Terminal Pleistocene Fish Remains from Homestead Cave, Utah, and Implications for Fish Biogeography in the Bonneville Basin

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Eleven fish species were identified from Homestead Cave, Utah. The remains, concentrated in the lowest stratum of the deposit, were accumulated by owls between approximately 11,200 and 10,100 ^{14}C yr B.P. and likely represent fish associated with the final die-off of the Lake Bonneville fauna. Four of the species (*Salvelinus confluentus, Prosopium abyssicola, Catostomus discobolus, Richardsonius balteatus*) represent their first records for Lake Bonneville. The *S. confluentus* premaxilla is the first Quaternary specimen record for the genus in the Great Basin and suggests a southern range extension during the Pleistocene. The *C. discobolus* specimens represent the first fossil records for the subgenus *Pantosteus* in the Great Basin; their presence in Lake Bonneville documents a Pleistocene connection between two presently disjunct populations. The hyomandibulars of *Prosopium gemmifer* are different from Recent specimens in a pattern suggesting Holocene introgression with *Prosopium spilonotus*. The lack of *Cottus echinatus* and the presence of both *Cottus bairdi* and *Cottus extensus* may suggest the former species evolved in Utah Lake over the last approximately 10,000 yr B.P. The abundance of *Catostomus ardens* and the absence of *Chasmistes liorus* may reflect a restricted spatial distribution of the latter in Lake Bonneville.

JUST over 30 years have past since our first glimpse of Lake Bonneville's fish fauna was provided by the fish materials described from the Black Rock Canyon and Hot Springs sites of the northern Bonneville Basin (Smith et al., 1968). A total of eight fish species were identified from these deposits, and the taxonomic composition revealed that Lake Bonneville, the largest pluvial lake in the western hemisphere, contained a fauna strikingly similar to that of modern Bear Lake, a cold, high-elevation body of water located on the Utah-Idaho border. This clearly confirmed physiographic evidence that suggested Bear Lake was tributary to Lake Bonneville during pluvial times. The analysis also documented that the high degree of isolation and endemism evident among modern fishes of the Bonneville Basin is very recent in origin and that differentiation had occurred among several taxa during the Holocene. The exact ages of the deposits that produced these fish materials were not, however, well controlled. The Hot Springs locality is located near the Stansbury Shoreline Complex and thus may date to around 20,000 yr B.P. (Currey, 1990; Oviatt, 1997). The Black Rock Canyon locality is located below the Provo

shoreline, and gastropod shells associated with the fish remains there provided a single radiocarbon date of 12,860 ± 400 yr B.P. (Smith et al., 1968).

Since the description of these materials, only a few isolated fish bones derived from Lake Bonneville (Oviatt, 1984; Murchison, 1989) or its tributary streams (Mead et al., 1982) have been reported, and no additional species have been identified among them. The precisely dated ichthyofauna from Homestead Cave reported here represents the largest, well-stratified, and richest Pleistocene fish assemblage from the entire Bonneville Basin. Thus, this collection is unique in its potential to shed light on late Quaternary fish biogeography in the Bonneville Basin.

MATERIALS AND METHODS

Homestead Cave (HC) is a wave-constructed cavern in a limestone ridge located on the northwestern margin of the Lakeside Mountains, several kilometers west of the Great Salt Lake (Fig. 1). This ridge reaches a maximum elevation of 1615 m and lacks active springs or
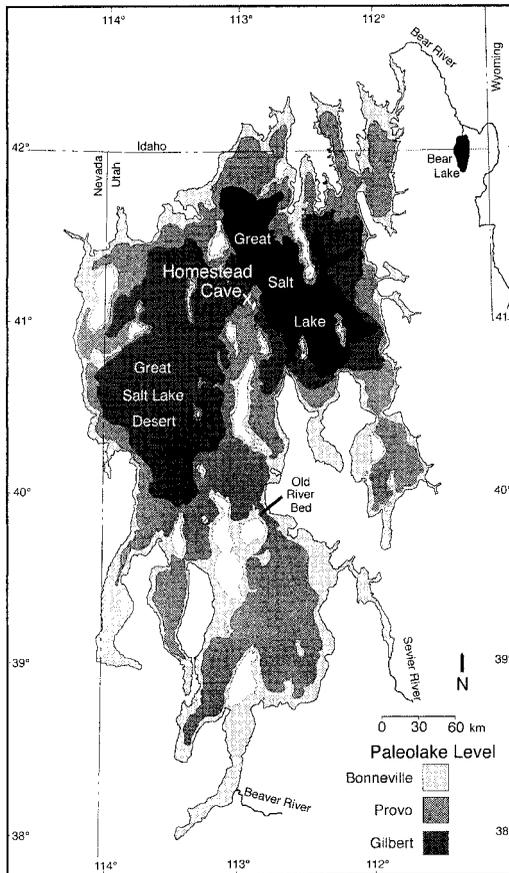
Fig. 1. Map of Bonneville Basin showing major paleolake levels and the location of Homestead Cave (adapted from Currey, 1990:202).

ward the back of the cave (Madsen et al., 2000). Materials excavated from the column were passed through a nested series of 1/4'' (6.4 mm), 1/8'' (3.2 mm), and 1/16'' (1.6 mm) screens. Twenty-one ^{14}C dates were obtained from organic materials (mostly mammal fecal pellets) recovered from the deposits and range from approximately 11,200 to 1000 ^{14}C yr B.P. The coherency of the ^{14}C results suggests that the deposits, where sampled, were laid down sequentially and cover the latest Pleistocene and virtually the entire Holocene (Madsen et al., 2000).

Although bone is extremely abundant throughout the HC sediments, fish remains were heavily concentrated in Stratum I, the basal stratum of the deposit which consists primarily of degraded organic material, including vast quantities of unfossilized bone. Samples were taken from the upper and lower divisions of the deposit to examine change in the fauna in relation to terminal Pleistocene lake level fluctuations and climate change. In addition to the fishes described below, 19 species of small mammals (Grayson, 1998; Madsen et al., 2000) and 28 species of birds (Livingston, 2000) have been identified from the Stratum I deposits.

Reported here are the fish remains from the 1/4'' and 1/8'' fractions of Stratum I and five noteworthy specimens present in higher strata of the cave. Six radiocarbon dates constrain the deposition of the materials from Stratum I between approximately 11,200 and 10,100 ^{14}C yr B.P (Table 1). These dates encompass the terminal Pleistocene stages of Lake Bonneville, including the post-Provo regression and the rise and fall of the Gilbert level (Currey 1990; Oviatt, 1997; Rhode and Madsen, 1995).

The vertebrate materials from HC appear to have been accumulated by owls. Owl pellet cones were observed on the floor of the cave when the excavation began, and many of the bones themselves, including the fish bones, still have owl pellet material (e.g., fur) adhering to

permanent streams. HC sits at an elevation of 1406 m: approximately 100 m below the Provo level of Lake Bonneville and approximately 90 m above the Gilbert level. The cave itself is 17 m in length and varies from 1 to 4.5 m wide and 5 to 6 m high.

