mountain glaciers and snowfields (Cavender, 1978).



**Figure 80.** Bull trout (*Salvelinus confluentus*).

No specimens, fossil or otherwise, have previously been collected for *Salvelinus* in the Great Basin. The nearest modern specimen record for *Salvelinus confluentus* is from the Jarbidge drainage, a tributary of the Snake River in northeastern Nevada (Miller and Morton, 1952; Cavender, 1978). The *Salvelinus* clade is known from Miocene deposits in both central Nevada and the Snake River Plain (referred to as *Hucho larsoni*; Smith, G. R., in press). A single historical account of char in the Bonneville basin was, however, provided in the early 19th century by John Kirk Townsend, a trained zoo-

logist. Townsend was traveling as an assistant to the English botanist Thomas Nuttall on a scientific collecting expedition across the Rocky Mountains to the Columbia River. Encamped along the Bear River on July 6, 1834, about 19 km miles south (upstream) of Soda Springs, Idaho, Townsend (1978, p. 89) reported that: "Trout, grayling, and a kind of char are very abundant here - the first very large." Nuttall was familiar with fishes of the Great Lakes, which included grayling and char (Smith, G. R., in press), and since char are so easily distinguished from trout - char are dark with light spots, while trout are light with dark spots - there is little reason to dispute Townsend's record. Hubbs and Miller (1948, p. 76) have also reported a "glacial relict" population of *Salvelinus* from the Lost River system on the eastern Snake River Plain, located about 180 km north of where Townsend reported these fish.

*O. clarki* (figure 81), divided into six regional subspecies, is native to most of the major river drainages of montane western North America. *O. clarki* is the only native trout species of the Great Basin, with the exception of *O. mykiss gairdneri*, redband trout, of southeastern Oregon, which displays a composite of *O. mykiss* and *O. clarki* characters (Smith, G. R., in press). In the Bonneville basin, and most other locations within its range, *O. clarki* occurs in cold freshwater lakes, rivers and streams. However, certain populations outside of the Bonneville basin have adapted to higher-salinity conditions. Some stocks inhabiting coastal drainages are anadromous, spending summer months well out to sea. *O. clarki henshawi*, Lahontan cutthroat trout, have adapted to the moderately saline waters of Pyramid Lake (5300 ppm, [mg/l] TDS) and Walker Lake (10,300 ppm TDS). Populations inhabiting lakes spawn up inflow streams. *O. clarki* can reach substantial sizes; records for Nevada and Utah are 18.6 kg (41 lb) and 12.1 kg (26 lb, 12 oz), respectively (Sigler and Sigler, 1996).

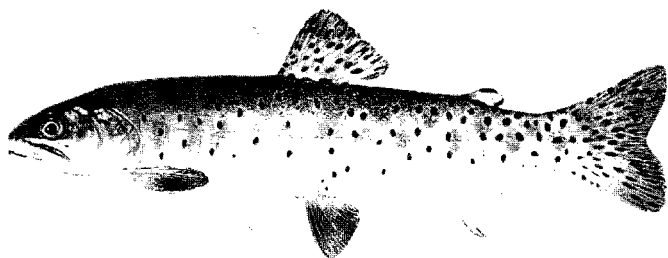


Figure 81. Cutthroat trout (*Oncorhynchus clarki*).

*O. clarki* is known from several other late Pleistocene deposits in the Bonneville basin. Smith and others (1968) described *O. clarki* specimens from the Black Rock Canyon locality of the northeastern Bonneville basin. *O. clarki* materials have also been derived from deposits of the Old River Bed, located between the northern and southern portions of Lake Bonneville (Oviatt, 1984, p. 59). Mead and others (1982, p. 7) report *O. clarki* specimens from the late Pleistocene deposits of Smith Creek Canyon in the Snake Valley of eastern Nevada.

### Coregoninae—Whitefishes

*P. spilonotus* - Bonneville Whitefish, *P. abyssicola* - Bear Lake Whitefish, and *P. gemmifer* - Bonneville Cisco

**Osteological notes:** Four whitefish species are native to the

Bonneville basin: *Prosopium williamsoni*, *P. spilonotus*, *P. abyssicola* and *P. gemmifer*. Both *P. abyssicola* and *P. gemmifer* are small whitefish. *P. gemmifer* rarely attains lengths over 216 mm (Sigler and Workman, 1978, p. 6). *P. abyssicola* rarely exceeds 254 mm in length (McConnell and others, 1957); the historical size record is 305 mm (Snyder, 1919). The other two whitefish that occur in the Bonneville basin, *P. williamsoni* and *P. spilonotus*, can reach much larger sizes: for both species, fish larger than 400 mm are not uncommon (McConnell and others, 1957; Sigler, 1951). Accordingly, I used the size of the Homestead whitefish specimens as an identification criteria for specimens that lacked other diagnostic characters.

I used the shape and orientation of the hyomandibular fossa of the opercle to separate *P. spilonotus* and *P. abyssicola* from *P. williamsoni*. In *P. williamsoni*, the medial margin of this fossa is squared-off; in *P. spilonotus* and *P. abyssicola* the medial margin of this feature is rounded. I found no criteria to separate the opercles of *P. abyssicola* and *P. spilonotus*. The hyomandibular fossa of the opercle in *P. gemmifer* is, however, distinct from all of the other whitefish. Specifically, the postero-dorsal margin of the hyomandibular fossa is more elevated, extending to or very near the dorsal margin of the opercle. The fossa thus appears to sit more directly atop the dorsal margin of the bone in *P. gemmifer* than in the other species of *Prosopium*.

I used the orientation of the coronoid process to identify the *Prosopium* dentaries. This feature varies systematically among the Bonneville basin whitefish along a gradient consistent with the phylogenetic relationships of these species (figure 79D, E, F; see Smith and Todd, 1993). Representing the ancestral condition, the coronoid process in *P. williamsoni* rises (dorsally) at a steep angle from the symphysis. The most derived condition is represented by *P. gemmifer* where the coronoid process is deflected posteriorly and rises at a very shallow angle from the symphysis. This condition is associated with the specialized elongation of the anterior portion of the cranium in *P. gemmifer* (see Smith and others, 1968, figure 3; Smith and Todd, 1993, figure 1). *P. spilonotus* and *P. abyssicola* represent the intermediate states of this feature. However, the orientation of the coronoid process in *P. spilonotus* is more similar to *P. williamsoni*, while this feature in *P. abyssicola* is more similar to *P. gemmifer*.

The articular-angular is distinctive in *P. gemmifer*. In *P. gemmifer*, the dorsal margin of the body of the articular-angular rises anteriorly at a very shallow angle from the quadrate articulating surface; this angle is much steeper in all of the other Bonneville basin whitefish. I used this feature, as well as size, to identify the *Prosopium* articular-angulars. The basioccipital in *P. gemmifer* is narrow relative to its length, compared to all of the other Bonneville basin whitefish. Among the reference material available to me, I found no criteria to securely separate the other *Prosopium* species using this element.

In *P. gemmifer*, the ceratohyal is more slender (dorsoventrally compressed) for its length compared to the other Bonneville basin *Prosopium*. I distinguished *P. spilonotus* from *P. williamsoni* by the relative length of the ceratohyal foramen: the foramen is longer, relative to the total length of the bone, in *P. spilonotus*. The relative length of the ceratohyal foramen is still longer in *P. abyssicola* compared to *P. spilonotus*.

The mesially deflected premaxillary process of the maxilla with a pointed condyle allows the secure identification of *P. gemmifer* with this element. I was unable to isolate characters that distinguished the remaining whitefish species using the maxilla. The quadrate is also quite distinct in *P. gemmifer*. Specifically, the latero-ventral margin of the articular process does not project laterally in *P. gemmifer* as it does in the other whitefish. In addition, a marked concavity is present in *P. gemmifer* on the latero-ventral margin of the quadrate just posterior to the articular process. I separated the two larger whitefish on the basis of the morphology of the quadrate as well. In *P. williamsoni*, a shallow concavity is present on the medial surface of the quadrate just dorsal to the articular process. *P. spilonotus* lacks this concavity.

The morphology of the hyomandibular allows secure separation of *P. gemmifer* (figure 79F) from the other Bonneville basin whitefish. In *P. gemmifer*, the postero-lateral ridge is less flared posteriorly than in the other *Prosopium*. In addition, the angle formed between the main axis of the ventral body of the hyomandibular and the margin formed between the opercular condyle and the dorsal condyle is less acute in *P. gemmifer* than in the other whitefish. I was unable to identify characters of the hyomandibular that would allow the consistent identification of *P. williamsoni*, *P. abyssicola* and *P. spilonotus* among the modern reference material of these taxa.

I used a variety of characters of the prootic to identify the Homestead whitefish. A pronounced concavity is evident on the postero-medial surface of *Prosopium* prootics. In *P. spilonotus* and *P. abyssicola*, the anterior and dorsal margins of this concavity are well defined and elevated; the corresponding margin in *P. gemmifer* is poorly defined and depressed. In *P. abyssicola* and *P. spilonotus*, the protuberance on the lateral aspect of the sphenotic condyle is situated more dorsally on the body of the prootic and projects less anteriorly than in *P. williamsoni*. In addition, the medial surface of the prootic is porous in *P. abyssicola* and *P. spilonotus*. The mesial surface of *P. williamsoni* is smooth.

I used the degree of porosity on the endocranial surface of the exoccipital to distinguish *P. abyssicola* and *P. spilonotus* as a group, from *P. williamsoni*. Specifically, the antero-lateral surface between the pterotic and epiotic condyles is porous in *P. abyssicola* and *P. spilonotus* but smooth in *P. williamsoni*. Since I identified no *P. williamsoni* from the Homestead material based on other diagnostic criteria, while *P. spilonotus* is well represented in the collection, I assigned all the *Prosopium* materials too large for *P. gemmifer* and *P. abyssicola* as *P. cf. spilonotus*.