In 1993 and 1994, a 1 m³ sample column was excavated to a depth of approximately 3 m to-

TABLE 1.   RADIOCARBON AND CALIBRATED AGES FROM STRATUM I, HOMESTEAD CAVE.

Provenience	Age (^{14}C yr B.P.)	Age (cal yr B.P.)[a]	Lab. No.
Upper 5 cm	10,160 + 85	11,706–12,105	AA 14819
Upper 5 cm	10,350 + 80	11,948–12,600	AA 14818
General	10,910 + 60	12,878–13,005	Beta 72205
Lower 5 cm	11,065 + 105	12,919–13,160	AA 14817
Lower 5 cm	11,181 + 85	13,018–13,187	AA 16808
Lower 5 cm	11,263 + 83	13,142–13,397	AA 16809
Lower 5 cm	11,270 + 135	13,039–13,431	AA 14816

[a] At 1 SD; calibrations from Stuiver et al., 1998.

them. Human artifacts are extremely rare in the deposits, and none of the bones exhibited evidence of human processing, such as cut-marks or burning. Evidence for carnivore involvement in the accumulation of the fauna is limited to three gnawed artiodactyl phalanges (Madsen et al., 2000). There is no evidence for water-laid deposits in Stratum I and no suggestion that the fish materials washed into the cave as the lake descended past its mouth.

Although the diet of most owls is predominantly comprised of small mammals, some species (e.g., *Tyto alba* and *Bubo virginianus*) use fish opportunistically, such as when they are stranded (dead or alive) on shorelines or partially exposed in shallow streams (Errington et al., 1940; Gallup, 1949; W. Klippel, pers. comm.). The bones of both *T. alba* and *B. virginianus* were present in the lower strata of HC (Livingston, 2000). Because the Stratum I vertebrate materials appear to have been accumulated by scavenging owls and date precisely to the very end of the Bonneville Lake cycle, and fish remains are comparatively rare in the upper, Holocene-aged deposits of the cave, the Stratum I fishes of HC likely represent the final die-off (or die-offs) of the Lake Bonneville ichthyofauna.

The fish remains from HC are presently housed at the Utah Geological Survey, Salt Lake City, Utah; the materials have not been assigned catalog numbers. The identifications were based largely on comparisons with Recent fish specimens from the following collections: UMMZ, CAS, UMNH, USNM, and BYU. Institutional abbreviations are as listed in Leviton et al. (1985). Diagnostic osteological characters were derived from the examination of multiple individuals (typically five or more) per species.

From a total of 13,537 fish specimens identified to at least the order level (Broughton, 2000; Broughton et al., 2000), 1994 were identified to below the generic level; only the latter are described here. Osteological specimens are listed under Material; the numbers of identified specimens are provided in parentheses. Taxonomy follows Robins et al. (1991).

RESULTS

Salmonidae—Trouts

cf. *Salvelinus confluentus* Suckley, 1858
Bull Trout

Material.—Premaxilla (1 fragment).

Oncorhynchus cf. *clarki* Richardson, 1836
Cutthroat Trout

Material.—Vomer (15), basioccipital (2), maxilla (2), premaxilla (31), ceratohyal (1), glossohyal (9).

Oncorhynchus clarki Richardson, 1836
Cutthroat Trout

Material.—Basibranchial (2).

Remarks—The cranial elements of the salmonines are heavily abraded and fragmentary. Accordingly, species level identifications were not possible for many elements that are diagnostic when they are intact. The single premaxilla fragment (Fig. 2A–B) identified as cf. *S. confluentus* closely matches Recent material and differs from that of *O. clarki*. The teeth of the premaxilla project mesially, as in *S. confluentus*, rather than vertically (i.e., 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 ridge 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); *O. clarki* lacks this feature. Unfortunately, the portion that bears the ascending process, a diagnostic feature of *S. confluentus*, is missing in the specimen (Norden, 1961). G. R. Smith (pers. comm.) concurs with the probable identification as *S. confluentus*. It is a remote possibility, however, that the specimen represents an aberrant *O. clarki*.

The elements identified as *O.* cf. *clarki* exhibit features that closely match with both *O. clarki* and *O. mykiss* but are unlike those of *S. confluentus*. The designation as *O.* cf. *clarki* for these specimens is based on the known distribution of trout in the Great Basin. Prior to their widespread anthropogenic dispersal in historic times, *O. mykiss* is known only from the extreme northwest of the Great Basin, and there is no suggestion that they ever could have occurred in the Bonneville Basin (Behnke, 1992; Smith, 1978).

The glossohyals were assigned to *Oncorhynchus* based on the pronounced medio-lateral ridge on the antero-ventral surface; the corresponding surface in *S. confluentus* is smooth. The vomers were identified as *Oncorhynchus* because the specimens exhibited a long, zigzag row of substantial teeth on an elongated vomeral shaft (Stearley and Smith, 1993). In *Salvelinus*, teeth occur in a patch on the head of the vomer, and the posterior extension of teeth is
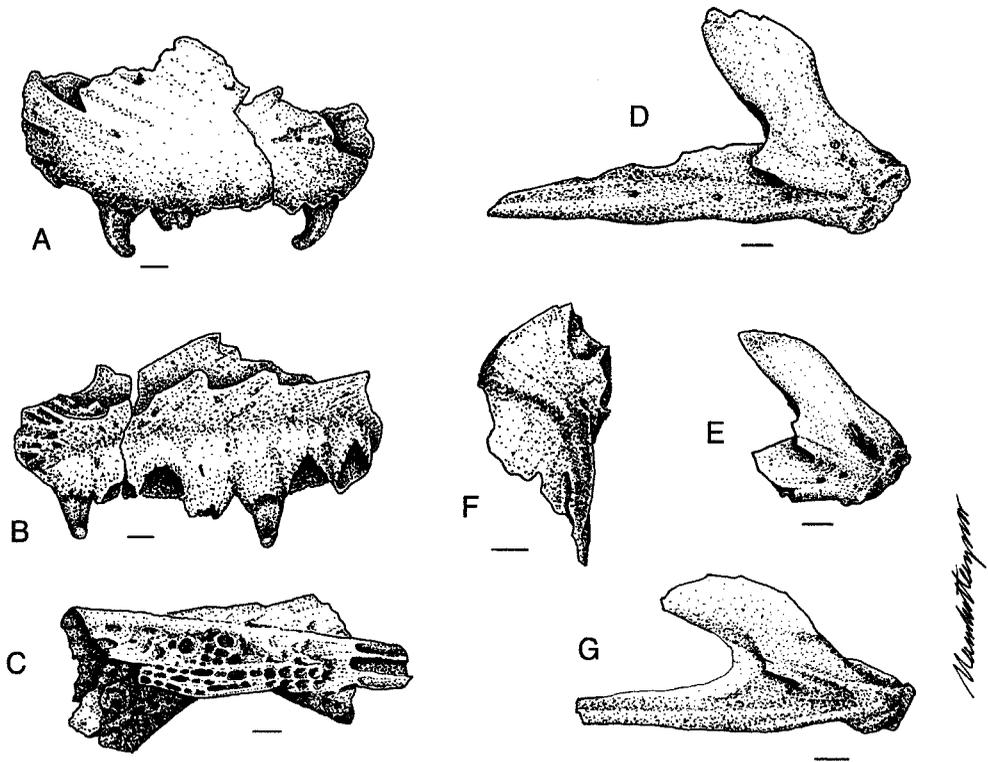
Fig. 2. Selected diagnostic salmonid elements from Homestead Cave. (A) Lateral view of right premaxilla of cf. *Salvelinus confluentus*; (B) mesial view of right premaxilla of cf. *S. confluentus* (same specimen as A); (C) basibranchial of *Oncorhynchus clarki* (dorsal view); (D) left dentary of *Prosopium spilonotus*; (E) left dentary of *Prosopium abyssicola* (the ventral ramus is broken off); (F) left hyomandibular of *Prosopium gemmifer* (the postero-lateral ridge is on the lower, right margin of the bone), (G) left dentary of *P. gemmifer*. Scale: bar length = 1 mm.

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). The ceratohyals are relatively deep for their length, as in *Oncorhynchus*; in *S. confluentus* these elements are more dorso-ventrally compressed (Stearley and Smith, 1993). The maxillae are referable to *Oncorhynchus* based on the orientation of the premaxillary process. In *Oncorhynchus,* this feature extends dorsally less than 10° from the main axis of the maxilla. In *Salvelinus*, the premaxillary process extends greater than 10° from the main axis of the maxilla (Stearley and Smith, 1993). As in *Oncorhynchus*, the basioccipitals represented at HC bear paired ventro-lateral walls that form a deep V-shaped furrow along the ventral portion of the element. In *Salvelinus*, the ventro-lateral walls are not as deep and are flattened ventrally to form a shelf for articulation with the posterior parasphenoid.

Two basibranchials (Fig. 2C) were identified as *O. clarki* because the dorsal surfaces have tooth bases; the basibranchials are untoothed in

O. mykiss (Norden, 1961; Stearley and Smith, 1993). The basibranchials also lack the sharp-edged ventral keel of *S. confluentus*.

The *Salvelinus* clade is known from Miocene deposits in both central Nevada and the Snake River Plain (Smith, 2000), yet no Quaternary-aged specimens, fossil or living, have previously been collected for *Salvelinus* in the Great Basin. The nearest modern specimen records for *S. confluentus* are from the Jarbidge drainage, a tributary of the Snake River in northeastern Nevada (Miller and Morton, 1952; Cavender, 1978) and from the Lost River system of the Snake River Plain (Hubbs and Miller, 1948). *Oncorhynchus clarki* is known from several other late Pleistocene deposits in the Bonneville Basin (Smith et al., 1968; Oviatt, 1984; Mead et al., 1982).

Prosopium spilonotus or *abyssicola* Snyder, 1919
Bonneville or Bear Lake Whitefish

Material.—Opercle (80), prootic (45), exoccipital (29), dentary (17), quadrate (7), ceratohyal (4).

Prosopium cf. *spilonotus* Snyder, 1919
Bonneville Whitefish

Material.—Dermethmoid (1), frontal (1), parietal (3), prootic (1), epiotic (2), maxilla (3), infraorbital (2), basioccipital (1), articular (5), quadrate (1), epihyal (3) ceratohyal (3), hyomandibular (11), preopercle (3), subopercle (3), supracleithrum (5), basipterygium (1), vertebrae (40).

Prosopium spilonotus Snyder, 1919
Bonneville Whitefish

Material.—Prootic (1), ceratohyal (6), opercle (4), dentary (23), quadrate (4).

Prosopium abyssicola Snyder, 1919
Bear Lake Whitefish

Material.—Dentary (8).

Prosopium gemmifer Snyder, 1919
Bonneville Cisco

Material.—Articular (29), basioccipital (23), ceratohyal (10), dentary (302), maxilla (42), opercle (286), prootic (9), hyomandibular (58), parasphenoid (2).

Remarks.—Four *Prosopium* species are native to the Bonneville Basin: *Prosopium williamsoni, P. spilonotus, P. abyssicola,* and *P. gemmifer*; the latter three are now endemic to Bear Lake. *Prosopium gemmifer* rarely attains lengths over 216 mm (TL), and *P. abyssicola* rarely exceeds 254 mm (McConnell et al., 1957; Sigler and Sigler, 1996). *Prosopium williamsoni* and *P. spilonotus* can exceed 400 mm (Sigler, 1951; McConnell et al., 1957). Because *P. williamsoni* was not identified, whereas *P. spilonotus* is well represented, all the *Prosopium* materials too large for *P. gemmifer* and *P. abyssicola* that lacked other diagnostic criteria were referred to as *P.* cf. *spilonotus*.

In *P. williamsoni*, the medial margin of the hyomandibular fossa of the opercle is squared-off; in *P. spilonotus* and *P. abyssicola* the medial margin of this feature is rounded. No reliable criteria were found to separate the opercles of *P. abyssicola* and *P. spilonotus*. The posterior-dorsal margin of the hyomandibular fossa in *P. gemmifer* uniquely extends to or very near the dorsal margin of the opercle. Thus, the fossa sits more atop the dorsal margin of the bone in *P. gemmifer* than in the other *Prosopium* species.

The coronoid process of the dentary varies systematically among the Bonneville Basin whitefish (Fig. 2D–E, G). Representing the an-

cestral condition, the coronoid process in *P. williamsoni* rises (dorsally) at a steep angle from the ventral ramus. 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 ventral ramus (Smith and Todd, 1993). *Prosopium spilonotus* and *P. abyssicola* represent the intermediate states of this feature in which (Smith and Todd, 1993) *P. spilonotus* is more similar to *P. williamsoni*, and *P. abyssicola* is more similar to *P. gemmifer*.

Because the anterior neurocranium is elongate in *P. gemmifer*, several features are distinctive. The dorsal margin of the body of the articular rises anteriorly at a very shallow angle from the quadrate fossa; this angle is much steeper in all of the other Bonneville Basin whitefish. The basioccipital in *P. gemmifer* is narrow relative to its length, compared to all of the other Bonneville Basin whitefish which had no distinguishing characters. In *P. gemmifer*, the ceratohyal is more elongate compared to the other local *Prosopium*.

The foramen in the ceratohyal is longer, relative to the length of the bone, in *P. spilonotus* than in *P. williamsoni,* but 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,* but this element lacked distinguishing characters in the remaining *Prosopium* species.