**Distribution and habitat:** Of the four species of whitefish that occur in the Bonneville basin today, three are present in the Homestead Cave ichthyofauna: *P. spilonotus* (figure 82), *P. abyssicola* (figure 83) and *P. gemmifer* (figure 84). Each of these three species are presently endemic to Bear Lake. At an elevation of 1805 m, Bear Lake is a fresh, deep, cold and infertile (oligotrophic) body of water with over 50 percent of the lake registering a depth of more than 30.5 m; the maximum depth is 64 m (Sigler and Sigler, 1996, p. 13, p. 194). The fourth Bonneville basin whitefish, *P. williamsoni*, was not demonstrably present in the Homestead deposits. This species is widespread in western North America where it is most abundant in cold mountain rivers and streams. Some lake populations, however, do exist. *P. williamsoni* has been

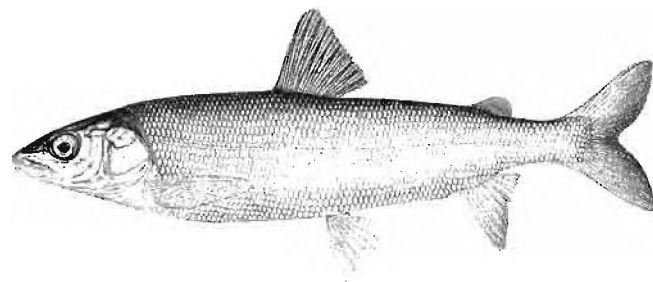


Figure 82. Bonneville whitefish (*Prosopium spilonotus*).

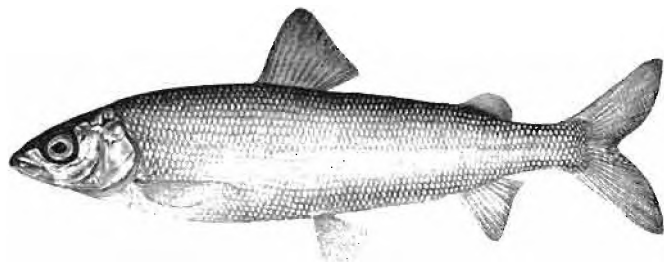


Figure 83. Bear Lake whitefish (*Prosopium abyssicola*).

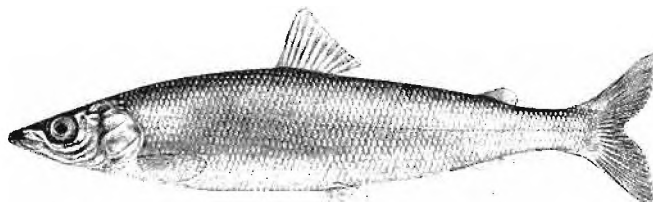


Figure 84. Bonneville cisco (*Prosopium gemmifer*).

reported in Bear Lake (Kemmerer and others, 1923), but they have been extremely rare in that setting throughout historical times. McConnell and others (1957, p. 20) suggested that the few *P. williamsoni* reported in Bear Lake may have drifted in from the Bear River.

*P. spilonotus* is the large wide-ranging whitefish of Bear Lake. *P. spilonotus* usually occurs in waters between 12.2 to 30.5 m and deeper but moves into shallower water near the shore between mid-February to early March to spawn in water temperatures of about 7.2°C. The species is primarily insectivorous, with chironomid (midge) larvae and pupae forming the dominant component of their diet (McConnell and others, 1957, p. 53). Smith and others (1968) identified *Prosopium spilonotus* from the late Pleistocene Hot Springs and Black Rock Canyon localities, both of the northeastern Bonneville basin, on the basis of basioccipital specimens.

*P. abyssicola* is a dwarf, deep-water whitefish of Bear Lake. They rarely frequent inshore areas. Spawning takes place from late December to early February in depths ranging from 15 to 30 m when water temperatures drop between 2.2 to 3.9°C. A diet of ostracodes, copepods, midge larvae and aquatic oligochaetes reflects a dependence on the deep, soft marl bottom of Bear Lake (Wurtzbaugh and others, 1989; McConnell and others, 1957). The Homestead Cave specimens of *P. abyssicola* represent the first records of this species for Lake Bonneville.

*P. gemmifer*, a small planktivorous species, is the most abundant fish species in modern Bear Lake; it is also the best



represented fish in the Homestead Cave ichthyofauna. Although they normally occur in water temperatures lower than 14.4°C, they require temperatures between 0.5 and 5.6°C to spawn. *P. gemmifer* inhabits the deep offshore waters of Bear Lake for most of the year, but moves inshore (from 0.9 to 2.4 m) to shallow waters for a brief (~ 2 week) period in winter to spawn (Perry, 1943; Sigler and Workman, 1978). Because of their adaptation to deep and cold waters, attempts have been made to stock this fish in a number of cold high-elevation lakes in western North America (for example, Lake Tahoe, Nevada/California, and Twin Lakes, Colorado). Survival in these settings has not been documented (Sigler and Sigler, 1987, 1996). *P. gemmifer* has been identified from two other late Pleistocene Lake Bonneville deposits, both in the northeastern Bonneville basin (Smith and others, 1968).

Based on measurements of the hyomandibular, Smith and others (1968), documented significant differences between the populations of *P. gemmifer* that inhabited Lake Bonneville and those that occur in Bear Lake today. Those differences were interpreted as evidence for specialization of the jaw structure in *P. gemmifer* over the last ~11 ka (Smith and others, 1968). Alternatively, this pattern may reflect introgression of *P. gemmifer* with the other Bear Lake *Prosopium* during the Holocene. Ongoing analysis of the sample of *P. gemmifer* hyomandibulars from Homestead Cave will allow this issue to be examined in further detail.

### Cyprinidae - Minnows

*Gila atraria* - Utah Chub, and  
*Richardsonius balteatus* - Redside Shiner

**Osteological notes:** Six cyprinid species are native to the Bonneville basin: *Gila atraria*, *Gila copei*, leatherside chub, *Iotichthyes phlegenthontis*, least chub, *Rhinichthys cataractae*, longnose dace, *Rhinichthys osculus*, speckled dace, and *Richardsonius balteatus*. With the exception of *Gila atraria*, these are very small fishes, rarely attaining lengths over 150 mm. *Gila atraria*, however, can reach lengths up to 559 mm, but typically range from 127 to 305 mm (Sigler and Sigler, 1996). Accordingly, I used size and robusticity of elements to identify *Gila atraria* from the Homestead materials for elements that lacked other diagnostic criteria.

*Gila atraria* can be easily separated from the other Bonneville basin cyprinids on the basis of the morphology of the pharyngeal teeth. The pharyngeal teeth of *Gila atraria*, in addition to having a unique tooth formula (2,5 - 4,2), are exceptionally robust, exhibit pronounced grinding surfaces and ter-

minally hooked tips (figure 85A). With one exception, all of the identifiable pharyngeal specimens from Homestead Cave are *G. atraria*. A single pharyngeal specimen is referable to *Richardsonius balteatus* (figure 85B) on the basis of the delicate and slender body and teeth and the distinctively squared-off margin of the lateral surface of the bone.<sup>2</sup>

The cyprinid maxillae are referable to *Gila atraria* on the basis of (1) the steep anterior and posterior margins of the dorsal ramus, and (2) the wide breadth and flattened dorsal extremity of this process. The basioccipital of *Gila atraria* is also distinctive among the Bonneville basin minnows. Specifically, the postero-ventral platform of the basioccipital is relatively narrow for its length in *Gila atraria* and the lateral margins decurve ventrally to form a pronounced concavity.

**Distribution and habitat:** *Gila atraria* (figure 86) is native to the Bonneville basin, the Snake River above Shoshone Falls, and the lower Wood River system, Idaho. It is abundant in a diversity of environments: from deep, cold, high-mountain lakes, such as Bear Lake, to small, warm (up to 31°C), moderately saline springs (up to 2.5% NaCl [sodium chloride]) on the desert floor. Laboratory experiments also indicate that these fish can tolerate saline waters (Na, 213 meq/l; Westenfelder and others, 1988). During the spring, lake populations move from deep to shallow water (less than