The ventro-lateral margin of the condyle of the quadrate 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 condyle. In *P. williamsoni*, a shallow concavity is present on the medial surface of the quadrate just dorsal to the condyle, but *P. spilonotus* lacks this feature.

In *P. spilonotus* and *P. abyssicola*, the anterior and dorsal margins of the pronounced concavity on the postero-medial surface of the prootic is 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 ectocranial aspect of the sphenotic condyle of the prootic is situated more dorsally on its body and projects less anteriorly than in *P. williamsoni*. In addition, the endocranial surface of the prootic is notably porous in *P. abyssicola* and *P. spilonotus* but smooth in *P. williamsoni*.

The degree of porosity on the endocranial surface of the exoccipital distinguishes *P. abys-*

TABLE 2.   HYOMANDIBULAR CONDYLAR RATIOS FOR LAKE BONNEVILLE AND RECENT *Prosopium gemmifer* AND *Prosopium spilonotus*.

Species (sample)	n	Mean	Range	SD	SE
P. gemmifer (HC)	17	0.49	0.35–0.15	0.064	0.015
P. gemmifer (Hot Springs)	27	0.45	0.38–0.54	—	0.017
P. gemmifer (Recent A)[a]	22	0.57	0.51–0.65	—	0.015
P. gemmifer (Recent B)	23	0.56	0.48–0.65	0.047	0.010
P. cf. *spilonotus* (HC)	11	0.53	0.46–0.61	0.050	0.015
P. spilonotus (Recent)	25	0.55	0.44–0.67	0.068	0.014

[a] From Smith et al. (1968:811)

sicola and *P. spilonotus*, as a group, from *P. williamsoni*. The anterior surface between the pterotic and epiotic condyles is porous in *P. abyssicola* and *P. spilonotus* but smooth in *P. williamsoni*.

In *P. gemmifer*, the postero-lateral ridge of the hyomandibular is less flared posteriorly than in the other *Prosopium* (Fig. 2F; Smith et al., 1968). In addition, the angle formed between the main axis of the ventral margin 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. The hyomandibular lacks distinguishing characters in the remaining *Prosopium* species.

Smith et al. (1968) identified differences in the shape of the hyomandibular between *P. gemmifer* from Lake Bonneville and those from Recent Bear Lake. The fossil hyomandibulars of *P. gemmifer* from the Hot Springs locality differed from Recent specimens in having a more perpendicular postero-lateral ridge and a narrower gap between the dorsal and opercular condyles. The latter difference was evident in the ratio of the distance between the two condyles and the length of the dorsal condyle, which was substantially lower in the fossil form than in the sample
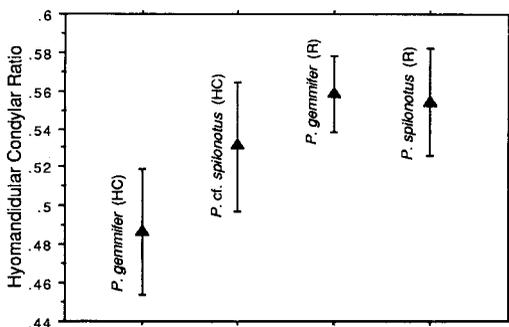

Fig. 3.   Comparison of the ratios of the distance between the dorsal and opercular condyles to the length of the dorsal condyle of the hyomandibular for the HC and Recent (R) *Prosopium gemmifer* and *Prosopium spilonotus*. Black triangles indicate the means; vertical bars indicate 95% confidence intervals.

of Recent specimens from Bear Lake. Those differences were interpreted as evidence for the further specialization (i.e., elongation) of the jaw structure in *P. gemmifer* over the last approximately 11,000 yr and were substantial enough to suggest that the Pleistocene and Recent forms may even represent separate species (Smith et al., 1968; Smith, 1981).

Table 2 provides the hyomandibular condylar ratios for the fossil and Recent *P. gemmifer* materials provided by Smith et al. (1968) as well as those from the HC *P. gemmifer* and an additional Recent sample from Bear Lake. The ratios are also provided for the sample of *P.* cf. *spilonotus* hyomandibulars recovered from HC as well as a Recent sample of *P. spilonotus* from Bear Lake. These data show that the hyomandibular morphology of the two Lake Bonneville samples of *P. gemmifer*, Hot Springs and HC, are similar with ratios of 0.45 ± 0.017 and 0.49 ± 0.015, respectively. The ratios from the two Recent samples of this species are nearly identical and are substantially higher (sample A = 0.57 ± 0.015, sample B = 0.56 ± 0.010) than the Pleistocene samples. The increase in this ratio documented between the fossil and Recent samples of *P. gemmifer* is toward *P. spilonotus* (Fig. 3). The sample of *P. gemmifer* from HC is different from Recent *P. gemmifer* (sample B; $t = -4.13$, $P < 0.001$) and both *P. spilonotus* from HC ($t = -1.96$, $P = 0.06$) and Recent *P. spilonotus* ($t = -3.25$, $P < 0.01$). However, Recent *P. gemmifer* does not differ from either the HC sample of *P. spilonotus* ($t = -1.57$, $P > 0.10$) or the Recent sample of the latter ($t = 0.25$, $P > 0.50$). There is also no difference between the HC and Recent samples of *P. spilonotus* ($t = -1.01$, $P > 0.30$).

Insofar as these differences are reflecting approximately 11,000 yr of time, *P. gemmifer* has come to be phenotypically more similar to *P. spilonotus* over this interval; *P. spilonotus,* however, has not changed. Although the evolutionary mechanisms and significance of this are not clear, it is possible that introgression of morphological characters from *P. spilonotus* to *P. gem-*

mifer has occurred during their Holocene occupation of Bear Lake. Indeed, many examples of hybridization are known among coregonid populations (Svardson, 1970; Smith, 1992) including *Prosopium* populations from Bear Lake. Sigler and Miller (1963) reported three fish from Bear Lake they believed to be *P. gemmifer/ P. spilonotus* hybrids. White (1974) also reported ''*P. gemmiferum*-like'' fish from Bear Lake, suggesting they resulted from combinations of *P. gemmifer* and either *P. spilonotus* or *P. abyssicola*.

Of the four species of whitefish that occur in the Bonneville Basin today, the three Bear Lake endemics are present in the HC fauna: *P. spilonotus, P. gemmifer,* and *P. abyssicola.* The former two have previously been identified from Lake Bonneville deposits (Smith et al., 1968), but this represents the first records for *P. abyssicola* for the lake.

Prosopium williamsoni, was not identified in the HC deposits. The widespread *P. williamsoni* has been reported in Bear Lake (Kemmerer et al., 1923) but has been extremely rare in that setting throughout historic times. McConnell et al. (1957) suggested that the few *P. williamsoni* reported in Bear Lake may have drifted in from the Bear River.