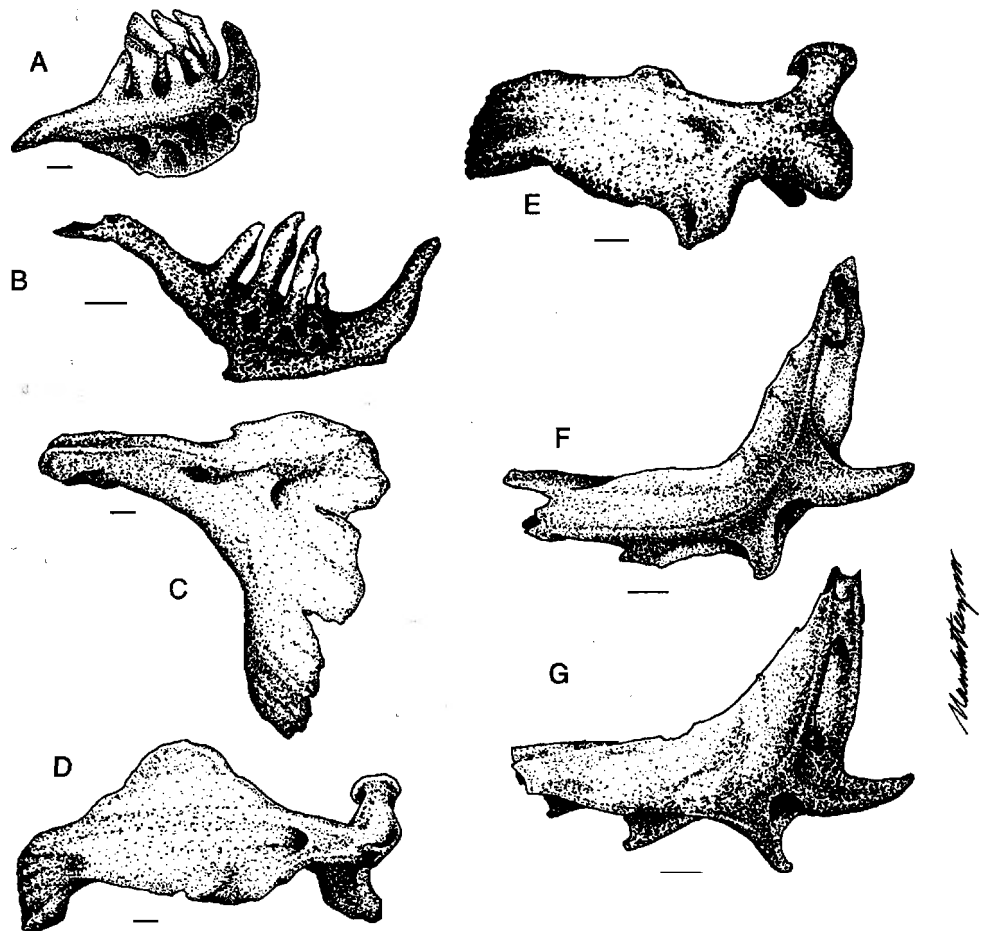


Figure 85. Selected diagnostic cyprinid, catostomid, and cottid elements from Homestead Cave. (A) left pharyngeal of *Gila atraria*, (B) right pharyngeal of *Richardsonius balteatus*, (C) left dentary of *Catostomus ardens*, (D) right maxilla of *Catostomus ardens*, (E) right maxilla of *Catostomus discobolus*, (F) left preopercle of *Cottus bairdi*, (G) left preopercle of *Cottus extensus*. Scale: bar length = 1 mm.

0.61 m) to spawn (Sigler and Sigler, 1987, 1996). *Gila atraria* is omnivorous, feeding on plant material, a variety of invertebrates, and occasionally even small fish. In desert spring settings, they will feed on green algae and their own eggs (Sigler and Sigler, 1996, p. 76).

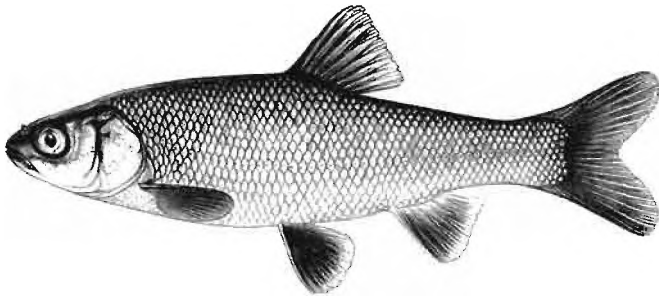


Figure 86. Utah chub (*Gila atraria*).

*Gila atraria* has been reported from three other late Pleistocene fossil localities in the Bonneville basin: Black Rock Canyon (Smith and others, 1968), Smith Creek Canyon (Mead and others, 1982) and the Public Shooting Grounds (Murchison, 1989a). Specimens of *Gila atraria* from the Public Shooting Grounds were derived from a matrix of transgressive lacustrine sands and silts rich in gastropod remains and were underlain by freshwater marsh deposits. *Lymnaea stagnalis* shell from the layer containing the chub materials provided a date of  $10,990 \pm 110$  yr B.P. The *Gila atraria* specimens represented here may have been derived from freshwater marshes (Murchison, 1989a) or may have come from a lake setting.

*Richardsonius balteatus* (figure 87) is a small, short-lived minnow; most individuals are under 127 mm and attain ages of no more than 5 years. They are widely distributed west of the Rocky Mountains, east from the Bonneville and Snake systems, and west to the Columbia and Malheur-Harney Basins. They occur in a wide variety of habitats, from cold mountain lakes, such as Bear Lake, to warm (up to 24°C) ponds and springs. *Richardsonius balteatus* is omnivorous, feeding on a variety of aquatic and terrestrial insects, algae, mollusks, zooplankton, as well as their own eggs and fry (Sigler and Miller, 1963, pp. 76-78; Sigler and Sigler, 1996, pp. 119-122). The Homestead Cave specimen represents the first record of this species in Lake Bonneville.

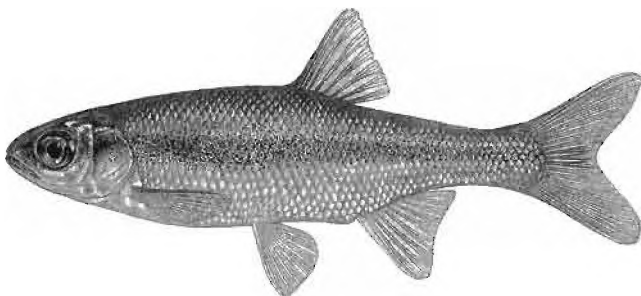


Figure 87. Redside shiner (*Richardsonius balteatus*).

### Catostomidae—Suckers

*Catostomus ardens* - Utah Sucker, and  
*Catostomus discobolus* - Bluehead Sucker

**Osteological notes:** Four sucker species are native to the

Bonneville basin: *Chasmistes liorus*, June sucker, *Catostomus ardens*, *Catostomus discobolus* and *Catostomus platyrhynchus*. Both *Chasmistes liorus* and *Catostomus ardens* can reach substantial sizes (>600 mm in length), while *Catostomus discobolus* and *Catostomus platyrhynchus* (subgenus *Pantosteus*) are smaller fishes, reaching maximum lengths of 305 mm and 457 mm, respectively (Sigler and Sigler, 1996). Hence, I used size to rule out the latter two species for certain large-sized sucker specimens (see below) that lacked other diagnostic criteria.

The morphology of the dentary allows easy separation of the Bonneville basin catostomids. The angle and length of the gnathic ramus relative to the posterior body of the dentary is slightly obtuse and short in *Catostomus ardens* (figure 85C), but is more obtuse and longer in *Chasmistes liorus*. This gives *Chasmistes* a longer, more curved ramus than *Catostomus ardens*. In addition, the angle of the dentary symphysis is parallel to the gnathic ramus in *Catostomus ardens* but is subparallel in *Chasmistes liorus* (Miller and Smith, 1981, p. 37). In *Catostomus platyrhynchus* and *Catostomus discobolus*, the gnathic ramus is dramatically foreshortened and mesially deflected, as in all species of the subgenus *Pantosteus* (Smith, 1966, p. 14). In *C. discobolus* a substantial protuberance sits at the lateral-posterior margin of the gnathic ramus; this feature is far less developed in *C. platyrhynchus*. Two sucker dentaries from Homestead are assignable to *C. discobolus* based on these criteria; all the others are *C. ardens*.

The maxillae are sufficiently distinct among these species to allow secure identifications as well. The anterior constriction or neck of the maxilla is thicker in *Catostomus ardens* (figure 85D) compared to *Chasmistes liorus* (Miller and Smith, 1981, p. 36). A nearly semi-hemispherical ridge is present along the antero-ventral margin of the neck in *C. ardens*, whereas this feature is not well developed in *Chasmistes*. The antero-ventral (premaxillary) process projects at a right angle from the long axis of the maxilla posterior to the head in *C. ardens*. In *Chasmistes liorus*, this process projects anteriorly at an obtuse angle from the long axis of the bone and is more directly ventral to the head of the maxilla (Miller and Smith, 1981, p. 36). The ventral keel is also better developed in *C. ardens* compared to *C. liorus* (Miller and Smith, 1981, p. 36); both these species have well-developed dorsal keels. The maxillae of *C. discobolus* and *C. platyrhynchus* are robust, lack dorsal keels and are distinctively dissimilar to either *C. ardens* or *C. liorus* (Smith, 1966, p. 14). The posterior margin of the ventral keel slopes anteriorly more steeply in *C. platyrhynchus* compared to *C. discobolus*. Based on these criteria, both *C. ardens* and *C. discobolus* are represented at Homestead Cave (figure 85D, E).

Finally, the premaxillae of *Catostomus ardens* and *Chasmistes liorus* are distinctive. In *Chasmistes liorus*, the maximum medio-lateral length (horizontal limb) of the premaxilla is longer than the maximum ventro-dorsal (vertical limb) length. In *Catostomus ardens*, the maximum medio-lateral length of the premaxilla is considerably shorter than the maximum dorso-ventral length (see Miller and Smith, 1981, figure 10, A and B). In *C. discobolus* and *C. platyrhynchus* the relative lengths of the premaxillary limbs are near equal or the horizontal limb is longer. In addition, the dorsal extremity of the vertical limb exhibits an antero-medial protuberance and is anteriorly deflected; *C. ardens* lacks this feature.

Finally, the horizontal limbs of *C. discobolus* and *C. platyrhynchus* are more curved, producing a marked convexity of the anterior surface. All of the Homestead catostomid premaxillae are referable to *Catostomus ardens* based on these criteria. Since only *Catostomus* was demonstrably present in the diagnostic Homestead sucker elements, I assigned the remaining catostomid materials to *Catostomus* sp.

**Distribution and habitat:** *Catostomus ardens* (figure 88) is distributed widely in the Bonneville basin and upper Snake system above Shoshone Falls. *Catostomus ardens* thrives in a diversity of habitat types, from large deep, cold lakes, such as Bear Lake, to relatively small, warm (above 26.7°C) streams. For lake populations, spawning migrations may occur up inflow streams or in shallow inshore settings within the lake itself. *Catostomus ardens* populations that occupy large lakes, such as Bear lake, are benthic browsers, taking both plant and animal material along the bottom of the lake at all depths (McConnell, and others 1957, p. 47; Sigler and Sigler, 1987, 1996).

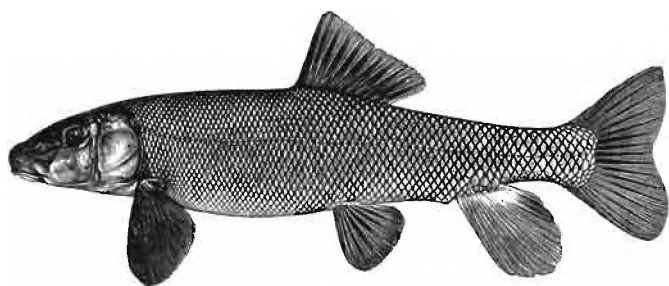


Figure 88. Utah sucker (*Catostomus ardens*).