Cyprinidae—Minnows

Gila atraria Girard, 1856
Utah Chub

Material.—Frontal (40), ethmoid (4), infraorbital (2), vomer (6), parietal (29), pterotic (30), basioccipital (29), parasphenoid (2), articular (9), dentary (43), premaxilla (1), maxilla (11), posttemporal (7), quadrate (25), epihyal (14), ceratohyal (23), urohyal (8), pharyngeal (154), hyomandibular (34), opercle (49), preopercle (26), cleithrum (45), supracleithrum (3), pectoral fin spine (9), basipterygium (9), scapula (5), coracoid (3), supraorbital (1), supraoccipital (1), 1st vertebra (8), 2nd vertebra (16), 3rd vertebra (4), 4th vertebra (2), Weberian apparatus (8).

Richardsonius balteatus Richardson, 1836
Redside Shiner

Material.—Pharyngeal (1).

Remarks.—Six cyprinid species are native to the Bonneville Basin: *G. atraria, Gila copei, Iotichthyes phlegethontis, Rhinicthys cataractae, Rhinichthys osculus,* and *R. balteatus.* With the exception of *G. atraria*, these fishes rarely attain total 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, the size and robusticity of elements was used to identify *G. atraria* from the HC materials for elements that lacked other diagnostic criteria.

The pharyngeals of *G. atraria* have a unique tooth formula (2,5-4,2), are exceptionally robust, and exhibit pronounced grinding surfaces and terminally hooked tips (Fig. 4A). The pharyngeals of *R. balteatus* (Fig. 4B) have delicate and slender bodies and teeth and a distinctively squared-off margin of the lateral surface of the bone. The cyprinid maxillae are referrable to *G. atraria* based on the steep anterior and posterior margins of the dorsal ramus, and the wide breadth and flattened dorsal extremity of this process. The postero-ventral plate of the basioccipital is relatively narrow for its length in *Gila atraria* and the lateral margins decurve ventrally to form a pronounced concavity.

Gila atraria is native to the Bonneville Basin, the Snake River above Shoshone Falls, and the lower Wood River system, Idaho (Rosenfeld, 1991). *Gila atraria* has been reported from three other late Pleistocene fossil localities in the Bonneville Basin (Smith et al., 1968; Mead et al., 1982; Murchison, 1989).

Richardsonius balteatus is widely distributed in western North America (Sigler and Miller, 1963; Sigler and Sigler, 1996). The HC specimen represents the first record of this species for Lake Bonneville.

Catostomidae—Suckers

Catostomus ardens Jordan and Gilbert, 1881
Utah Sucker

Material.—Dentary (73), maxilla (74), premaxilla (16).

Catostomus discobolus Cope, 1872
Bluehead Sucker

Material.—Dentary (1), Stratum VI; maxilla (3), Stratum IX; dentary (1), Stratum X.

Remarks.—Four catostomid species are native to the Bonneville Basin: *Chasmistes liorus, C. ardens, C. discobolus*, and *Catostomus platyrhynchus*. Both *C. liorus* and *C. ardens* can reach substantial sizes (> 600 mm TL), whereas *C. discobolus* and *C. platyrhynchus* (subgenus *Pantosteus*) reach maximum lengths of 457 mm 305 mm, respectively (Sigler and Sigler, 1996). Hence, size was used to rule out the latter two species for certain large-sized catostomid specimens that lacked other diagnostic criteria.
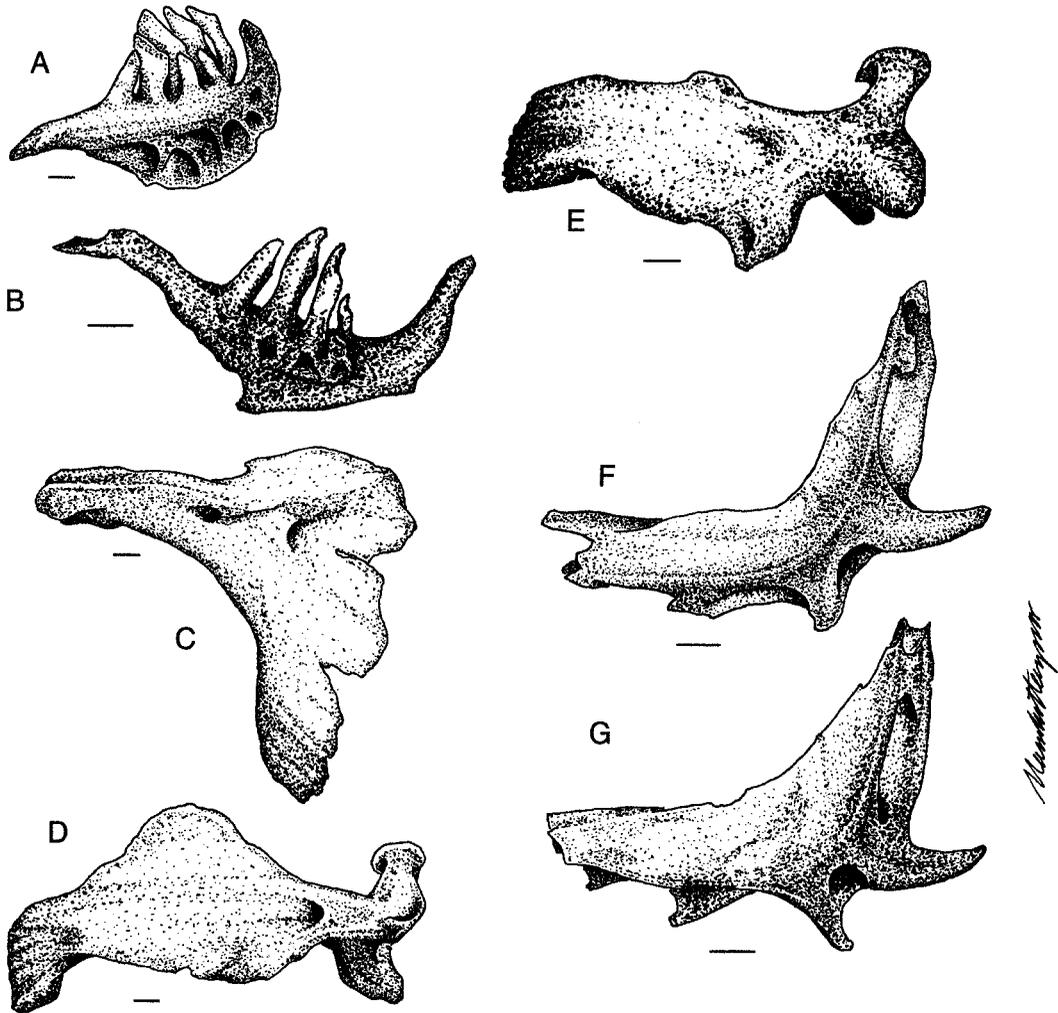
Fig. 4. Selected diagnostic cyprinid, catostomid, and cottid elements from Homestead Cave. (A) Left pharyngeal tooth of *Gila atraria*; (B) right pharyngeal tooth of *Richardsonius balteatus*; (C) left dentary of *Catostomus ardens*; (D) right maxilla of *Catostomus ardens*; (E) right maxilla of *Catostomus discobolus*; (F) left preopercle of *Cottus bairdi*; (G) left preopercle of *Cottus extensus*. Scale: bar length = 1 mm.