*Catostomus ardens* is known from two other Lake Bonneville deposits: the Hot Springs locality (Smith and others, 1968) and the Old River Bed (Oviatt, 1984). Both of these samples are represented by single skeletal elements.

*Catostomus discobolus* (figure 89), the most specialized and derived species in the subgenus *Pantosteus* (Smith, 1966; Smith and Koehn, 1971), is found in the upper Colorado River drainage, the Weber and Bear River drainages in the Bonneville basin, and in the upper Snake drainage (Sigler and Miller, 1963, p. 99; Smith, G. R., in press). Suckers in the *Pantosteus* subgenus are river and stream fish and show a variety of morphological adaptations to fluvial environments (Smith, 1966; Powers, 1972). *Catostomus discobolus* occurs in a variety of fluvial environments, from small cool (20°C or less) creeks in the headwaters of the Weber River to the warm (up to 27.8°C) torrent of the main stem of the Colorado River (Smith, 1966, p. 94; Sigler and Miller, 1963, pp. 100-103; Sigler and Sigler, 1996, pp. 133-136). *Catostomus discobolus* feeds along the bottom using the chisel-like cartilaginous ridges of their jaws to scrape algae, aquatic insects

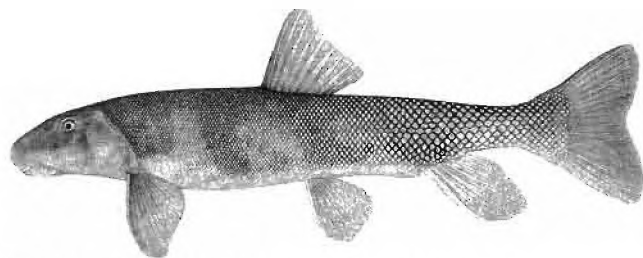


Figure 89. Bluehead sucker (*Catostomus discobolus*).

and other invertebrates from rocks. No other *Pantosteus* fossils are known from the Great Basin.

## Cottidae—Sculpins

*Cottus bairdi* - Mottled Sculpin, and *Cottus extensus* Bear Lake Sculpin

**Osteological notes:** Four species of sculpin are known from the Bonneville basin: *Cottus beldingi*, Paiute sculpin, *C. bairdi*, *C. extensus* and *C. echinatus*, Utah Lake sculpin. *C. echinatus* is a Utah Lake endemic that is now extinct. As a result, osteological comparative material is extremely limited for this species. Features of the preopercle provide the most reliable osteological means of distinguishing these species (Bailey and Bond, 1963; Smith and others, 1968) and I relied on this element exclusively to identify the sculpin species represented in the Homestead fauna.<sup>3</sup>

The preopercle of *C. beldingi* is distinctive in possessing only a single, blunt, posteriorly directed preopercular spine. The preopercle of *C. bairdi* is also unique in exhibiting an anteriorly deflected second (from the dorsal) spine (figure 85F; see also Smith and others, 1968, figure 5B). The second spine in both *C. extensus* and *C. echinatus* is deflected posteriorly, allowing them, as a group, to be readily distinguished from *C. bairdi*. Securely distinguishing *C. extensus* from *C. echinatus* is more difficult owing to the strong osteological similarity of these species and the small number of recent *C. echinatus* reference specimens available for comparison. I used the orientation of the third (from the dorsal) spine to distinguish these species. In *C. echinatus*, the third spine projects more ventrally (less anteriorly) compared to *C. extensus* (figure 85G). I observed this feature on three *C. echinatus* specimens [UMMZ 156794, BYU 29212, and BYU 29213]. Gerald R. Smith (personal communication 1999) observed this feature on the four *C. echinatus* housed at the UMMZ. Using these criteria, *C. bairdi* and *C. extensus* are demonstrably represented in the Homestead ichthyofauna, but *C. beldingi* and *C. echinatus* are not.

**Distribution and habitat:** *Cottus bairdi* (figure 90) is widely distributed in the Bonneville and Columbia drainages and across much of northeastern North America as well. *C. bairdi* may reach a maximum length of ~150 mm; adults in the Logan River, Utah, range between 76 and 102 mm (Sigler and Sigler, 1996, p. 231). In the Bonneville and Columbia drainages, *C. bairdi* is found principally in clear, cold, well-oxygenated streams with rapid to moderate currents. They prefer summer water temperatures between 12.8 to 18.3°C and gravel or rocky substrates. Their diet consists primarily of aquatic insects (Wydoski and Whitney, 1979, p. 163; Sigler and Sigler, 1996, p. 231). In eastern North America, *C. bairdi* also inhabits cold streams but many populations are adapted to lacustrine settings as well. Most of the eastern lake populations of *C. bairdi* inhabit shallow-water shoreline settings (Hubbs and Lagler, 1964, p. 118; Becker, 1983, p. 970). However, deep-water lake populations, such as in Lake Erie, are known to occur for this species as well (Trautman, 1981, pp. 708-710; Keleher, 1952, cited in Scott and Crossman, 1973). *C. bairdi* has also been identified from the Hot Springs (four specimens) and Black Rock (two specimens) localities of Lake Bonneville (Smith and others, 1968).

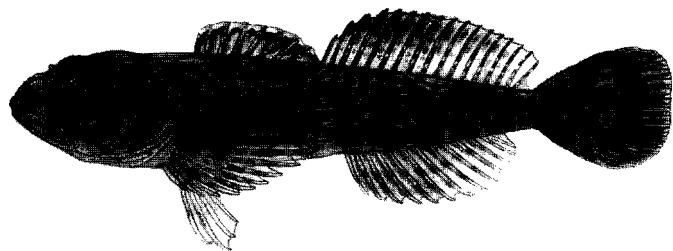


Figure 90. Mottled sculpin (*Cottus bairdi*).

*Cottus extensus* (figure 91) is presently endemic to Bear Lake, where they are the second most abundant fish in the lake. This is a very small fish with an average length of 76 mm. For most of the year, most *Cottus extensus* individuals occur in very cold, deep (15–53 m [50 to 175 ft]) water where they burrow into the soft marl bottom for cover; late winter and spring brings them to rocky nearshore settings to spawn. They feed primarily on ostracodes and cyclopoid copepods (McConnell and others, 1957; Dalton and others, 1965; Sigler and Sigler 1987, 1996). *Cottus extensus* has been identified from both the Hot Springs and Black Rock Canyon localities of Lake Bonneville (Smith and others, 1968).

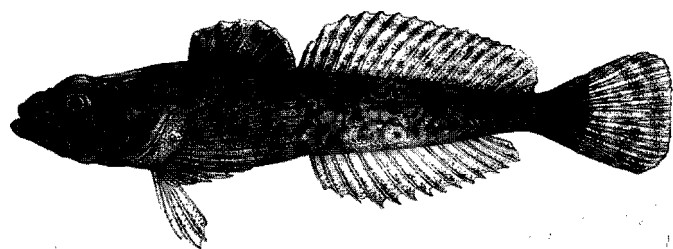


Figure 91. Bear Lake sculpin (*Cottus extensus*).

## BIOGEOGRAPHIC IMPLICATIONS

In the 1960s, G.R. Smith described the fish materials from the Black Rock Canyon and Hot Springs sites, two late Pleistocene fossil localities in the Bonneville basin (Stokes and others, 1964; Smith and others, 1968). Those materials represented the first Lake Bonneville fish assemblages ever described and hence provided a wealth of information on the Quaternary biogeographic history of fishes in the Bonneville basin. Since that time, only a few isolated fish bones derived from the sediments of Lake Bonneville have been reported, and no new species have been identified among them (Oviatt, 1984; Mead and others, 1982). The Homestead Cave fauna is thus extremely unique in its potential to help explain issues of fish biogeography in the Bonneville basin.

Four fish species previously unknown to have inhabited Lake Bonneville are represented in the Homestead Cave ichthyofauna: *Salvelinus confluentus*, *Prosopium abyssicola*, *Catostomus discobolus* and *Richardsonius balteatus*. There are also several species that are noteworthy for their absence in the Homestead fauna: *Chasmistes liorus* and *Cottus echinatus*. Here, I discuss the biogeographic significance of the presence/absence of these taxa in the Homestead ichthyofauna.

From a biogeographic standpoint, one of the most

important aspects of the Homestead fauna is the identification of a single *Salvelinus confluentus* specimen. Again, this represents the first specimen record for the genus *Salvelinus* in the Great Basin and supports Townsend's early historical period report of char in the Bear River – an account that has previously been considered “dubious” (see Hass and McPhail, 1991, p. 2204). The Bonneville system may have been colonized by *Salvelinus confluentus* from the Snake River system when Lake Bonneville overflowed into the Snake ~15 ka. Alternatively, *Salvelinus confluentus* could have reached Lake Bonneville sometime around 27 ka when the Bear River was diverted from the Snake River drainage system into the Bonneville basin by lava flows in southern Idaho (Bright, 1963, 1967; Smith, G. R., in press; but see Bouchard and others, 1998).

Today, *Salvelinus confluentus* is restricted to cold streams and lakes fed by mountain glaciers and snowfields and has declined dramatically in the southern portions of their range during historical times (Cavender, 1978; Hass and McPhail, 1991; Riemen and McIntyre, 1995). Petitions for listing under the U.S. Endangered Species Act have been issued (Reiman and others, 1997). For a species as large as *Salvelinus confluentus*, the presence of only a single specimen at Homestead Cave suggests that even by ~11.3 ka, they were uncommon in Lake Bonneville. Since the Homestead fishes were apparently derived from a low-elevation lake (~1300 m), it may be that by the time the Homestead fauna began to accumulate, water temperatures were already too warm and *Salvelinus confluentus* populations had already begun to decline in Lake Bonneville. The indication that *Salvelinus confluentus* is a native species to cold waters of the Bonneville basin has implications for the modern management of this species in decline.

Homestead Cave has provided the first record of *Catostomus discobolus* in Lake Bonneville and the only fossil record of the subgenus *Pantosteus* in the Great Basin. *Catostomus discobolus* occurs almost exclusively in stream or river habitats; a single lake population has been reported for Lower Green River Lake, Wyoming (Sigler and Miller, 1963, p. 102). Today, two disjunct populations occur in swift, cool mountain streams of the Bonneville basin: one in the upper Weber River drainage and one in the Bear River drainage. This present distribution pattern led Smith (1966, p. 121) to suggest that the Weber River population must have colonized that system before the Bear and Weber Rivers were isolated by the desiccation of Lake Bonneville at the end of the Pleistocene. This argument requires that *Catostomus discobolus* had occupied Lake Bonneville, at least along its stretch of shoreline between the Bear River and Weber Rivers, but evidence of their presence in the lake has heretofore been lacking. The presence of *C. discobolus* at Homestead Cave indicates not only that they occurred in Lake Bonneville, but that they ranged widely across the lake. Since *C. discobolus* is a stream-adapted species, their presence also implies that populations of these fish had either adapted to some aspect of the lacustrine environments of Lake Bonneville and/or suitable fluvial environments occurred near Homestead Cave in the past.

The distribution patterns of stream fishes in the Great Lakes region provide insight into how *C. discobolus* may have adapted to lacustrine environments of Lake Bonneville. High-energy wave action along the shorelines of the Great

Lakes creates substrate types and associated benthic algal and diatom communities that are analogous to those found in riffle sections of stream environments. As a result, fish species in northeastern North America that are primarily restricted to swift streams, or rivers with rock or gravel substrates, also occur in certain high-energy shoreline settings of the Great Lakes (Hubbs and Lagler, 1964). Wave-swept shorelines clearly characterized Lake Bonneville and may have provided suitable habitat for *C. discobolus* in those settings.

It is also possible that stream habitats may have existed near Homestead Cave in late Pleistocene times even though they do not occur there today. In this context, I note that avian taxa associated with riparian vegetation have been reported for the basal deposits of Homestead Cave (Livingston, chapter eight) and may reflect the presence of local fluvial habitats in the past. I also note that an ancient stream channel that would have drained much of the western margin of Lakeside Mountains is located ~0.5 km from the mouth of the cave (chapter two).

*Prosopium abyssicola* is the last of the four Bear Lake endemics to be identified in Lake Bonneville sediments. *Prosopium abyssicola*, *Prosopium spilonotus* and *Prosopium gemmifer* apparently evolved from a *Prosopium williamsoni* ancestor, the more widespread and morphologically least-derived western whitefish species. When and where the endemic Bonneville basin whitefish speciated has remained unknown, although the previous documentation of *Prosopium spilonotus* and *Prosopium gemmifer* in Lake Bonneville sediments has indicated that they have been around since the late Pleistocene. The documentation that *Prosopium abyssicola* also inhabited Lake Bonneville indicates they too evolved sometime before the late Pleistocene and eliminates the possibility that this species diverged more recently (that is, over the last ~11,000 years) in Bear Lake.

A single pharyngeal of *Richardsonius balteatus* was identified from the Homestead deposits. *Richardsonius balteatus* is abundant in a variety of lacustrine and fluvial habitats in the Bonneville basin. These are very small fish and their rarity in the sample may in part be a function of recovery bias. Analysis of the entire 1.6 mm fraction would shed light on this suggestion and may also indicate the presence of *Rhinichthys osculus*, another widespread diminutive minnow of the Bonneville basin absent in the Homestead sample. The fact that *Richardsonius balteatus* specimens were previously unknown from Lake Bonneville fossil fish faunas but were present in sediments derived from Pliocene Lake Idaho has led to the suggestion that this species entered the Bonneville basin from the Snake system very recently (~12 ka; Sigler and Sigler, 1996, p. 24). Additional older Lake Bonneville fish fossils will be required to evaluate this suggestion, but it is certainly clear now that this species was part of the Lake Bonneville fauna.

The fact that *Cottus echinatus* was not demonstrably present in Homestead deposits is noteworthy. This species was endemic to Utah Lake in historical times but is now extinct. This sculpin has now failed to appear in the all of Lake Bonneville fish assemblages that have been studied. This fact, along with the close morphological similarity between *C. echinatus* and *C. extensus*, suggests that the former diverged from a relictual *C. extensus* population in Utah Lake over the last ~11,000 years (Rosenfeld, 1996, p. 32;

Smith, G. R., in press).

*Chasmistes liorus* is noteworthy for its absence in the Homestead ichthyofauna as well. This species is also endemic to the shallow eutrophic waters of Utah Lake today. *Chasmistes liorus* is a large, planktivorous lake sucker; it spawns in June (hence its common name) up the Provo River. Miller and Smith (1981, p. 33) report a fragmentary coracoid and dentary referable to *Chasmistes* cf. *liorus* from the Black Rock Canyon locality. Hyomandibulars assigned to *Chasmistes* sp. were reported by Bright (1967) from late Pleistocene sediments in the Thatcher Basin (Miller and Smith, 1981, p. 33).

The absence of *C. liorus* in the abundant catostomid collection from Homestead deposits is thus intriguing. That absence may reflect a restricted spatial distribution of these fish in late Pleistocene Lake Bonneville. Perhaps they were restricted to warmer, shallower bays of Lake Bonneville near major input rivers.

### FISH LIFE HISTORY ADAPTATION AND BODY SIZE CHANGE IN A REGRESSING LAKE BONNEVILLE

The demographic structure of vertebrate populations is determined by age-specific patterns in fertility and mortality. Variation in these parameters can not only mechanically alter the distribution and abundance of individuals across age classes in a population, but can provide the selective context for the emergence and persistence of different life history strategies as well (Gadgil and Bossert, 1970; Stearns, 1992). It is well known, for example, that intraspecific variation in mortality and life expectancy among fishes is directly correlated with, among other variables, the age of initial reproduction and adult body size. The relationships between these variables and the fitness related trade-offs that underlie them, have been well explored through mathematical modeling (see Stearns and Crandall, 1981, 1984; Roff, 1984, 1992; Stearns and Koella, 1986; Charnov, 1993). In this section, I explore how change in the size of fish represented at Homestead Cave might inform on the nature of the extinction of Lake Bonneville's ichthyofauna.

In the context of intermountain fishes, Smith (1981) has developed a specific model linking intraspecific variation in life history strategies to local regimes of habitat stability, adult mortality and ultimately variation in adult body sizes:

Many intermountain minnows, suckers, and trouts are selected locally for large size by increased adult survival and consequent late reproduction in large habitats. Annual fluctuations that reduce habitats seasonally, thus causing heavy mortality, lead to persistence of phenotypes that reproduce early at the expense of later growth...When adult mortality is low individuals leave more descendants by growing larger and producing more young over several seasons (Smith, 1981, p. 126, p. 162).

Smith has documented significant positive relationships between habitat size, as a measure of environmental stability, and maximum adult size in many western fish species, including some of the cypriniform taxa represented at Home-

stead Cave, namely, *Gila atraria* and *Catostomus discobolus*. In large stable rivers and lakes with limited adult mortality and high life expectancy, these species mature later, live longer and attain larger sizes. In smaller, less stable aquatic settings, where adult mortality is at least seasonally high, these fishes reproduce at younger ages and attain smaller maximum sizes. According to this model, the mortality rate is the critical variable affecting the selection of different life history phenotypes that ultimately constrain adult body size. This model has clear implications for change in the size structure of Lake Bonneville's fish populations as the lake regressed at the end of the Pleistocene.

The taxonomic composition of the Homestead fishes suggests that during the deposition of Stratum I, the lake was, at least periodically, a fresh, cold, oligotrophic body of water similar to modern high-elevation lakes that are fed by mountain glaciers and snowfields. If the Homestead Cave fish assemblage was derived from a process involving a series of die-offs that occurred either seasonally or over periods of many years during which lower lake levels exceeded the temperature or salinity tolerances of the fishes, then selection should have increasingly favored early maturing, smaller-sized fishes across this period of elevated mortality. If this was the case, it follows from Smith's model that the fish materials from Homestead Cave representing populations that resulted from later die-offs (that is, Stratum Ib) should be skewed to smaller size classes, compared to fish representing the initial die-offs (that is, Stratum Ia). If, on the other hand, the fish materials from Homestead Cave represent a single relatively instantaneous die-off event, no change in size structure should be evident across the divisions of Stratum I.

The sample of Cypriniformes vertebrae identified from Strata Ia and Ib was selected for analysis of change in fish size. Table XXX provides the summary statistics for the maximum diameters of cypriniform vertebral centra derived from these strata.<sup>4</sup>

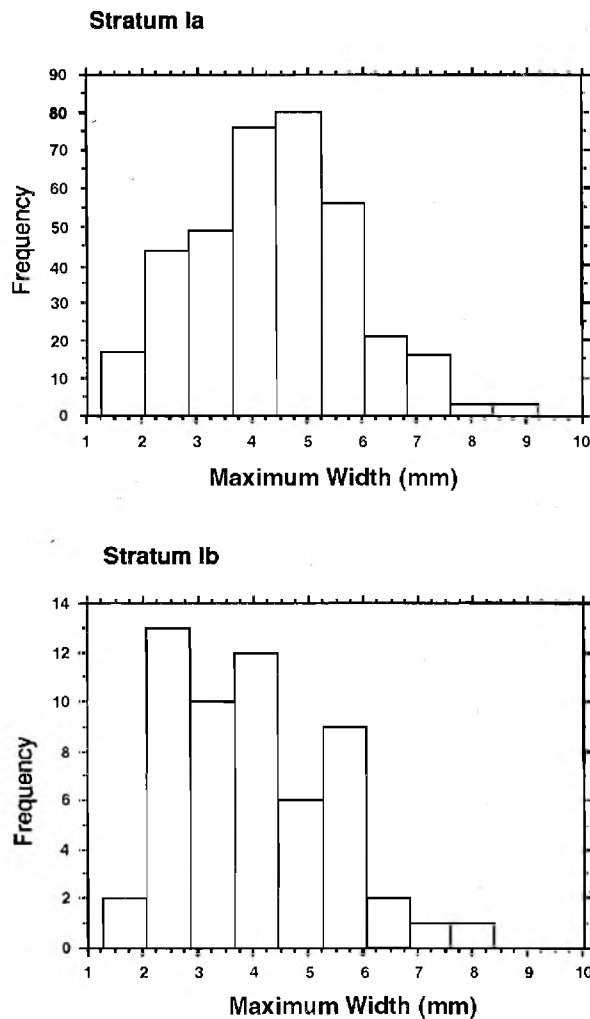
Figure 92 shows the frequency distributions of the maximum diameters of cypriniform vertebral centra, as a measure of size, for Stratum Ia and Stratum Ib. The distributions are clearly distinct: the later deposits (Stratum Ib) are skewed to smaller-sized fishes, have a smaller maximum size, and exhibit a significantly smaller mean size than do those in Stratum Ia (Mann-Whitney  $U = 8546.5$ ,  $P < 0.05$ ).