The angle and length of the gnathic ramus relative to the posterior body of the dentary is slightly obtuse and short in *C. ardens* (Fig. 4C) but is more obtuse and longer in *C. liorus*. This gives *Chasmistes* a longer more antero-mesially curved ramus than *C. ardens*. In addition, the angle of the dentary symphysis is parallel to the gnathic ramus in *C. ardens* but is subparallel in *C. liorus* (Miller and Smith, 1981). In *C. platyrhynchus* and *C. discobolus,* the gnathic ramus is dramatically foreshortened and mesially deflected, as in all species of the subgenus *Pantosteus* (Smith, 1966). 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.*

The anterior constriction or neck of the maxilla is thicker in *C. ardens* (Fig. 4D) compared to *C. liorus* (Miller and Smith, 1981). A nearly semihemispherical ridge is present along the antero-ventral margin of the neck in *C. ardens,* whereas this feature is not well developed in *Chasmistes*. The anteroventral (premaxillary) process projects at a right angle from the long axis of the maxilla posterior to the dorso-anterior process (head) in *C. ardens*. In *C. 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). The ventral keel is also more well developed in *C. ardens* compared to *C. liorus* (Miller and Smith, 1981); both these species

have well-developed dorsal keels. The maxillae of *C. discobolus* (Fig. 4E) and *C. platyrhynchus* are robust, lack dorsal keels, and are dissimilar to both *C. ardens* or *C. liorus* (Smith, 1966) and to each other. The posterior margin of the ventral keel slopes more steeply (anteriorly) in *C. platyrhynchus* compared to *C. discobolus*.

In *C. liorus*, the maximum medial-lateral length (horizontal limb) of the premaxilla is longer than the maximum dorso-ventral (vertical limb) length. In *C. ardens*, the maximum medial-lateral length of the premaxilla is considerably shorter than the maximum dorsal-ventral length (Miller and Smith, 1981). 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 anterior-medial protuberance and is anteriorly deflected; *C. ardens* lacks this feature. The horizontal limbs of *C. discobolus* and *C. platyrhynchus* are more curved, producing a marked convexity of the anterior surface.

Catostomus ardens is known from two other Lake Bonneville deposits (Smith et al., 1968; Oviatt, 1984), whereas no other *Pantosteus* fossils are known from the Great Basin (Smith, 2000).

Cottidae—Sculpins

Cottus cf. *bairdi* Girard, 1850
Mottled Sculpin

Material.—Preopercle (1).

Cottus bairdi Girard, 1850
Mottled Sculpin

Material.—Preopercle (6).

Cottus extensus or *echinatus* Bailey and Bond, 1963
Bear Lake or Utah Lake Sculpin

Material.—Preopercle (12).

Cottus extensus Bailey and Bond, 1963
Bear Lake Sculpin

Material.—Preopercle (5).

Remarks.—Four species of sculpin are known from the Bonneville Basin: *Cottus beldingi, C. bairdi, C. extensus*, and *C. echinatus*, a Utah Lake endemic that is now extinct. Features of the preopercle provide the most reliable osteological means of distinguishing these species (Bailey and Bond, 1963; Smith et al., 1968) and were used exclusively to identify the sculpin species represented.

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 (Fig. 4F; see also Smith et al., 1968). 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 because of the strong osteological similarity of these species and the small number (n = 3) of Recent *C. echinatus* reference specimens available for comparison.

In *C. echinatus*, the third spine projects more ventrally (less anteriorly) compared to *C. extensus* (Fig. 4G). Using these criteria, *C. bairdi* and *C. extensus* are demonstrably represented in the HC fauna, but *C. beldingi* and *C. echinatus* are not. Both *C. bairdi* and *C. extensus* have been identified from the Hot Springs and Black Rock Canyon localities of Lake Bonneville (Smith et al., 1968).

DISCUSSION

In their landmark synthesis of the biogeographic history of Great Basin fishes, Hubbs and Miller (1948:25) concluded that a clearer understanding of this subject would emerge ''if we had more than the present dribble of paleontological data on the fishes.'' Yet, unfortunately, Pleistocene-aged fish assemblages are still extremely uncommon. The rich, well-dated fish collection from HC provides a rare snapshot of the fishes that inhabited Lake Bonneville as it receded at the close of the Pleistocene and adds to our knowledge of the Quaternary biogeographic history of the region.

A total of 1994 fish bones identifiable to below the generic level were recovered from HC. The bones, concentrated in lowest stratum (I) of the cave, appear to have been deposited by scavenging owls between approximately 11,200 and 10,100 ^{14}C yr B.P. These dates encompass the final regressions of Lake Bonneville at the very end of the Pleistocene, and the assemblage probably represents the final die-off or die-offs of the Lake Bonneville fish fauna. Eleven species are represented in the collection, five more than the total derived from the previously described Lake Bonneville collections. *Prosopium gemmifer* is the best represented species in the assemblage (761 specimens), followed by *G. atraria* (660 specimens), and the conjoined sample of *P. spilonotus* and *P. abyssicola* (309). *Proso-*

pium gemmifer was also the best represented taxon at Hot Springs and Black Rock Canyon (Smith et al., 1968) and has been one of the most abundant species in Bear Lake throughout historic times (McConnell et al., 1959).

Four fish species previously unknown to have inhabited Lake Bonneville are represented: cf. *S. confluentus, P. abyssicola, C. discobolus,* and *R. balteatus. Chasmistes liorus* and *C. echinatus* are noteworthy for their absence.

The most surprising aspect of the HC fauna is the probable presence of *S. confluentus.* This represents the first specimen record for the genus *Salvelinus* in the Great Basin during Quaternary times. A single historic account of char in the Bonneville Basin was, however, provided in the early 19th century by J. K. Townsend (1978) whose account has also been considered "dubious" (Hass and McPhail, 1991:2204).

The Bonneville system may have been colonized by *S. confluentus* from the Snake River system when Lake Bonneville overflowed into the Snake approximately 15,000 yr ago. Alternatively, *S. confluentus* could have reached the Bonneville system sometime after approximately 50,000 yr ago when Lake Thatcher of southern Idaho, filled by the Bear River, began to spill southward into the Bonneville Basin (Bouchard et al., 1998; but see also Bright 1963, 1967).

For a species as large as *S. confluentus,* the presence of only a single specimen at HC suggests that even by approximately 11,200 ^{14}C yr B.P., they were uncommon in the Bonneville Basin, or at least in Lake Bonneville. If *S. confluentus* was ever abundant in the Bonneville system, their decline appears to have begun before the Pleistocene-Holocene transition. The suggestion that *S. confluentus* was once a native species to cold waters of the Bonneville Basin may have implications for the modern management of this species.

Prosopium abyssicola, P. spilonotus, and *P. gemmifer,* apparently evolved from a *P. williamsoni-* like ancestor, the more widespread and morphologically less-derived western whitefish species (Smith and Todd, 1993). Where and when the lacustrine whitefish now endemic to Bear Lake speciated remains unknown, but most likely it occurred in one of three lakes: Lake Bonneville, Pleistocene Lake Thatcher, or Bear Lake itself (Miller 1965:578). The previous documentation of *P. spilonotus* and *P. gemmifer* from Lake Bonneville deposits has indicated that they existed in that lake since the late Pleistocene. The evidence presented here that *P. abyssicola* also inhabited Lake Bonneville indicates they too evolved sometime before the late Pleistocene and eliminates the possibility that this spe-

cies diverged during the Holocene in Bear Lake.

Differences are evident in the morphology of the hyomandibular between the HC sample of *P. gemmifer* and their modern counterparts in Bear Lake. The change is in the direction toward the morphology of *P. spilonotus,* a less specialized member of the genus. This suggests that introgression of characters from *P. spilonotus* to *P. gemmifer* has occurred during the Holocene.

The presence of only a single pharyngeal of the tiny *R. balteatus* may in part be function of recovery bias. Analysis of the as yet unexamined 1/16" fraction of the HC fish materials may also document the presence of *R. osculus,* another widespread diminutive minnow of the Bonneville Basin, and additional *Cottus* spp. Because *R. balteatus* specimens were previously unknown from Lake Bonneville faunas but were present in Pliocene Lake Idaho has led to the suggestion that this species entered the Bonneville Basin from the Snake system as recently as about 12,000 yr ago (Sigler and Sigler, 1996:24). 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 fauna from HC has also provided the initial record of *C. discobolus* in Lake Bonneville and the only fossil record of the subgenus *Pantosteus* in the Great Basin. Although five specimens were recovered from Strata VI, IX, and X, contexts that provided mid-Holocene-aged radiocarbon dates, they probably owe their presence in those strata to mixing with Stratum I.

Although *C. discobolus* occur almost exclusively in stream or river habitats, a lake population has been reported for Lower Green River Lake, Wyoming (Sigler and Miller, 1963). Today, two disjunct sets of 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 distribution pattern led Smith (1966) to suggest that the Weber River populations 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 *C. 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 HC indicates not only that they occurred in Lake Bonneville but that they ranged widely across the lake. Because *C. discobolus* is a stream-adapted species, their presence also im-

plies that populations of these fish had adapted to some aspect of the lacustrine environments of Lake Bonneville or suitable fluvial environments occurred near HC in the past.

Chasmistes liorus is endemic to the shallow eutrophic waters of Utah Lake today, where it has experienced substantial introgression with *C. ardens* and is noteworthy for its absence at HC (Miller and Smith, 1981). Miller and Smith (1981) reported a fragmentary coracoid and dentary referable to *C.* cf. *liorus* from the Black Rock Canyon locality. Hyomandibulars assigned to *Chasmistes* sp. were also reported by Bright (1967) from Late Pleistocene sediments in the Thatcher Basin (Miller and Smith, 1981). Its absence might suggest a restricted spatial distribution of these fish in Lake Bonneville, resulting from unknown environmental factors, at least during terminal Pleistocene times. *Chasmistes liorus* may already have been sequestered in the Utah Lake basin by approximately 11,200 ^{14}C yr B.P.

Smith et al. (1968) suggested that *C. extensus* occurred in Lake Bonneville and Bear Lake during the late Pleistocene and underwent little evolution in the relatively cold and stable environment of Bear Lake during the Holocene. In contrast, they argued that in Utah Lake—the shallow, unstable low-elevation remnant of Lake Bonneville—*C. echinatus* diverged from a relictual *C. extensus* population over the last approximately 11,000 yr. This scenario was based on the historical distributions of these fishes as well as the fact that *C. extensus* was known from the fossil record of Lake Bonneville, but *C. echinatus* was not. Because the HC deposits failed to produce the remains of *C. echinatus* but *C. extensus* is demonstrably present in the assemblage, the scenario of Smith et al. (1968) is supported.

LITERATURE CITED

BAILEY, R. M., AND C. E. BOND. 1963. Four new species of freshwater sculpins, genus *Cottus*, from western North America. Occ. Pap. Mus. Zool. Univ. Mich. 634:1–27.

BEHNKE, R. J. 1992. Native trout of western North America. American Fisheries Society Monograph 6, Bethesda, MD.

BOUCHARD, D. P., D. S. KAUFMAN, A. HOCHBERG, AND J. QUADE. 1998. Quaternary history of the Thatcher Basin, Idaho, reconstructed from the ^{87}Sr/^{86}Sr and amino acid composition of lacustrine fossils: implications for the diversion of the Bear River into the Bonneville Basin. Palaeogeogr. Palaeoclimatol. Palaeoecol. 141:95–114.

BRIGHT, R. C. 1963. Pleistocene Lakes Thatcher and Bonneville, southeastern Idaho. Unpubl. Ph.D. diss., Univ. of Minnesota, Minneapolis.

———. 1967. Late-Pleistocene stratigraphy in Thatcher basin, southeastern Idaho. Tebiwa 10:1–7.

BROUGHTON, J. M. 2000. The Homestead Cave ichthyofauna. *In*: Late Quaternary paleoecology in the Bonneville Basin. D. B. Madsen, D.K. Grayson, and D. Rhode (eds.). Utah Geological Survey Bulletin 130, Salt Lake City.

———, D. B. MADSEN, AND J. QUADE. 2000. Fish remains from Homestead Cave and lake levels of the past 13,000 years in the Bonneville Basin. Quat. Res. 52:xxx–xxx.

CAVENDER, T. M. 1978. Taxonomy and distribution of the bull trout, *Salvelinus confluentus* (Suckley), from the American northwest. Calif. Fish Game 64:139–174.

CURREY, D. R. 1990. Quaternary paleolakes in the evolution of semidesert basins, with emphasis on Lake Bonneville and the Great Basin, U.S.A. Palaeogeogr. Palaeoclimatol. Palaeoecol. 76:189–214.

ERRINGTON, P., F. HAMMERSTROM, AND F. N. HAMMERSTROM JR. 1940. The Great horned owl and its prey in north-central United States. Iowa Agric. Exp. Stn. Res. Bull. 277:757–850.

GALLUP, F. N. 1949. Banding recoveries of *Tyto alba*. Bird-Banding 20:150.