It is also evident that neither of these distributions display ideal "catastrophic" profiles, that is, a decreasing number of individuals represented in progressively larger (older) size classes: both divisions of Stratum I are underrepresented by the smaller (< 2 mm) size classes. Catastrophic profiles are expected to result if individuals are sampled in direct proportion to their abundance in the living population and thus should be produced from death assemblages representing mass die-offs such as those represented at Homestead Cave. Since these materials were collected with 1.6 mm screen mesh, the underrepresentation of very small cypriniform vertebrae in both Ia and Ib is not likely due to recovery bias. Instead, very small individual fish may have consistently been outside the diet breadth of the owls that accumulated the fauna.

While the size change between Stratum Ia and Ib is consistent with Smith's model of life history adaptation, the same pattern would also be expected to result mechanically from a set of at least two catastrophic die-offs in which the

**Table XXX**  
Vertebral widths (mm) of the Homestead Cave  
Cypriniformes in Strata Ia and Ib

Stratum	N	$\bar{x}$	Range	s
Ia	365	4.40	1.26 - 9.20	1.46
Ib	56	4.02	1.74 - 7.62	1.38



**Figure 92.** Frequency distribution of the maximum diameters of cypriniform vertebral centra for Strata Ia and Ib at Homestead Cave.

population resulting from the second one had not occurred long enough in the lake to grow individuals of larger size classes. The smaller size of fishes in Stratum Ib, in this scenario, would thus represent a historical vestige derived from a previous period of substantial mortality. In either case, the data suggest that the Homestead Cave ichthyofauna represents multiple fish die-offs rather than a single die-off event.

The data also do not allow a determination of the precise nature of fish mortality during the extinction process. It is unknown, for instance, whether Lake Bonneville ever completely lost its fish populations during any one of the initial die-offs; even during periods of mass mortality, remnant populations may have persisted in colder, less saline water, perhaps in deeper portions of the lake or in settings near major

input rivers. The periodicity of the die-offs is also unknown: they may have occurred seasonally during low-level conditions or during low-level periods spanning many years or decades during which salinities or temperatures consistently exceeded the tolerances of the lake's fish populations. Determination of the seasonality of fish deaths through analyses of annuli formation on the Homestead fish elements could shed light on this issue. Such analyses could also potentially indicate changes in the age and size of initial reproduction of these fishes to more definitively test Smith's model of life history adaptation.

### CHANGE IN TAXONOMIC ABUNDANCE IN RELATION TO SALINITY AND TEMPERATURE

Decreasing lake levels and associated increases in water temperature and salinity are the likely cause of the fish die-offs and ultimately the permanent loss of Lake Bonneville's fishes that occurred sometime within the deposition of Stratum Ib (see below). Comparisons of the relative abundance of fishes with different temperature and salinity tolerances between Stratum Ia and Stratum Ib might inform on the dynamics of the die-off(s) in relation to these variables. Although the precise temperature and salinity tolerances of most of these fishes are, unfortunately, not well known, broad categories of tolerance to these variables can be defined from what data are available.

#### Salinity

The fishes represented within Stratum I of Homestead Cave can be divided into two groups on the basis of their relative tolerance to salinity. Species intolerant of saline waters include *Prosopium gemmifer*, *Prosopium abyssicola*, *Prosopium spilonotus*, *Catostomus ardens*, *Cottus bairdi* and *Cottus extensus*. These species have never been known to occur in even moderately saline waters. By contrast, *O. clarki* is represented by anadromous stocks in coastal drainages where individuals spend considerable portions of their lives well out to sea (see Wydoski and Whitney, 1979, p. 41). *Gila atraria* presently inhabit springs in the Great Salt Lake Desert of widely varying salinity (freshwater to 2.5% NaCl). In addition, laboratory experiments conducted on these fish indicate they can readily tolerate waters with salt (Na) con-

tents as high as 213 meq/L (Westenfelder and others, 1988).

Although most members of the large and diverse sculpin family (Cottidae) are benthic marine fishes, sculpins of the genus *Cottus* have invaded and adapted to inland freshwater lakes and streams. Both the cottids represented at Homestead Cave, *C. bairdi* and *C. extensus*, are found strictly in freshwater settings. Although it is possible these sculpin might be able to tolerate elevated salinities based on their evolutionary pedigree<sup>5</sup>, their modern distributions clearly indicate they prefer freshwater environments. Thus, I consider them salinity-intolerant taxa in the analyses that follow.

Table XXXI shows the relative abundance in Strata Ia and Ib of the two groups of fishes that differ in their tolerance to salinity.<sup>6</sup> The salinity-intolerant taxa dominate both Strata Ia and Ib and, assuming both *C. extensus* and *C. bairdi* are represented by the *Cottus* sp. materials in Stratum Ib, no extinctions of species susceptible to high salinities are evident within the Stratum I fauna. There is, however, a significant decline in the relative abundance of salinity intolerant taxa across the two divisions of Stratum I ( $X^2 = 4.31$ ,  $P < 0.05$ ). That relationship remains significant if the sculpin, taxa whose tolerance to salinity remains in some question, are excluded from the analysis ( $X^2 = 4.01$ ,  $P < 0.05$ ). In sum, taxa intolerant of elevated salinities dominate both components of Stratum I, but they are significantly underrepresented in the upper portion of that deposit (Stratum Ib). At least upon initial inspection, a declining lake level and associated increase in salinity appear to be registered in the Homestead Cave ichthyofauna.

#### Temperature

The Homestead fishes can also be divided into two groups according to their relative sensitivity to high water temperatures. *Catostomus ardens* and *Gila atraria* are known to thrive in water temperatures over 26.7°C and 31.1°C, respectively. The other fishes represented at Homestead Cave are, as a group, much more sensitive to high water temperatures.

*O. clarki* is most commonly found in cold water lakes and streams in western North America. Even though *O. clarki* occurs in Pyramid Lake, where surface water temperatures can reach as high as 23°C in the summer, the profundal water temperature of this lake remains a constant 6°C (Galat and others, 1981). Based on laboratory experiments, the upper lethal temperature for *O. clarki henshawi* is 23°C (Vigg and Koch, 1980). However, Behnke (1981, p. 101) reports an

Table XXXI

Numbers of identified specimens of salinity-tolerant and salinity-intolerant fish taxa from Strata Ia and Ib at Homestead Cave

	Stratum Ia	%	Stratum Ib	%
Salinity Tolerant				
<i>Gila atraria</i>	226	3.0	29	4.9
Salmoninae	279	3.7	23	3.9
Total	505	6.7	52	8.9
Salinity Intolerant				
<i>Prosopium</i>	6551	87.0	491	84.2
<i>Catostomus</i>	321	4.2	31	5.3
<i>Cottus</i>	197	2.6	9	1.5
Total	7069	93.0	531	91.1

unnamed subspecies of cutthroat trout in the headwaters of the Humboldt River, Nevada in waters up to 25.5°C. Optimum growth temperatures for trout are of course far lower (~16.5°C) than these lethal limits (Jobling, 1981).

Like virtually all members of the genus *Cottus*, both *C. bairdi* and *C. extensus* are found strictly in cool or cold water settings. There is no suggestion that these fish can tolerate warm water temperatures. The three *Prosopium* species represented at Homestead Cave are now endemic to Bear Lake where water temperatures do not exceed 14°C. In laboratory settings, *P. abyssicola*, *P. spilonotus*, and *P. gemmifer* develop debilitating abnormalities of the jaws when eggs are reared in temperatures over 5°C (Nielson, personal communication, 1998).

Table XXXII provides the abundance in Strata Ia and Ib of fishes that are sensitive to high water temperatures (*O. clarki*, *Cottus* and *Prosopium*) and those that are not (*Gila atraria* and *Catostomus ardens*). Although *O. clarki*, *Cottus* and *Prosopium* are present in both Strata Ia and Ib, there is a highly significant decline in their relative abundance across these stratigraphic divisions ( $X^2 = 7.41$ ,  $P < 0.01$ ). In other words, taxa that are intolerant of high water temperatures are underrepresented in Stratum Ib compared to Stratum Ia. Thus, an increase in water temperature also appears to be registered in the Homestead fish sequence.

### Temperature Versus Salinity

Because the whitefish and sculpin species are sensitive to both high temperatures and salinities and because *Gila atraria* is tolerant of both of these conditions, change in the relative frequencies of these taxa cannot help us discriminate which of these variables had the greatest influence on Lake Bonneville's fish populations as the lake regressed during the late Pleistocene. As a result, it is possible that one or the other of these variables alone caused the mass mortality and

extinctions of these fishes. Discriminating between the effects of temperature and salinity thus requires an analysis of change among taxa that are tolerant of one variable but not of the other. Of the major taxonomic groups represented at Homestead Cave, only *O. clarki* and *Catostomus ardens* meet this criteria. *O. clarki* is intolerant of high water temperatures but can readily adapt to increased salinity. *Catostomus ardens*, by contrast, can tolerate elevated water temperatures but is sensitive to increases in salinity. Change in the relative frequencies of *O. clarki* and *Catostomus ardens* across Strata Ia and Ib would allow us to estimate whether temperature or salinity provided the stronger limiting factor on fish rebounds or recolonizations across the period over which these materials accumulated.