GRAYSON, D. K. 1998. Moisture history and small mammal community richness during the latest Pleistocene and Holocene, northern Bonneville Basin, Utah. Quat. Res. 49:330–334.

HASS, G. R. AND J. D. McPHAIL. 1991. Systematics and distributions of dolly varden (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*) in North America. Can. J. Fish. Aquat. Sci. 48:2191–2211.

HUBBS, C. L., AND R. R. MILLER. 1948. Zoological evidence: correlation between fish distribution and hydrographic history in the desert basins of the western United States, p. 17–144. *In:* The Great Basin, with emphasis on glacial and postglacial times. Univ. of Utah Biology Series 10, Salt Lake City.

KEMMERER, G., J. F. BOVARD, AND W. R. BOORMAN. 1923. Northwestern lakes of the United States; biological and chemical studies with reference to possibilities in production of fish. U.S. Bur. Fish. Fish Bull. 39:51–140.

LEVITON, A. E., R. H. GIBBS JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology. Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.

LIVINGSTON, S. 2000. The Homestead Cave avifauna. *In:* Late Quaternary Paleoecology in the Bonneville Basin. D. B. Madsen, D. K. Grayson, and D. Rhode (eds.). Utah Geological Survey Bulletin 130, Salt Lake City.

MADSEN, D. B., D. K. GRAYSON, AND D. RHODE. 2000. Late Quaternary paleoecology in the Bonneville Basin. Utah Geological Survey Bulletin 130, Salt Lake City.

MCCONNELL, W. J., W. J. CLARK, AND W. F. SIGLER. 1957. Bear Lake: its fish and fishing. Utah State Department of Fish and Game, Idaho Department of Fish and Game, Wildlife Management Department of Utah State Agricultural College, Logan.

MEAD, J. I., R. S. THOMPSON, AND T. R. VAN DEVENDER. 1982. Late Wisconsinan and Holocene fauna from Smith Creek Canyon, Snake Range, Nevada. Trans. San Diego Soc. Nat. Hist. 20:1–26.

MILLER, R. R. 1965. Quaternary freshwater fishes of North America, p. 569–581. *In:* The Quaternary of the United States. H. E. Wright Jr. and D. G. Frey (eds.). Princeton Univ. Press, Princeton, NJ.

———, AND W. M. MORTON. 1952. First record of the dolly varden *Salvelinus malma* from Nevada. Copeia 1952:207–208.

———, AND G. R. SMITH. 1981. Distribution and evolution of *Chasmistes* (Pisces: Catostomidae) in western North America. Occasional Papers of the Museum of Zoology, Univ. of Michigan. 696, Ann Arbor.

MURCHISON, S. B. 1989. Utah chub (*Gila atraria*) from the latest Pleistocene Gilbert shoreline, west of Corrine Utah. Great Basin Nat. 49:131–133.

NORDEN, C. R. 1961. Comparative osteology of representative salmonid fishes with particular reference to the grayling (*Thymallus arcticus*) and its phylogeny. J. Fish. Res. Bd. Can. 18:679–791.

OVIATT, C. G. 1984. Lake Bonneville stratigraphy at the Old River Bed and Leamington, Utah. Unpubl. Ph.D. diss., Univ. of Utah, Salt Lake City.

———. 1997. Lake Bonneville fluctuations and global climate change. Geology 25:155–158.

RHODE, D. AND D. B. MADSEN. 1995. Late Wisconsin vegetation in the northern Bonneville Basin. Quat. Res. 44:246–256.

ROBINS, C. R., R. M. BAILEY, C. E. BOND, J. R. BROOKER, E. A. LACHNER, R. N. LEA, AND W. B. SCOTT. 1991. Common and scientific names of fishes from the United States and Canada. 5th ed. American Fisheries Society, Spec. Publ. 20., Bethesda, MD.

ROSENFELD, M. J. 1991. Systematic studies of members of the genus *Gila* (Pisces: Cyprinidae) from the Great Basin and Colorado River: protein electrophoretic and cytogenetic variation. Unpubl. Ph.D. diss., Univ. of Utah, Salt Lake City.

SIGLER, W. F. 1951. The life history and management of the mountain whitefish *Prosopium williamsoni* (Gi-
rard) in Logan River, Logan, Utah. Utah State Agricultural College Bulletin 347, Logan.

———, AND R. R. MILLER. 1963. Fishes of Utah. Utah State Department of Fish and Game, Salt Lake City.

———, AND J. W. SIGLER. 1996. Fishes of Utah: a natural history. Univ. of Utah Press, Salt Lake City.

SMITH, G. R. 1966. Distribution and evolution of North American catostomid fishes of the subgenus *Pantosteus*, genus *Catostomus*. Misc. Publ. Mus. Zool. Univ. Mich. 129:1–132.

———. 1978. Biogeography of intermountain fishes, p. 17–42. *In:* Intermountain biogeography: a symposium. Great Basin Naturalist Memoirs 2, Brigham Young Univ., Provo.

———. 1981. Late Cenozoic freshwater fishes of North America. Annu. Rev. Ecol. Syst. 2:163–193.

———. 1992. Introgression in fishes: significance for paleontology, cladistics, and evolutionary rates. Syst. Biol. 41:41–57.

———. 2000. Historical biogeography of Great Basin fishes. *In:* Great Basin aquatic systems history. R. Hershler, D. R. Currey, and D. B. Madsen (eds.). Smithsonian Contributions in Earth Science, Washington, DC.

———, AND T. N. TODD. 1993. Morphological cladistic study of coregonine fishes. Pol. Arch. Hydrobiol. 39:479–490.

———, W. L. STOKES, AND K. F. HORN. 1968. Some late Pleistocene fishes of Lake Bonneville. Copeia 1968:807–816.

STEARLEY, R. F., AND G. R. SMITH. 1993. Phylogeny of the Pacific trouts and salmons (*Oncorhynchus*) and genera of the family Salmonidae. Trans. Am. Fish. Soc. 122:1–33.

STUIVER, M., P. J. REIMER, E. BARD, J. W. BECK, G. S. BURR, K. A. HUGHEN, B. KROMER, G. MCCORMAC, J. VAN DER PLICHT, AND M. SPURK. 1998. INTCAL98 radiocarbon age calibration, 24,000–0 cal BP. Radiocarbon 40:1041–1084.

SVARDSON, G. 1970. Significance of introgression in coregonid evolution, p. 33–60. *In:* Biology of coregonid fishes. C. C. Lindsey and C. S. Woods (eds.). Univ. of Manitoba Press, Winnipeg, MB, Canada.

TOWNSEND, J. K. 1978. Narrative of a journey across the Rocky Mountains to the Columbia River. Univ. of Nebraska Press, Lincoln.

WHITE, R. G. 1974. Endemic whitefishes of Bear Lake, Utah-Idaho. Unpubl. Ph.D. diss., Utah State Univ., Logan.

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