Table XXXIII provides the numbers of identified salmonines (*O. clarki*) and *Catostomus* (*C. ardens*) for Strata Ia and Ib. *Catostomus ardens* are more abundant than *O. clarki* in both these sets of deposits and slightly more so in Stratum Ib (57%) compared to Stratum Ia (54%). That difference, however, is statistically insignificant ( $X^2 = 0.30$ ,  $P > 0.50$ ).

The analysis of change in fish size described above suggests that, as Lake Bonneville regressed episodically towards the end of the Pleistocene, its fish populations underwent a series of mass die-offs that were followed by brief rebounds or recolonizations. The analysis of change in relative abundance of species characterized by different salinity/temperature tolerances suggests that species tolerant of high salinities and/or temperatures were more successful at rebounding or reinvading the lake, although conditions were sufficiently fresh and cool to support the entire Bonneville fish fauna. It remains unclear, however, what the relative roles that temperature and salinity played in both limiting the success of these fish rebounds as the lake fluctuated and the ultimate extinction of the Lake Bonneville fish fauna.

Table XXXII

Numbers of identified specimens of temperature-tolerant and temperature-intolerant fish taxa from Strata Ia and Ib at Homestead Cave

	<u>Stratum Ia</u>	<u>%</u>	<u>Stratum Ib</u>	<u>%</u>
Temperature Tolerant				
<i>Gila atraria</i>	226	3.0	29	5.0
<i>Catostomus</i>	321	4.2	31	5.3
Total	547	7.2	60	10.3
Temperature Intolerant				
<i>Prosopium</i>	6551	86.5	491	84.2
Salmoninae	279	3.7	23	4.0
<i>Cottus</i>	197	2.6	9	1.5
Total	7027	92.8	523	89.7

Table XXXIII

Numbers of identified *Catostomus* and Salmonine specimens from Strata Ia and Ib at Homestead Cave

	<u>Stratum Ia</u>	<u>Stratum Ib</u>
<i>Catostomus</i>	321	31
Salmoninae	279	23



## CHRONOLOGY OF LATE QUATERNARY LAKE-LEVEL FLUCTUATIONS IN THE BONNEVILLE BASIN

It now seems clear that the Homestead Cave fish fauna resulted from a series of catastrophic die-offs associated with late Quaternary lake cycles in the Bonneville basin. Analysis of that fauna in relation to the detailed radiocarbon chronology provided by the Homestead deposits should thus shed light on our understanding of the timing of climatically controlled lake-level fluctuations in this region. To this end, I first examine the abundance of fish remains in the Homestead Cave deposits, relative to other vertebrates, to pinpoint the timing of the terminal Pleistocene extinction-recolonization cycles of Lake Bonneville's ichthyofauna. I then examine change in fish taxonomic composition across the Holocene sequence of deposits to inform on the chronology of fluctuations in Great Salt Lake. The results provide support for certain aspects of the lake-level chronologies based on core and shoreline data, but conflict with those chronologies in several important ways as well.

### Lake Level Fluctuations of Terminal Pleistocene Lake Bonneville

Table XXXIV provides the numbers of identified mammal and fish specimens for each of the Homestead strata. Figure 93 shows the abundance of fish remains, relative to mammals, throughout the Homestead sequence. As noted above, fish remains are clearly concentrated in Stratum I of Homestead Cave. They account for over 26% of the assemblage in Stratum I but comprise, in most cases, far less than 1% of the fauna in the higher strata.

To further pinpoint the stratigraphic break in the Homestead deposits after which fish remains become rare, I examined the distribution of fish materials within Stratum I itself. In the bulk sediment sample taken from the lower 10 cm of Stratum Ia, fish comprise 23.5% (807 of 3,434 specimens) of the entire vertebrate faunal assemblage. By contrast, fish comprise only 0.02% (10 of 3,896 specimens) of the vertebrate materials from the upper 10 cm of Stratum Ib: a figure very similar to the relative abundance of fishes throughout the rest of the column. The difference in the frequencies of fish and non-fish vertebrate specimens across these divisions is astronomically significant ( $X^2 = 955.34$ ,  $P < 0.0001$ ). Fish remains are thus largely confined to Stratum Ia, and the lower microlaminae of Stratum Ib.

Fecal pellets of woodrats (*Neotoma* sp.) from the lowest 5 cm of Stratum Ia, directly overlying bedrock, date to  $11,270 \pm 135$  yr B.P. (AA 14816),  $11,263 \pm 83$  yr B.P. (AA 16809),  $11,181 \pm 85$  yr B.P. (AA 16808), and  $11,065 \pm 105$  yr B.P. (AA 14817). Fecal pellets of woodrats taken directly from the upper 5 cm of Stratum Ib provided dates of  $10,350 \pm 80$  yr B.P. (AA 11818) and  $10,160 \pm 85$  yr B.P. (AA 11819). The die-offs of Lake Bonneville's fishes thus appear to have begun shortly after  $\sim 11.3$  ka<sup>7</sup> but were over sometime before  $\sim 10.4$  ka.

Based on studies of shoreline features and sediment stratigraphy, it has been suggested that Lake Bonneville declined to elevations approaching those of the modern Great Salt Lake soon after 13 ka. Sometime after 12.2 ka, the lake

Table XXXIV

Numbers of identified mammal and fish specimens by stratum at Homestead Cave

Stratum	Mammals	Fish	% Fish
XVIII	1047	8	0.08
XVII	15,548	117	0.08
XVI	6292	29	0.05
XV	—	5	—
XIV	—	57	—
XIII	—	101	—
XII	22,860	330	1.42
XI	10,096	65	0.06
X	6601	24	0.04
IX	22,088	52	0.02
VIII	8289	21	0.03
VII	13,905	36	0.03
VI	24,330	54	0.02
V	5109	8	0.02
IV	26,615	114	0.04
III	2884	51	1.73
II	7855	257	3.17
I*	10,275	3702	26.48
Total	183,798	5031	2.66

(\* ) Includes specimens from FS-63, the only provenience unit of Stratum I for which mammal materials were identified.

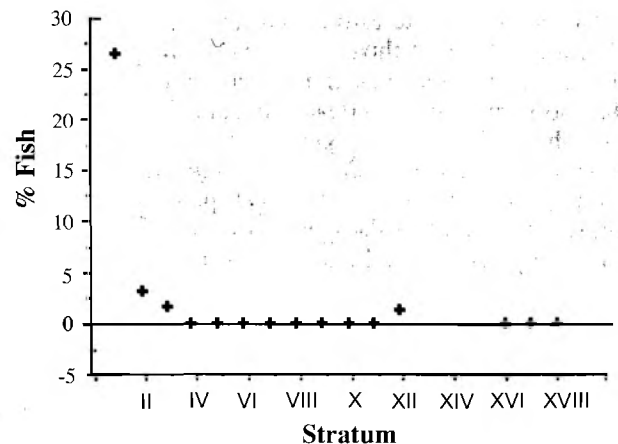


Figure 93. Abundance of fish specimens, relative to mammals, across the Homestead strata.

rebounded again to form the Gilbert shoreline complex, peaking between 10.9 and 10.3 ka (Benson and others, 1992; Currey, 1990; Oviatt and others, 1992; Thompson and others, 1990). The plant macrofossil record, however, indicates that summer temperatures and evaporation rates were substantially depressed between  $\sim 13$  and 11 ka, and suggests that a larger lake would have likely existed at this time (Rhode, chapter eleven).

Cold-water lake fish are extremely abundant at the very base of Stratum I, a context that provided four radiocarbon dates with a weighted average of  $11,201 \pm 76$  yr B.P. Thus, lake levels appear to have been sufficiently high ( $> \sim 1300$  m based on the strontium isotope analysis; Quade, chapter two) to support the entire Lake Bonneville fish fauna from Provo

times until ~11.2 ka. In the global climate scheme, this date corresponds with a brief, sharp, dry period, which Haynes (1991) has locally called the Clovis drought.

This was not, however, the end of fishes in Lake Bonneville and, subsequent to this first catastrophic die-off, at least one recolonization or rebound period occurred. The presence of this second, younger age-dominated, fish fauna can be interpreted in two ways. A Younger Dryas-age lake may have been too saline to contain fish and the fauna may simply represent a short period of lake-level fluctuation immediately following the initial die-off. Alternatively, there has been some suggestion that the lake may have supported fish populations during this period (Rosenfeld, 1991, p. 45, 1996; Grayson, 1993). Theoretical modeling and empirical analyses suggest that the uptake of salt by a growing lake from crustal efflorescences or from pore fluids found in lake basin sediments is a fairly slow process on the order of decades where it has been analyzed empirically (Lerman and Jones, 1973; Spencer and others, 1985). While it is not possible to estimate the rates of salinity uptake, it is possible a growing lake could have remained fresh for some time, closer to decades than centuries (B. Jones, personal communication, 1998), and may have supported the entire Lake Bonneville fish fauna, at least during the early to middle stages of its rise to the Gilbert level.

### Lake-Level Fluctuations of Great Salt Lake

As described above, Lake Bonneville was inhabited primarily by fishes now restricted to cold and freshwater habitats. However, the lake also supported populations of *Gila atraria*, a species that thrives in those settings, but is also abundant today in marshes and warmer, moderately saline, creeks and springs of the Great Salt Lake Desert. Based in part on the high degree of genetic similarity documented among now isolated populations of *Gila atraria* in the northern Bonneville basin, Rosenfeld (1991, p. 89) suggested that during wetter periods of the Holocene, Great Salt Lake may have become sufficiently diluted in places to support populations of the saline-tolerant *Gila atraria*. Even if *Gila atraria* could not have invaded Great Salt Lake during wetter cycles, the extent of local freshwater marshes, habitats these fish certainly would have inhabited, might be expected to vary positively with the extent of regional moisture and the elevation of the lake. Alternatively, if salinities of Great Salt Lake remained above the threshold of tolerance for *Gila atraria* even during its transgressions, an expanding lake may have drowned local freshwater marshes with highly saline water producing fish die-offs in these settings. In any case, *Gila atraria* frequencies should be linked to higher elevations of Great Salt Lake.<sup>8</sup>

Materials representing the Lake Bonneville fish fauna occur in very low frequencies above Stratum I in Homestead Cave and likely owe their presence in those contexts to limited mixing with that stratum. However, the *Gila atraria* materials in these upper strata may be derived not only from limited mixing with Stratum I but from Holocene-aged scavenging activities of owls as well. Insofar as substantial owl-based deposition of *Gila atraria* occurred in tandem with Holocene transgression-regression cycles of Great Salt Lake, then major peaks in the frequencies of *Gila atraria* within the Homestead deposits should signal those cycles.

Figure 94 shows the NISP values of *Gila atraria* across the Holocene-aged strata at Homestead Cave. The absolute abundances of *Gila atraria* exhibits two marked peaks: first within Stratum XII and second within Stratum XVII. While the absolute frequencies of any taxon can be expected to vary positively with the total sample of recovered bone, this factor does not appear to be the source of the two spikes in *Gila atraria* frequencies at Homestead Cave; the NISPs of *Gila atraria* are not significantly correlated with either the total mammal ( $r_s = -.284, P = .30$ ) or the total bird NISPs ( $r_s = .41, P = .10$ ) within the Homestead strata.

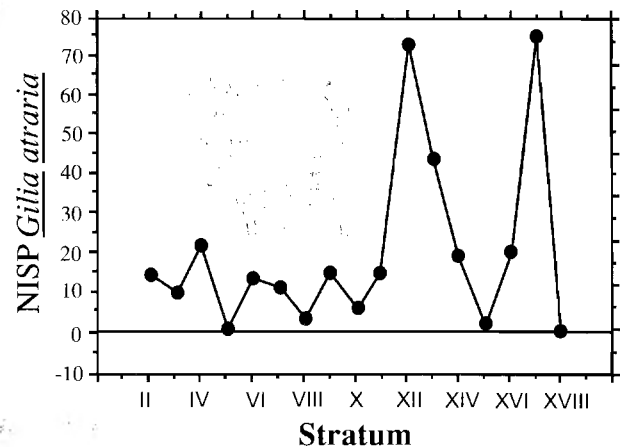


Figure 94. NISP of *Gila atraria* through the Holocene deposits of Homestead Cave (Stratum I is not included).

Several Holocene highstands of Great Salt Lake have been proposed. According to core and shoreline data, the most notable among them occurred between ~3 and 2 ka when the lake appears to have transgressed to a highstand of 1287 m and flooded the Great Salt Lake Desert (see chapter two; Murchison, 1989b; Currey, 1990; McKenzie and Eberlie, 1987; Mehringer, 1985). Although this transgression was clearly not high enough to allow the recolonization of the Lake Bonneville fish fauna, it may be recorded by the substantial increase in *Gila atraria* within Strata XII and XIII, contexts that provided radiocarbon dates of ~3400 and ~3480 yr B.P., respectively. The more dramatic increase in *Gila atraria* abundance occurs within Strata XVI and XVII, strata that provided radiocarbon dates of ~1200 B.P. and ~1020 B.P., respectively. Although a highstand of Great Salt Lake at this time has been documented from shoreline data, those data suggest it reached only to an elevation of ~1283 m and did not flood the Great Salt Lake Desert (Murchison, 1989a; Currey, 1990).

### SUMMARY

1. The substantial fish fauna from Homestead Cave appears to have been accumulated by scavenging owls. The limited available evidence suggests that owls utilize fish resources only in very unusual circumstances, such as when fish are stranded on shorelines or exposed in very shallow water. North American owls are not known to take live fish from deep, open water but will readily scavenge stranded

fish carcasses. An owl-based accumulation thus suggests that the Homestead fishes were derived from die-offs of local fish populations.

2. The Homestead Cave fish assemblage is represented by 11 species of mostly cold- and freshwater-adapted species; four of these represent the first records for Lake Bonneville. The *Salvelinus confluentus* and *Catostomus discobolus* specimens provide the first fossil evidence for these species in the entire Great Basin; the *Salvelinus* premaxilla also represents the first specimen record of any kind for this genus in the Great Basin. These records provide a wealth of information on fish biogeography in the Bonneville basin; the *Salvelinus* specimen should have implications for fisheries management in the region.

3. A model of life history evolution of Great Basin minnows and suckers (Smith, 1981) suggests that these fish attain sexual maturity earlier and attain smaller adult body sizes in unstable environments characterized by high adult mortality. A significant decline in the mean and maximum size of minnows and suckers was documented across the Stratum I deposits. This pattern suggests that the fauna resulted from a process involving a series of fish die-offs.

4. Taxa intolerant of high water salinities and temperatures are significantly underrepresented in Stratum Ib compared to Stratum Ia, even though these taxa dominate both sets of deposits. A clear signal of decreasing water depth and increasing temperature and/or salinity is thus registered in the fauna. The data do not, however, allow us to tease apart the relative roles that temperature and salinity played in affecting fish die-offs and subsequent recolonizations of the lake's fish fauna.

5. The initial post-Provo die-off of the Lake Bonneville fish fauna occurred at ~11.2 ka, suggesting that climatically controlled lake levels were sufficiently high to support this fauna until that time. This result calls into question current models of lake-level history that posit a substantial regression beginning at 13 ka. The entire Bonneville fish fauna may have rebounded or recolonized the lake with the Gilbert transgression, but was permanently eliminated from the lake shortly before ~10.4 ka, toward the middle or the end of the Gilbert cycle. A late Holocene highstand of Great Salt Lake appears to have occurred around ~3.4 ka to judge from a substantial increase in *Gila atraria* within Stratum XII. This is roughly consistent with the proposed transgression of Great Salt Lake between ~3 and 2 ka based on core and shoreline data, albeit slightly earlier. An even more dramatic increase in *Gila atraria* occurs within Stratum XVII, deposits that date to ~1 ka, and suggests that a transgression-regression cycle of Great Salt Lake occurred at this time as well. Such an event has also been recorded in shoreline and core data.

## ENDNOTES

<sup>1</sup> The identifications were based largely on comparisons with Recent fish specimens from the following collections: Division of Fishes, Museum of Zoology, University of Michigan; Department of Ichthyology, California Academy of Sciences; Division of Fishes, National Museum of Natural History; and The Utah Museum of Natural History.

<sup>2</sup> The single pharyngeal of *Richardsonius balteatus* was derived from deposits (F-17, FS-10-11) outside the column

sample representing either Stratum I or II, but mostly likely Stratum I. Aside from this specimen, materials from this provenience unit have not been identified.

<sup>3</sup> Only nine specimens of *Cottus echinatus* were collected prior to its extinction in the 1930s: the holotype UMMZ 177376, UMMZ 156794 (two specimens), USNM 197681 (two specimens), USNM 30808, USNM 27414 (Bailey and Bond, 1963, p. 2) BYU 29212, and BYU 29213. All of these specimens are preserved whole in fluid, with the exception of UMMZ 156794: G. Smith cleared and stained a partial (Ridewood dissection) cranium of this specimen. I had access to the latter specimen, BYU 29212, and BYU 29213. Diagnostic features of the preopercle can be readily examined from fluid-preserved specimens.

<sup>4</sup> As a frame of reference, the mean vertebral widths of a modern 450 mm SL *Catostomus ardens* and a 202 mm SL *C. discobolus* are 8.76 and 2.84 mm, respectively.

<sup>5</sup> Several *Cottus* species (see *C. asper*, prickly sculpin, *C. gulosus*, ruffle sculpin and *C. perplexus*, reticulate sculpin) that occupy coastal drainages in the Pacific Northwest are known to tolerate brackish waters (Wydoski and Whitney, 1979).

<sup>6</sup> In the analyses of temperature and salinity that follow, I assume the specimens identified as Salmoninae represent *O. clarki* since that species was the only member of this subfamily present in the materials of Strata Ia and Ib. Even if *Salvelinus confluentus* is represented in the salmonine material, this species has very similar temperature and salinity tolerances as *O. clarki*. Similarly, the materials identified as *Catostomus* sp. are assumed to represent *Catostomus ardens*. There is also no cost if this assumption is incorrect; the other *Catostomus* species represented at Homestead Cave, *C. discobolus*, has similar temperature and salinity tolerances to *C. ardens*.

<sup>7</sup> All of the following dates in this section refer to <sup>14</sup>C yr B.P.

<sup>8</sup> In this analysis, I assume the specimens identified as Cyprinidae represent *Gila atraria*, since *Gila atraria* represents well over 99% of the identified cyprinids at Homestead Cave.

## ACKNOWLEDGMENTS

I thank Gerald Smith for his generous assistance on many aspects of this project, including the examination of the specimen reported here as cf. *Salvelinus confluentus*, discovering the *Richardsonius balteatus* specimen and providing reference specimens. I also thank Virginia Butler, Richard E. Broughton, Dominique Rampton, Shannen Robson and Andrew Ugan for helpful comments on the manuscript; Bryce Nielsen and Scott Tolentino for help in the collection of reference specimens at Bear Lake; Dominique Rampton for helpful assistance in the lab; Marlene Lambert-Tempest for figures 79 and 85; Monson Shaver III for his work on the Homestead fish posters; Walter Klippel for unpublished information on the Caney Creek owl roost; Dennis Shiozawa for help with the *C. echinatus* specimens at Brigham Young University; and the following museums for access to reference material: Division of Fishes, Museum of Zoology, University of Michigan; Department of Ichthyology, California Academy of Sciences; Division of Fishes, National Museum of Natural History; and The Utah Museum of Natural History.